

Genomic selection for feed efficiency traits

Kashly Schweer, University of Nebraska-Lincoln

Introduction

Feed costs comprise the majority of variable expenses in beef cattle systems making feed efficiency an important economic consideration within the beef industry (Koch et al., 1963; Dickerson et al., 1974). Aside from the direct economic impact of this trait complex at the individual producer level, the projections of global population growth provide extra pressure for efficient beef cattle production as producers try to combat the growing food demand with limited resources (Eggen, 2012). Improved feed efficiency also has an environmental impact through a decreased carbon footprint as more efficient cattle have fewer days to finish, emitting less methane throughout their lifetime (Freetly, 2013).

There are multiple measures of feed efficiency. The most common used in the fed cattle sector is feed conversion ratio (FCR), the ratio of feed to gain (F:G), or gain to feed (G:F). This ratio is simply the raw pounds of feed required for raw pounds of weight gained, or the reciprocal. It makes no adjustments for age and weight differences of the cattle or energy content differences of the diet being fed. For these reasons, unadjusted FCR should be limited to use within contemporary groups. Due to the positive genetic correlation between feed intake and gain, selection to improve FCR has the potential to lead to larger, more maintenance intensive animals in the breeding herd (Archer et al., 1999).

One proposed alternative to FCR is residual feed intake (RFI). The concept of RFI was introduced by Koch et al. (1963) by suggesting that feed intake should be adjusted for body weight and weight gain, making RFI the difference between actual feed intake and the predicted feed intake of an animal based its requirements for maintenance and gain. More desirable or efficient animals will have a negative RFI value with an average individual having an RFI of zero (Koch et al., 1963; Archer et al., 1999). The prediction equation is developed by regressing actual feed intakes, gains and weights of the animal's contemporaries, meaning the sum of RFI values across the contemporary group in which it was calculated should equal zero and thus contemporary group definition becomes vital. It is sometimes considered the preferred definition of feed efficiency because RFI is phenotypically independent of the production traits (growth and body weight) used in the prediction equation (Kennedy et al., 1993). Ultimately, selection on RFI is equivalent to using a restricted selection index containing the component traits. Since genetic variation in RFI exists, genetic progress towards more efficient cattle through selection on this trait is possible.

The use of RFI as a measure of feed efficiency is occasionally contested for a variety of reasons including difficult interpretation and differences in the frequency of recording for the component traits. Additionally, if any genetic or residual correlations exist between feed intake and maintenance traits, the resulting heritability estimates can be flawed (Lu et al., 2015; Kennedy et al., 1993). In the dairy industry, Lu et al. (2015) proposed a multi-trait model as an alternative approach to feed efficiency. This may represent a more robust measure of feed efficiency and comprehensive investigation into the genetic relationship between intake and gain.

Feed intake, and consequently feed efficiency traits, are difficult to obtain and expensive to measure. Consequently a genomics approach seems warranted. Although it is an expensive initiative, the detection of genetic markers for feed efficiency has the potential for great returns in the beef industry.

Review of Literature

Genetic Parameters for Feed Efficiency Traits

Moderate heritability estimates for average daily gain (ADG), dry matter intake (DMI), metabolic mid-test body weight (MMBW; lb0.75) and RFI suggest genetic variation exists and genetic progress can be garnered. Average daily gain is defined as the difference between the start and end test weights divided by the total number of days on feed. Arthur et al. (2001a) used data from 1,180 young Angus bulls and heifers on performance tests to estimate genetic and phenotypic parameters. Direct heritability of ADG was estimated as 0.28 (Arthur et al., 2001a). Heritability estimates were higher from data on young Charolais bulls. The heritability of ADG was calculated at 15 and 19 months of age on Charolais bulls. Heritability estimates were moderate at 0.34 and 0.41, respectively, for the two ages (Arthur et al., 2001b). These estimates are similar to previous reports from Robinson and Oddy (2004) and Schenkel et al. (2003) of 0.23 and 0.35, respectively.

Daily DMI is the cumulative on-test feed intake on a dry matter basis divided by the total days on feed. Nkrumah et al. (2007) estimated the heritability of daily DMI as 0.54 using crossbred beef steers, which is higher than a previous estimate of 0.44 by Schenkel et al. (2003). Feed intake can also be measured on an as-fed basis. Heritability estimates for feed intake as total feed consumed (as-fed) are also moderate with reports of 0.27, 0.48 and 0.39 from Robinson and Oddy (2004), Arthur et al. (2001b) and Arthur et al. (2001a), respectively.

Mid-test body weight (MBW) can be calculated by the average of the initial and end weights or through regression techniques. Metabolic mid-test body weight (MMBW) is $MBW \times 0.75$. Arthur et al. (2001a) reported the direct heritability estimate of 0.40 for MMBW. This agrees with the estimates of 0.35 and 0.41 from Schenkel et al. (2003), and Robinson and Oddy (2004), respectively.

Direct heritability estimates are moderate for RFI. Arthur et al. (2001a) estimated a heritability of 0.39. Schenkel et al. (2003) used two definitions of RFI. The first was the classical definition of the trait, the difference between actual feed intake and expected feed intake required for body weight and growth (RFIP), and the second included an adjustment for end of test backfat thickness (RFIb). Heritability estimates for both versions of RFI were very similar at 0.38 and 0.39 for RFIP and RFIb, respectively. Robinson and Oddy (2004) reported heritability estimates much lower for RFI (0.18) when cattle from varying breed types (temperate and tropical) at near market-ready weights were fed an ad libitum feedlot diet. Estimates for other feed efficiency related traits including FCR, feeding time and number of eating sessions per day are also moderate (Robinson and Oddy, 2004; Herd and Bishop, 2000; Arthur et al., 2001a; Arthur et al., 2001b).

Two of the main causes for genetic correlations between traits are the existence of pleiotropy and linkage (Bolormaa et al., 2014). Genetic and phenotypic correlations exist among feed efficiency traits and between feed efficiency and production traits. Phenotypic and genetic correlations between MMBW and ADG were 0.24 and 0.53, respectively (Arthur et al., 2001a). Moderate-to-strong positive genetic correlations exist between ADG and feed intake (as-fed or dry matter basis) with estimates of 0.54 (Arthur et al., 2001a), 0.87 (Nkrumah et al., 2007) and 0.50 (Schenkel et al., 2004). Several authors have reported moderate phenotypic correlations between gain and feed intake ranging from 0.41 to 0.60 (Arthur et al., 2001a; Nkrumah et al., 2007; Schenkel et al., 2004). Additionally, MMBW has been reported to be positively correlated with feed intake both phenotypically ($r_p=0.77$), and genetically ($r_g=0.71$) by Schenkel et al. (2004). By definition, RFI should be phenotypically independent of its component traits (Koch et al., 1963). Estimates from Arthur et al. (2001a) illustrate this with reported phenotypic correlations between RFI and MMBW ($r_p=0.02$) and between RFI and ADG ($r_p=-0.06$). Nkrumah et al. (2007) reported RFI was also genetically independent of its component traits, ADG and MMBW, with estimates close to zero ($r_g=-0.04$, $r_g=-0.06$). Nkrumah et al. (2007) reported that the genetic correlation between RFI and feed intake was 0.72, while feed intake was genetically correlated with F:G to a lesser degree ($r_g=0.31$). Schenkel et al. (2003) also found RFI to be more strongly genetically correlated with feed intake than F:G, thus suggesting selecting for low RFI could decrease feed intake more substantially than selecting for FCR.

Feed intake tends to be positively genetically correlated with postweaning growth traits including 200-d weight direct and 400-d weight direct with estimates of $r_g = 0.28$ and 0.56, respectively (Arthur et al., 2001a). Additionally, RFI was negatively correlated with 200-d weight direct ($r_g=-0.45$) and 400-d weight direct ($r_g=-0.26$; Arthur et al., 2001a). Both FCR and RFI are negatively correlated with longissimus muscle area (LMA). This suggests more efficient cattle have larger LMA (Schenkel et al., 2003). More efficient cattle may also produce a leaner product, as RFI is genetically correlated with intra-muscular fat percentage ($r_g=0.22$) and rump fat ($r_g=0.72$) (Robinson and Oddy, 2004). Robinson and Oddy (2004) further investigated the association between RFI and fat by holding age and carcass weight constant. Regardless of adjustment, the magnitude and sign of the relationships were similar.

Methods for genomic prediction

Traditionally, genetic selection to improve economically relevant traits in livestock has been based on phenotypic records and pedigree information. Estimated breeding values (EBV) are an estimate of the additive genetic merit of an individual for a given trait. The genetic value of a parent is one-half of its EBV, referred to as an expected progeny difference (EPD) in the U.S. beef cattle industry. The calculation an EPD combines pedigree information, the individual's own performance records and the performance records of one's offspring or relatives. Selection based on EPD has been successful. For animals to have EPD with high accuracy, many offspring with performance records are typically needed. In terms of feed intake, this is often not plausible due to the expense of recording phenotypes. The length of the generation interval is also a limiting factor on the timeliness of the genetic progress. The concept of identifying genes to improve certain traits and selecting candidates for breeding based on the presence of favored alleles is advantageous (Goddard and Hayes, 2009).

One of the primary hurdles which must be overcome with the current genomic advances is continuing to develop methodology to accurately estimate marker effects in a computationally efficient manner. The evolution of methodology is almost as vast as the changes in technology, or possibly parallel to some degree. Historically, BLUP has given animal breeders a powerful tool for the prediction of breeding value based on performance records. Henderson (1984) realized the advantages of prediction with BLUP over least squares, regressed least squares or selection index due to the reduction of error and the greater correlations between the predictors and the predictions.

The BLUP methodologies were augmented to include marker effects into breeding value predictions through mixed models for the introduction of genomic BLUP (GBLUP; Fernando and Grossman, 1989). With BLUP, pedigree information is used to derive the relationship matrix making full sibs have the same EBV (parent average value). If instead, genomic information (i.e. SNP genotypes) is used to form the relationship matrix, the Mendelian Sampling term is taken into account and allows for individual deviation from the parent average. This increases the accuracy of the EBV and consequently, the response to selection (Hayes et al., 2009). As with most linear predictions, GBLUP assumes that all markers contribute to the overall genetic variance therefore meaning each of the SNP have small effects (VanRaden, 2008).

Regression techniques were also used as a method for MAS where least square analysis was used as a way to estimate marker effects. Lande and Thompson (1990) found MAS to be feasible through the multiple regression of phenotype on genotype at a given marker loci to determine markers associated with a given trait due to LD with the QTL. If a sufficient amount of markers are linked with the QTL and a large enough sample size of individuals exist, the regression should be able to account for most of the additive genetic variance within the trait due to a particular QTL (Lande and Thompson, 1990). In reality, the massive amount of marker effects cannot be estimated to be included into the standard regression model. With the advent of high-density genotyping platforms, the number of markers exceeds the number of genotyped individuals within the population. In order to overcome the challenge of dimensionality, only a subset of the marker effects are estimated to be included in the regression model and results in larger errors and poor estimates of the genetic value of an individual (Zhang and Smith, 1992; Whittaker et al., 2000).

Ridge regression is a method that has better predictive ability than when only a subset of markers can be used (Breiman, 1995) as more markers are able to be included with the estimates of marker effects shrunk towards zero by a constant factor (λ) known as the smoothing factor (Whittaker et al., 2000). However, Xu (2002) demonstrated that this penalty approach may not be a valid method for QTL mapping when genome-dense SNP are used. Through a simulation study, Whittaker et al. (2000) showed ridge regression outperformed regression with a subset of marker effects estimated and traditional phenotypic selection.

Perhaps the most appealing method for genomic prediction lies within the “Bayesian alphabet.” Bayesian analysis has captured the attention of animal breeders for a number of reasons. First, Bayesian procedures have the ability to handle situations where the number of markers exceeds the number of observations (Gianola et al., 2009). Meuwissen et al. (2001) demonstrated how to make the transition from traditional BLUP estimation to analysis of marker effects with each SNP having a specific variance through Bayesian techniques. Bayesian analysis takes into account the degree of uncertainty revolving around each of the unknowns within the model (Gianola et al., 2009). Nonlinear equations, such as those within Bayesian methods, assume a prior distribution of SNP effects. This may be a more realistic approach as the effects from each marker may not all contribute small effects as assumed with linear predictions. In fact, major genes may exist on some chromosomes therefore having corresponding markers that explain a greater amount of genetic variance (VanRaden, 2008).

In Bayesian models, all unknown parameters are treated as random variables each with its own distribution. Variables are further classified as observables or unobservables. The observable variables include the phenotype (y_i for $i=1, \dots, n$ where n number of individuals) and the marker information. The QTL effect (b_j) and the variance of each marker effect (σ_j^2 for $j=1, \dots, p$ where p is the total number of markers) are considered unobservable. The distribution of the unobservable variables is referred to as the prior distribution, $f(\Theta)$. The distribution of the observable variables is a function of the unobservables; the likelihood function, $f(y|\Theta)$. The likelihood function represents the contribution of the phenotypic information to knowledge of the prior (Θ). The posterior distribution is the conditional distribution of the parameters given the observable variables or simply the combination of the likelihood function and the prior distribution, $f(\Theta|y)$. The Markov Chain Monte Carlo (MCMC) sampling technique draws samples from the posterior distribution to estimate the posterior means and variances (Xu, 2002; Gianola and Fernando, 1986).

Meuwissen et al. (2001) proposed two Bayesian methods with the advent of genomic selection; BayesA and BayesB. BayesA shares similarities with the previous regression models as it assumes that all markers have an effect and the prior distribution of the marker effects is normal with a marker-specific variance from a scaled inverse chi-square distribution. The normal distribution of SNP effects allows for some SNP to have larger effects than others, but with BayesA every SNP is treated as though it has a non-zero effect. However, if the number of QTL is substantially less than the number of markers and, given the multitude of SNP on current genotyping arrays, it seems logical to assume some markers will have no effect (Meuwissen et al., 2001; Goddard et al., 2010). For this reason, BayesB was introduced. BayesB allows for a proportion of the markers to have an effect ($1-\pi$) following a normal distribution and a proportion of the markers to have no effect (π). The proportion of markers that have no effect (π) is assumed a priori. The variance of the marker effects is sampled from a scaled inverse chi square distribution similar to the BayesA approach. One of the criticisms of BayesA and BayesB is the magnitude of influence the prior has on the shrinkage of

the marker effects (Gianola et al., 2009). BayesC assumes that every marker will not have an effect parallel to BayesB, but BayesC uses an equal variance for all SNP. BayesC can be extended by assuming that π is not known and instead is estimated from the data (BayesC π). Estimating π requires additional samples (Habier et al., 2011). The Bayesian alphabet continues to expand for animal breeding prediction.

Methods of genomic prediction primarily exploit linkage disequilibrium (LD) between SNP markers and QTL. Although SNP-based models offer promise to discover genomic regions associated with traits of interest, models utilizing haplotypes consisting of multiple SNP markers may provide greater power for association experiments. This is primarily justified as haplotypes may be in greater LD with the QTL than the individual SNP marker. As the number of SNP markers within a chromosomal segment increase, the likelihood that identical haplotypes carried by different animals are identical by descent increases as well. Given haplotypes are identical by descent, QTL alleles would be conserved within the haplotype (Hayes, 2013).

Inclusion of Genomic Information into National Cattle Evaluations

The augmentation of genomic information into National Cattle Evaluations (NCE) is critical for the progression of breeding programs. The advent of SNP panels to genotype large numbers of animals at a reasonable cost has made genomic prediction feasible. The QTL can be detected through LD with the markers, even though in practice the position of the QTL and the effects are not known. Summation of the product of the marker effects and SNP genotypes across all loci can estimate the breeding value of an individual based on markers effects only, or the molecular breeding value (MBV). This estimation focuses on the total genetic value of the animal instead of the precise discovery of QTL (Goddard et al., 2010).

Molecular breeding values have been augmented into NCE for the majority of popular beef cattle breeds. Genomically-enhanced expected progeny differences (GE-EPD) are calculated similarly to traditional EPDs with the addition of genomic test results. The way the genomic information is augmented into EPDs differs and can be divided into multi-step and single-step approaches. The multi-step approach requires the estimation of marker substitution effects, the prediction of the MBV and the combination of MBV with EPD. Single-step approaches include all phenotypic, pedigree and genomic information by modifying the relationship matrix of the mixed model equations (Fernando and Garrick, 2013).

In order to augment genomic information into NCE for one succinct value for selection decisions, a method referred to as “blending” was proposed. Blending is an index-like approach that utilizes traditional matrix calculations to establish the weighting factors b from $Pb=g$. These weightings will differ for each trait according to the accuracy of the MBV and for each animal according to the EBV reliability (Garrick and Saatchi, 2013). For most breeds, blending is done post-evaluation and thus the MBV only influences the genotyped individual (Spangler, 2013).

Kachman (2008) introduced methodology to incorporate marker scores into NCE by integrating MBV as a correlated indicator trait in a multi-trait model. This approach was very adaptable for breed associations. Contrary to the blended approach, treating the MBV as a correlated trait had the ability for the genomic information to influence other animals in the pedigree that did not have genotypic data (Spangler, 2013). This approach was later adopted by MacNeil et al. (2010) for the use of incorporating ultrasound data and MBV as indicator traits for predicting carcass EBV. Exploiting the knowledge of genetic correlations among traits and between traits and MBV allow for multiple sources of information to be used to predict hard to measure traits, such as carcass traits that can only be obtained after an animal is slaughtered.

Recently, a single-step approach to GBLUP has been adopted. The single-step approach combines phenotypic, pedigree and SNP data in a single analysis. It creates the G relationship matrix using animals with genotypic data as with GBLUP and a sub-matrix using pedigree data for individuals without genotypic information. It combines those matrices into a relationship matrix, H. Evidence shows that single-step GBLUP (ssGBLUP) produces the same or improved accuracies of other genomic prediction models. It allows combined phenotypes from nongenotyped animal into the analysis. The limitations of ssGBLUP are the massive computing power needed. For large datasets, the inversion of the H matrix can be computationally expensive. Additionally, the G and A matrices need to be scaled appropriately (Misztal et al., 2013). Several breed associations are moving toward this single-step approach for their genetic analyses.

As with any method of genomic augmentation, animals with preexisting high accuracy EBV do not notice additional gains in accuracy by incorporating molecular information for a given trait. However, lowly accurate animals (i.e. those without progeny) do see gains in accuracy. The increase in accuracy through the incorporation of genomic information is directly related to the correlation between the phenotype and the MBV as the amount of genetic variance explained is equal to the square of the correlation. This is best illustrated by an example adopted from

Spangler (2011) using results reported by MacNeil et al. (2010). Assuming the correlation (r) for marbling score was 0.37, 13.7% ($r^2 \times 100$) of the additive genetic variance of marbling score was explained by the genomic test. Moreover, if the heritability of marbling is known to be moderate ($h^2=0.3$), the gain in accuracy for an animal with no ultrasound record or progeny information is now equivalent to the accuracy of having 5 progeny with carcass records in its pedigree or ultrasound information on the individual itself through the incorporation of genomic data (Spangler, 2011).

The primary justification for incorporating molecular information into traditional selection methods is the faster rate of genetic gain than could be achieved by phenotypic data alone (Meuwissen et al., 2001). Meuwissen and Goddard (1996) predicted 8-38% extra genetic gain through the incorporation of marker information into BLUP breeding values. Additional advantages of genomic selection include improved accuracy of young, unproven animals as selection candidates (Kachman et al., 2013) such as yearling bulls who have not produced offspring. In the dairy industry, it is estimated that the use of genomic selection will reduce the costs of bull testing by upwards of 90% (Eggen, 2012). The ability to make more accurate selection decisions at a younger age will in turn reduce the generation interval, speeding the rate of genetic progress as Meuwissen et al. (2001) anticipated. Within the beef industry, genomic predictors allow for selection of economically relevant traits that have phenotypes that are only expressed late in life, phenotypes that are expensive or difficult to measure, traits that are limited by sex, lowly heritable traits or phenotypes that can only be collected once the animal has been harvested (Dekkers, 2004; Bolormaa et al., 2013).

Conclusions and Implications to Genetic Improvement of Beef Cattle

In regards to feed efficiency, genomic prediction is conducted as the association between genotypic data and measures of feed efficiency such as FCR, RFI or component traits including DMI or ADG. Multi-trait models have been proposed in the dairy (Lu et al., 2015) and swine (Strathe et al., 2014) industries as a more comprehensive investigation of feed efficiency. Lu et al. (2015) modeled DMI with energy sink traits including milk and MMBW. The classical calculation of RFI assumes relationships at the genetic and nongenetic levels are constant. The proposed multi-trait model allows these relationships to differ. Aside from the gains in genetic prediction accuracies with the multi-trait model over RFI, the multi-trait model allows the inclusion of all animals, even those with missing records (Lu et al., 2015).

Given multi-trait models can be deployed for genetic merit prediction, it seems possible to use the same approach with genomic prediction. A multi-trait model for GWAS including intake and gain is currently an unexplored area in the beef cattle industry. The frequency of intake and gain phenotypes differ considerably with gain measured more routinely on-farm. Since a strong genetic correlation exists between the two traits, a bivariate model would exploit the knowledge of the highly recorded trait to inform the limited phenotype.

Genomics has proven to be an exciting time within the beef industry; however, it is not a cure-all type of solution. With expensive to measure phenotypes, such as feed intake, it is practical to assume that only superior animals will be chosen for feeding trials. This non-random selection creates a bias in the genomic predictions (Spangler, 2013). Genomic prediction requires a large number of animals with phenotypic and genotypic data for training. For traits that are routinely recorded and have existing EPD, the transition to GE-EPD has been made. However, novel traits require greater effort to build resource populations of thousands of animals representing multiple breeds to establish genomic predictions that are robust across beef cattle populations. This has been the focus of a multi-institutional research effort in beef cattle (Saatchi et al., 2014). Genomic information could also be improved by having a greater understanding of the underlying biological mechanisms of distinct phenotypes (Eggen, 2012). Molecular breeding values work well when used within the same cattle breed as training, but lose efficacy when applied across breeds (Kachman et al., 2013).

At its current state, genomics serves as a tool to compliment selection techniques in order to gain higher accuracies. Although genomics was unable to serve as the magic bullet for animal breeding, it does bring forth advantages. Aside from the expected genetic gains through greater accuracies and decreased generation intervals, genomics has the ability to aid in parent identification and traceability. As industry and social demands continue to increase, it is vital for livestock producers to implement all possible selection techniques to produce the most efficient animals. The world population is expected to increase 40 to 50% by 2020 to 2030. To accommodate the growing demand for protein with the decreasing land resources, cattle must be more efficient in converting feed to consumable product. Increased environmental awareness also drives the demand for greater feed efficiency with concerns of the carbon footprint resulting from livestock production (Green, 2008). Cattle producers will face these contests and many others in years to come, but the opportunities through beef cattle genomics are considerable.

Bibliography

- Archer, J.A., E.C. Richardson, R.M. Herd, and P.E. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. *Aust. J. Agric. Res.* 50:147-161.
- Arthur, P.F., G. Renand, and D. Krauss. 2001b. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. *Livest. Prod. Sci.* 68:131-139.
- Arthur, P.F., J.A. Archer, D.J. Johnston, R.M. Herd, E.C. Richardson, and P.F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in Angus cattle. *J. Anim. Sci.* 79:2805-2811.
- Bolormaa, S., J.E. Pryce, A. Reverter, Y. Zhang, W. Barendse, K. Kemper, B. Tier, K. Savin, B.J. Hayes, and M.E. Goddard. 2014. A multi-trait, meta-analysis for detecting pleiotropic polymorphisms for stature, fatness and reproduction in beef cattle. *PLOS Genetics* 10(3):e1004198.
- Bolormaa, S., J.E. Pryce, K. Kemper, K. Savin, B.J. Hayes, W. Barendse, Y. Zhang, C.M. Reich, B.A. Mason, R.J. Bunch, B.E. Harrison, A.Reverter, R.M. Herd, B.Tier, H.-U. Graser, and M.E. Goddard. 2013. Accuracy of prediction of genomic breeding values for residual feed intake and carcass and meat quality traits in *Bos Taurus*, *Bos indicus*, and composite beef cattle. *J. Anim. Sci.* 91:3088-3104.
- Breiman, L. 1995. Better subset selection using the nonnegative garrote. *Technometrics* 37:373-384.
- Dekkers, J.C.M. 2004. Commercial application of marker- and gene-assisted selection in livestock: Strategies and lessons. *J. Anim. Sci.* 82:ESuppl E313-328.
- Dickerson, G.E., N. Kunzi, L.V. Cundiff, R.M. Koch, V.H. Arthaud, and G.E. Gregory. 1974. Selection criteria for efficient beef production. *J. Anim. Sci.* 39:659-673.
- Eggen, A. 2012. The development and application of genomic selection as a new breeding paradigm. *Anim. Front.* 2:10-15.
- Fernando, R.L., and D.J. Garrick. 2013. Bayesian regression as an alternative implementation of genomic-enhanced genetic evaluation. *Proc. 10th Genetic Prediction Workshop. Kansas City, MO.* Pp. 38-43.
- Fernando, R.L., and M. Grossman. 1989. Marker assisted selection using best linear unbiased prediction. *Genet. Sel. Evol.* 21:467-477.
- Freetly, H.C., and T.M. Brown-Brandl. 2013. Enteric methane production from beef cattle that vary in feed efficiency. *J. Anim. Sci.* 91:4826-4831.
- Garrick, D.J., and M. Saatchi. 2013. Practical experiences in developing breed-specific predictions for genome-enhanced EPDs. *Proc. 10th Genetic Prediction Workshop. Kansas City, MO.* Pp. 24-34.
- Gianola D., and R.L. Fernando. 1986. Bayesian methods in animal breeding theory. *J. Anim. Sci.* 63:217-244.
- Gianola D., G. de los Campos, W.G. Hill, E. Manfredi, and R. Fernando. 2009. Additive genetic variability and the Bayesian alphabet. *Genetics* 183:347-363.
- Goddard, M.E., and B.J. Hayes. 2009. Mapping genes for complex traits in domestic animals and their use in breeding programmes. *Nature* 10:381-391.
- Goddard, M.E., B.J. Hayes, and T.H.E. Meuwissen. 2010. Genomic selection in livestock populations. *Genet. Res.* 92:413-421.
- Green, R.D. 2008. ASAS Centennial Paper: Future needs in animal breeding and genetics. *J. Anim. Sci.* 87:793-800.
- Habier, D., R. L. Fernando, K. Kizilkaya, and D.J. Garrick. 2011. Extension of the Bayesian alphabet for genomic selection. *BMC Bioinformatics* 12:186.
- Hayes, B.J. 2013. Overview of statistical methods for genome-wide association studies (GWAS). In: Cedric Gondro et al., editors, *Genome-Wide Association Studies and Genomic Prediction, Methods in Molecular Biology.* Springer Science+Business Media, LLC, p. 149-169.
- Hayes, B.J., P.M. Visscher, and M.E. Goddard. 2009. Increased accuracy of artificial selection by using the realized relationship matrix. *Genet. Res.* 91:47-60.
- Henderson, C.R. 1984. Best linear unbiased prediction of performance and breeding value. *Proc. 33rd National Breeders' Roundtable, St. Louis, Mo,* p. 172.

- Herd, R.M., and S.C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in British Hereford cattle. *Livest. Prod. Sci.* 63:111-119.
- Kachman, S.D. 2008. Incorporation of marker scores into national cattle evaluations. Proc. 9th Genetic Prediction Workshop, Kansas City, MO, p. 88-91.
- Kachman, S.D., M.L. Spangler, G.L. Bennett, K.J. Hanford, L.A. Kuehn, W.M. Snelling, R.M. Thallman, M. Saatchi, D.J. Garrick, R.D. Schnabel, J.F. Taylor, E.J. Pollak. 2013. Comparison of molecular breeding values based on within- and across-breed training in beef cattle. *Genet. Sel. Evol.* 45:30.
- Kennedy, B.W., J.H.J. van der Werf, and T.H.E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. *J. Anim. Sci.* 71:3239-3250.
- Koch, R.M., L.A. Swinger, D. Chambers and K.E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22:486-494.
- Lande, R., and R. Thompson. 1990. Efficiency of marker assisted selection in the improvement of quantitative traits. *Genetics* 124:743-756.
- Lu, Y., M.J. Vandehaar, D.M. Spurlock, K.A. Weigel, L.E. Armentano, C.R. Staples, E.E. Connor, Z. Wang, N.M. Bello, and R.J. Templeman. 2015. An alternative approach to modeling genetic merit of feed efficiency in dairy cattle. *J. Dairy Sci.* 98:6535-6551.
- MacNeil, M.D., J.D. Nkrumah, B.W. Woodward, and S.L. Northcutt. 2010. Genetic evaluation of Angus cattle for carcass marbling using ultrasound and genomic indicators. *J. Anim. Sci.* 88:517-522.
- Meuwissen, T.H.E., and M.E. Goddard. 1996. The use of marker haplotypes in animal breeding schemes. *Genet. Sel. Evol.* 28:161-176.
- Meuwissen, T.H.E., B.J. Hayes, and M.E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. *J. Anim. Sci.* 88:544-551.
- Misztal, I., S.E. Aggrey, and W.M. Muir. 2013. Experiences with single-step genome evaluation. *Poul. Sci.* 92:2530-2534.
- Nkrumah, J.D., J.A. Basarab, Z. Wang, C. Li, M.A. Price, E.K. Okine, D.H. Crews, Jr., and S.S. Moore. 2007. Genetic and phenotypic relationships of feed intake and measures of efficiency with growth and carcass merit of beef cattle. *J. Anim. Sci.* 85:2711-2720.
- Robinson, D.L., and V.H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Lvstk. Prod. Sci.* 90:255-270.
- Saatchi, M., J.E. Beever, J.E. Decker, D.B. Faulkner, H.C. Freetly, S.L. Hansen, H. Yampara-Iquise, K.A. Johnston, S.D. Kachman, M.S. Kerley, J. Kim, D.D. Loy, E. Marques, H.L. Neibergs, E.J. Pollak, R.D. Schnabel, C.M. Seabury, D.W. Shike, W.M. Snelling, M.L. Spangler, R.L. Weaber, D.J. Garrick, and J.F. Taylor. 2014a. QTLs associated with dry matter intake, metabolic mid-test weight, growth and feed efficiency have little overlap across 4 beef cattle studies. *BMC Genomics* 15:1004.
- Schenkel, F.S., S.P. Miller, and J.W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. *Can. J. Anim. Sci.* 84:177-185.
- Spangler, M.L. 2011. Integration of genomic information into genetic evaluation. NCBA Cattlemen's College.
- Spangler, M.L. 2013. Strengths and weaknesses of methods of incorporating genomics into genetic evaluations. Proc. 10th Genetic Prediction Workshop. Kansas City, MO, p. 1-4.
- Strathe, A.B., T. Mark, B. Nielsen, D.N. Doo, H.N. Kadarmideen, and J. Jensen. 2014. Deriving genomic breeding values for residual feed intake from covariance functions of random regression models. Proc 10th World Congr. Genet. Appk. Livest. Prod., Vancouver, Canada.
- VanRaden, P.M. 2008. Efficient methods to compute genomic predictions. *J. Dairy Sci.* 92:16-24.
- Whittaker, J.C., R. Thompson, and M.C. Denham. 2000. Marker-assisted selection using ridge regression. *Genet. Res., Camb.* 75:249-252.
- Xu, S. 2002. Estimating polygenic effects using markers of the entire genome. *Genetics* 163:789-801.
- Zhang, W. and C. Smith. 1992. Computer simulation of marker-assisted selection utilizing linkage disequilibrium. *Theor. and Appl. Genet.* 83:813-820.