

Genetic Correlations Between Carcass Traits And Molecular Breeding Values In Angus Cattle

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Introduction

American Angus Association (AAA) has collected data for genetic evaluation of marbling (MRB), longissimus muscle area (LMA), subcutaneous fat depth (SQF), and carcass weight (CWT) since 1974 (Wilson *et al.*, 1993). In 1997, that genetic evaluation was augmented with a separate evaluation of ultrasound indicator traits measured on yearling bulls and heifers. These data are now analyzed simultaneously in national cattle evaluation (NCE; MacNeil and Northcutt, 2008). Today, firms also genotype animals for breeders and estimate molecular breeding values (MBV) from multiple genetic markers. To date, use of MBV has been, for the most part, independent of NCE. This is not optimal and their joint consideration is a more powerful selection strategy (Dekkers and Hospital, 2002; Spangler *et al.*, 2007). Thallman (2004) envisioned incorporating MBV into NCE to increase its accuracy. The objective of this research was to elucidate genetic relationships between carcass traits, ultrasound indicator traits, and their respective MBV. Results are presented for two generations of MBV; the first developed primarily from candidate gene loci and the second developed from SNP associations determined from genome-wide association analysis.

Materials and methods

Phenotypic data. Carcass data were either from an AAA sponsored sire evaluation program or submitted directly to AAA by members who had obtained the data using a variety of commercial and private services. Dams were predominately commercial Angus-type cattle. However, unique identification of dams was not required and thus dams were considered unknown. The AAA defines carcass contemporary group as the concatenation of herd code, harvest date, breeder group code, and gender. Carcass data were adjusted to 480-d of age at harvest. There were 38,296 records from steer calves in 748 contemporary groups used in evaluating the first generation of MBV. In the evaluation of the second generation of MBV, the dataset was augmented by new data to total 42,493 records on the carcass traits.

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Yearling Angus bulls and heifers were scanned by certified technicians using ultrasound. The images were interpreted by centralized processing labs and results reported directly to AAA. Cattle were weighed at the time of scanning. Records were adjusted to 365-d of age for bulls and 390-d of age for heifers. Ultrasound imagery data from 33,857 bulls and 33,737 heifers were used in evaluating the first generation of MBV whereas; image data were from 82,985 bulls and 66,907 heifers for the second generation MBV.

A four generation pedigree for animals with a phenotypic record or MBV was extracted from the AAA herdbook.

Molecular breeding values. The MBV evaluated herein were produced specifically for Angus cattle and provided to the AAA by IGENITY®.

First generation MBV was developed from SNP targeting candidate genes and QTL for carcass traits. In all, SNP genotypes from 444 Angus bulls were evaluated for their univariate associations with EPD for the carcass traits published by AAA in 2008. The effect of each marker was estimated as a regression on the number of copies of the assigned first allele (based on alphabetic order, i.e., CC, CT, and TT from a C/T mutation were coded 2, 1, and 0, respectively). Each SNP that gave an indication of being at least tentatively associated with the trait ($P < 0.10$) was then evaluated for potential linkage disequilibrium (LD) with other SNP. To avoid redundancy, only one of each such pair of SNP with high LD ($r^2 > 0.80$) was chosen as a tagSNP to capture the effect of the targeted QTL (Carlson *et al.*, 2004). Final models for computing MBV were multi-marker compound covariate prediction equations (Tukey, 1993), with covariates defined by for each marker's coded genotype and weights corresponding to the allele substitution effect estimated for each marker.

Second generation MBV was developed using 1,710 Angus bulls born from 1955 to 2003 and genotyped with the Illumina BovineSNP50 assay (Matukumalli *et al.*, 2009). A total of 41,028 SNP passed QA/QC (minimum sample and SNP genotype call rates $\geq 90\%$ and minor allele frequency $> 5\%$). FastPhase (Scheet and Stephens, 2006) was used to impute missing genotypes and to phase the 29 autosomes and the pseudoautosomal X. Genome-wide association analysis was performed on EPDs provided by the AAA using weighted regression using accuracies as weights (Morsci *et al.*, 2006). Identification of reduced SNP subsets for further evaluation used several approaches, including forward selection and a Bayesian procedure. The 1,721 bulls were partitioned according to their sire into 3 equal subsets to avoid sibs being represented across subsets. Analyses were undertaken on 2 of the subsets and predictive ability validated in the third subset. This approach was repeated 3 times so that every bull was in 2 training analyses and 1 validation analysis. Each analysis used a Markov-chain Monte Carlo process to fit a mixture model with 0.9 of the SNP assumed to have zero effect on the trait and 0.1 probability of an association. Fitted SNP were treated as random effects with an unknown common variance. The 20 most informative SNP on each chromosome were identified for each trait on the basis of fitted model frequency. This resulted in 3 sets of 600 SNP for each trait. Final models for computing MBV were again set up as multi-marker compound covariate prediction equations (Tukey, 1993) yielding a single panel of SNP that provided whole genome coverage and included the most informative SNP for each of a portfolio of traits.

Statistical analyses. Animals whose MBV data were used here were not previously used in the development process. Variance and covariance components, genetic parameters, and their standard errors were estimated using ASReml v2.0 (Gilmour *et al.*, 2006). The linear model used can be described as:

$$\begin{bmatrix} Y_1 \\ Y_2 \\ Y_3 \end{bmatrix} = \begin{bmatrix} X_1\beta_1 \\ X_2\beta_2 \\ X_3\beta_3 \end{bmatrix} + \begin{bmatrix} Z_1u_1 \\ Z_2u_2 \\ Z_3u_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

where the Y_i are vectors of carcass traits, ultrasound indicator traits, and MBV, respectively; X_i and Z_i are design matrices relating the data to their respective fixed contemporary group effects, random animal effects, and random residual effects. The only fixed effect for MBV was the overall mean. Residual effects were assumed independent within and across traits.

Results and discussion

Table 1 shows estimates of heritability for the MBV and genetic correlations between the MBV and the economically relevant carcass traits and associated indicator traits.

Table 1: Estimates of heritability ($h^2 \pm SE$) of molecular breeding values for economically relevant traits (ERT) measured on carcasses of steers and their respective genetic correlations ($r_g \pm SE$) with the ERT and indicator traits measured using ultrasound or at the time of scanning.

Trait ¹	Generation I Candidate Gene MBV		Generation II Association MBV	
Carcass	h^2	r_g	h^2	r_g
CWT	0.92±0.09	0.10±0.15	0.99±0.00	0.54±0.04
LMA	0.93±0.09	0.34±0.14	1.00±0.00	0.58±0.04
FAT	0.86±0.09	0.40±0.14	1.00±0.00	0.50±0.04
MRB	0.92±0.09	0.35±0.14	0.99±0.00	0.65±0.03
Ultrasound		♂	♀	
				♂
UWT		0.17±0.13	0.07±0.14	0.34±0.03
				♀
ULM		0.47±0.12	0.31±0.14	0.40±0.03
				♂
SQF		0.07±0.12	0.22±0.14	0.20±0.03
				♀
IMF		0.39±0.12	0.43±0.12	0.38±0.03

¹ CWT = Carcass weight, LMA = Longissimus muscle area, FAT = Subcutaneous fat depth at 12th rib, MRB = Marbling score (Beef Improvement Federation, 2002), UWT = Live weight at scanning, ULM = Longissimus muscle area, SQF = Weighted average of subcutaneous fat depths at 12th rib and rump; IMF = estimated % intramuscular fat in longissimus.

The EPDs for animals used to develop these MBV spanned almost the full range of published accuracy values. Predicted rates of annual genetic gain (not shown) suggest that as the genetic correlation between MBV and targeted economically relevant trait approaches 0.6 there may be a disincentive to continue collecting phenotypic data. However, continued

data collection will be needed to update EPDs and MBV to account for erosion in LD, for changes in allele frequency that result from selection, and because some sires used to construct the MBV had low accuracy EPDs.

These data indicate that increased genetic correlations between MBV and the targeted economically relevant carcass traits were achieved between the first and second generation of MBV. These improvements arose without any substantial change in the relationships between MBV and the indicator traits obtained from candidates for selection using ultrasound. There were 1,264 animals genotyped with both MBV products. The correlations between the first and second generation MBV ranged from 0.28 for carcass weight to 0.42 for marbling. Further improvement in MBV products seems feasible as the cost of genotyping decreases and additional numbers of SNPs can cost-effectively be genotyped.

Conclusion

These results show MBV to be useful indicators of economically relevant traits in Angus cattle. The MBV derived from trait-associated SNP identified through genome-wide association analysis appear more useful than the MBV derived from SNP at candidate gene loci. However, the correlations between the pair of MBV for each of the traits suggest improvement is possible. To date, high accuracy EPDs continue to require the collection of phenotypic data for economically relevant traits. This data will also be important for the periodic re-evaluation of MBV as LD between tested SNP and targeted QTL changes.

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