National cattle evaluation system for combined analysis of carcass characteristics and indicator traits recorded using ultrasound in Angus cattle

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Running Head: Genetic analysis of carcass traits

National cattle evaluation system for combined analysis of carcass characteristics and indicator traits recorded using ultrasound in Angus cattle[1]

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ABSTRACT: Objectives were to 1) evaluate genetic relationships of sex-specific indicators of carcass merit obtained using ultrasound with carcass traits of steers, 2) estimate genetic parameters needed to implement combined analyses of carcass and indicator traits to produce unified national cattle evaluations (NCE) for longissimus muscle area, subcutaneous fat depth, and marbling with the ultimate goal of publishing only EPD for the carcass traits; and 3) compare resulting evaluations with previous ones. Four data sets were extracted from the records of the American Angus Association (AAA). Records from 33,857 bulls, 33,737 heifers, and 1,805 steers that had measures of intramuscular fat content (IMF), longissimus muscle area (uLMA), and subcutaneous fat depth (SQF) derived from interpretation of ultrasonic imagery, and weight recorded at the time of scanning. Also used were 38,296 records from steers with marbling (MRB), fat depth at the 12th-13th rib interface (FD), carcass weight, and longissimus muscle area (cLMA) recorded upon harvest. (Co)variance components were estimated with ASREML using the same models as used for NCE by AAA. Heritability estimates for carcass measures were 0.45±0.03, 0.34±0.02, 0.40±0.02, and 0.33±0.02 for MRB, FD, carcass weight, and cLMA, respectively. Genetic correlations of carcass measures from steers with ultrasonic measures from bulls and heifers indicated gender specific relationships for IMF (0.66±0.05 vs. 0.52±0.06) and uLMA (0.63±0.06 vs. 0.78±0.05), but not for weight at scanning (0.46±0.07 vs. 0.40±0.07) or SQF (0.53±0.06 vs. 0.55±0.06). For each trait, estimates of genetic correlations between bulls and heifers measured using ultrasound were greater than 0.8. Prototype national cattle evaluations were conducted using the estimated genetic parameters resulting in some re-ranking of sires relative to previous analyses. Rank correlations of high impact sires were 0.91 and 0.84 for the joint analysis of MRB and IMF with previous separate analyses of MRB and IMF, respectively. Corresponding results for FD and SQF were 0.90 and 0.90, and for cLMA and uLMA 0.79 and 0.89. Unified national cattle evaluation for carcass traits using measurements from harvested animals and ultrasonic imagery of seedstock in a combined analysis appropriately weights information from these sources and provides breeders estimates of genetic merit consistent with traits in their breeding objectives upon which to base selection decisions.

Key words: beef cattle, carcass, genetic parameters, ultrasound

INTRODUCTION

Price discrimination based on quality and yield grades provides economic incentive for selection of breeding stock based on carcass merit. Since 1974, the American Angus Association (**AAA**) has collected data for genetic evaluation of carcass traits (Wilson et al., 1993). More recently, similar data have been collected from yearling bulls and heifers using ultrasound (Crews and Kemp, 2002). To date, the AAA has conducted separate genetic evaluations using data from each source. Because genetic correlations between carcass traits typically measured on steers and corresponding indicator traits measured on yearling bulls and heifers may be less than 1.0 (Moser et al., 1998; Kemp et al., 2002; Crews et al., 2003) and different models are used in the analyses

(http://www.angus.org/sireeval/), potential exists for inconsistencies between these analyses and confusion on the part of producers using the results. Rank correlations of 0.52, 0.59, and 0.44 for sires (N = 1,523) evaluated in both systems for longissimus muscle area, intramuscular fat content, and subcutaneous fat depth quantify the problem. Joint evaluation of data from both sources to produce a single genetic evaluation for each relevant trait would alleviate this problem. Preliminary analysis of data from AAA also indicated potential heterogeneity of variance with gender for ultrasonically measured intramuscular and subcutaneous fat. In evaluation of Australian beef cattle, traits measured on bulls by ultrasonic scanning are considered different, but correlated, with those measured on steers and heifers (Graser, et al., 2005). Thus, our objectives were to: evaluate genetic relationships of gender-specific indicators of carcass merit obtained using ultrasound with carcass traits of steers, estimate genetic parameters needed to implement joint analyses of carcass and indicator traits to produce unified national cattle evaluations for longissimus muscle area, subcutaneous fat depth, and marbling; and compare the resulting evaluations with previous ones.

MATERIALS AND METHODS

Carcass data were either from an Angus Association sponsored sire evaluation program or submitted directly by members who had obtained the data using a variety of commercial and private services. Dams were predominately commercial Angus-type cattle, often with known Angus sires. However, unique identification of dams was not required. The American Angus Association defines carcass contemporary group as the concatenation of herd code, harvest date, breeder group code, and gender. Carcass weight (CWT), longissimus muscle area (cLMA), subcutaneous fat depth at the 12th rib (FD), and marbling (MRB) were adjusted to 480 d of age at harvest. There were 59,124 records available and 38,296 remained after editing to remove: 1) all heifers and bulls, 2) animals with 1 or more traits not recorded, 2) contemporary groups of less than 30 animals, 3) sire groups of less than 7 animals, and 4) observations more than 4 SD from their respective contemporary group mean. Thus, the 38,296 carcass records used herein were from steer calves by 1,470 Angus sires, and there were 748 contemporary groups.

Ultrasound images were collected by certified field technicians. Results from ultrasonic scanning of yearling Angus bulls, heifers, and steers were interpreted through centralized processing labs and reported to AAA for use in genetic evaluation. Measures included longissimus muscle area (uLMA), fat depth at the 12th rib and over the rump, and intramuscular fat (IMF).   Individual ultrasound measurements were adjusted by AAA to 365 d for bulls, 390 d for heifers, and 400 d for steers. Following Tait et al. (2002), the subcutaneous fat measurement (SQF) used in genetic evaluation was calculated as 0.6(rib fat) + 0.4(rump fat). For traits measured using ultrasound, the American Angus Association defines contemporary group as the concatenation of breeder herd code, weaning herd code, image processing date, calf type (embryo or natural), scanning date, technician, breeder group code, test type, gender, and diet. There were 1,926,207 pedigree records available and phenotypes from 33,857 bulls, 33,737 heifers, and 1,805 steers remained after editing to remove: 1) animals with carcass data, 2) animals sired by bulls that did not have progeny with carcass data, 3) animals with 1 or more traits not

recorded, 4) contemporary groups of less than 30 bulls, 20 heifers, or 3 steers, 5) sire groups of less than 7 animals, and 6) observations more than 4 SD from their respective contemporary group mean. Thus, the ultrasound imagery data from bulls, heifers, and steers used herein came from progeny of 430, 410, and 112 Angus sires, respectively. These cattle represented 708, 968, and 152 contemporary groups of bulls, heifers, and steers, respectively.

The 4 generation pedigree file for all animals having either carcass or live animal measures contained 1,926,207 records. From this file, pedigrees that included animal, sire, and maternal and paternal grandsires were extracted for each of the sets of data described above. The pedigree file associated with the carcass data contained 40,870 records. Pedigree files associated with the ultrasonically measured traits contained 44,067, 44,152, and 2,036 records for bulls, heifers, and steers, respectively. Thus, numerator relationship matrices used in bivariate analyses of the carcass and gender-specific ultrasound measures had ranks of 77,340, 77,719, and 42,702 for bulls, heifers, and steers, respectively.

Using the data sets described above, a series of bivariate analyses were conducted to estimate genetic variances and covariances to be used as input to the AAA National Cattle Evaluation (NCE). Given genetic correlations between traits of interest reported by Hassen et al. (1998) and Wilson et al. (1993), the NCE was envisioned to be comprised of 3 separate analyses. In each analysis, measures of the indicator traits were considered gender-specific. The first NCE would produce EPD for MRB using the carcass data described above and ultrasonically measured IMF. The second NCE would produce EPD for FD using the carcass data and SQF as described above. The final NCE would produce EPD for CWT and cLMA, again using the carcass data described above with weight at scanning and uLMA as indicator traits.

The linear model used in these analyses can be described as:

$$\begin{bmatrix} Y_1 \\ Y_2 \end{bmatrix} = \begin{bmatrix} X_1\beta_1 \\ X_2\beta_2 \end{bmatrix} + \begin{bmatrix} Z_1u_1 \\ Z_2u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix},$$

where Y_i is the vector of data for the ith trait, X_i and Z_i are design matrices relating the data to their respective fixed contemporary group effects (β_i), random animal effects (u_i), and random residual effects (e_1) (authors: should this be e_i?). The random animal effects were assumed to have null means and variances:

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} A\sigma_{u_1}^2 & A\sigma_{u_1u_2} \\ A\sigma_{u_1u_2} & A\sigma_{u_2}^2 \end{bmatrix},$$

where A represents the numerator relationship matrix appropriate to the specific pedigree associated with the pair of traits being analyzed. The random residual effects were assumed to have variances:

$$\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} I\sigma_{e_1}^2 & I\sigma_{e_1 e_2} \\ I\sigma_{e_1 e_2} & I\sigma_{e_2}^2 \end{bmatrix},$$

where I represents an identity matrix appropriate to the number of observations for the traits being analyzed. When the traits being analyzed were measured on different animals $\sigma_{e_1 e_2} = 0$. Estimates of the variance and covariance components and associated estimates of heritability and their standard errors were obtained using ASREML v2.0 (Gilmour et al., 2000). The value of various indicator traits measured with ultrasound to predict carcass traits was assessed using standard formulas for correlated response (e.g., Falconer, 1989), parameter estimates obtained as described above, and assuming constant selection intensity.

Because results from a series of 2-trait analyses were pooled to produce genetic and residual covariance matrices for NCE, a bending procedure (Jorjani et al., 2003) was required to make the genetic covariance matrices for MRB and cLMA/CWT positive definite before using them in NCE. This bending was necessary only when covariances from ultrasonic imagery of steers were added to the genetic covariance matrices. Squared SE of heritability and correlation estimates were used as weighting factors for the diagonal and off-diagonal elements of the variance-covariance matrix, respectively. After ensuring the (co)variance matrices were positive definite, prototype NCE were conducted using animal models and results were compared with the previous NCE conducted by AAA. Rank correlations between NCE were computed for sires that met the following criteria: at least 35 progeny with 365-d weights in proper contemporary groups on Angus Herd Improvement Records resulting in an accuracy of the 365-d weight EPD of at least 0.50 and a minimum of 5 calves recorded in the American Angus Association Herd Book since June 1, 2005 (high impact sires).

Predicted BV from the joint and prior national cattle evaluation analyses were standardized using genetic standard deviations for the respective traits. The standardized BV were plotted against birth year to illustrate genetic trends irrespective of differences in scale between carcass measures and data obtained using ultrasound.

RESULTS AND DISCUSSION

Summary statistics describing the data sets are presented in Table 1. Median birth year of the steers from which carcass data were obtained was 1997, with 90% of the data coming from steers born between 1991 and 2003. Median birth years of the bulls, heifers, and steers from which data were collected using ultrasound were 2001, 2002, and 2002; and 90% of these data came from calves born from 1998 to 2005, 1999 to 2006, and 1998 to 2005, respectively. Issues with heterogeneity of intra-contemporary group variances associated with gender were less pronounced in the edited data than they had been when all data were considered, as would be the case in the NCE. Still, the intra-contemporary group variance of IMF content was more than 2-fold greater for steers than for bulls, with heifers intermediate. Likewise, Meyer (2007) reported approximately 2-fold or greater additive genetic variance for IMF, P8, and rib fat in steers and heifers relative to that of bulls in Australian Angus cattle.

Results with data from American Angus cattle (Wilson et al., 1993; Hassen et al., 1998; Sapp et al., 2002) were interpreted to indicate 3 analyses could be used to model the traits of interest with relatively little loss of information from correlated traits. Use of this *a priori* information resulted in estimation of a specific subset of all possible covariances from these data. This approach also enhances the computational ease of conducting the Angus NCE.

Shown in Table 2 are estimates of genetic (co)variances and parameters derived from them for MRB and IMF percentages calculated from ultrasonic scanning of live animals. The present estimate of heritability for MRB, while greater than the 0.26±0.04 estimate of Wilson et al. (1993) and the 0.35±0.04 estimate of Devitt and Wilton (2001) from multiple breeds, is consistent with other estimates from Angus cattle (0.43, Reverter et al., 2000; 0.42, Kemp et al., 2002; 0.58±0.05, Meyer, 2007) and with the 0.46 average from 17 studies reviewed by Bertrand et al. (2001). Here, MRB had a marginally greater heritability than ultrasonically measured IMF. However, the literature is unsettled relative to this issue. Reverter et al. (2000) and Meyer et al. (2007) indicated greater heritability for MRB than for IMF in Australian Angus and Hereford cattle. Crews et al. (2003) reported similar estimates of heritability for MRB and IMF in American Simmental. Finally, Kemp et al. (2002) reported the heritability of MRB in American Angus cattle was less than its ultrasonically measured counterpart. Bertrand et al. (2001) reported 0.41 as the average estimated heritability for % IMF measured using ultrasound.

Using the rule of thumb that estimated genetic correlations ≥ 0.8 indicate alternative measures of the same trait or the absence of genotype-environment interaction (Robertson, 1959), ultrasonic measurement of IMF results in observation of the same phenotype irrespective of gender. This result is contrary to the 0.65±0.06 estimate of Meyer (2007), but consistent with results of Reverter et al. (2000). However, ultrasonically measured IMF does not appear to be the same trait as carcass MRB. As calculated from the ratio of predicted correlated responses to selection, these data suggest that ultrasound imagery of steers has 6% greater value in prediction of carcass MRB than scans of bulls and that scans of bulls are 19% more valuable than scans of heifers. In this regard, the advantage of ultrasonic imagery from bulls over that from heifers results primarily from the difference in genetic correlations; with the difference between genders in genetic correlations resulting from corresponding differences in additive genetic variance rather than the covariance. However, as a result of proportional scaling in genetic and phenotypic variance across genders, the estimates of heritability of IMF were similar for bulls and heifers. In contrast, the result of Meyer (2007) may be interpreted to suggest scans of bulls are 33% less valuable than those of steers and heifers combined. This difference in value results from the additive genetic variance of IMF in bulls being reduced to a greater degree relative to phenotypic variance than in heifers and steers (i.e., reduced heritability), and despite the marginally greater genetic covariance between carcass and ultrasound IMF in bulls. The presently estimated genetic correlations between MRB and IMF confirm similar reports of this correlation in the range of 0.59 to 0.80 (Devitt and Wilton, 2001; Crews et al., 2003; Meyer, 2007); the 0.90 estimate of Kemp et al. (2002) notwithstanding. All evidence suggests that IMF is a useful predictor

of marbling score. Therefore, and in agreement with Sapp et al. (2002), selection decisions based on ultrasonically measured IMF can be expected to increase marbling score and quality grade.

Shown in Table 3 are estimates of genetic (co)variances and parameters derived from them for FD of steer carcasses and SQF of live animals measured from ultrasonic imagery. The heritability for FD (0.337 ± 0.023) found in this study is consistent with (Bertrand et al., 2001; Kemp et al., 2002; Crews et al., 2003) or marginally greater than (Wilson et al., 1993; Reverter et al., 2000; Meyer, 2007) other estimates; the 0.41 ± 0.05 estimate of Devitt and Wilton (2001) notwithstanding. Based on the present results, heritability of SQF as measured with ultrasound may be gender specific and marginally greater than the heritability of FD. Results from Reverter et al. (2000) and Crews et al. (2003) seemingly support differences in heritability between bulls and heifers, although estimates of Meyer et al. (2007) indicate similar heritability of fat depth for bulls and for steers and heifers combined. Recent literature estimates of differences in heritability between ultrasound and carcass measurements of fat depth were consistently positive (i.e., ultrasound – carcass = 0.04, Kemp et al., 2002; 0.11, Meyer, 2007; 0.23, Reverter et al., 2000; and 0.26, Crews et al., 2003). Taking into account any scaling effect associated with differences in fat depth of steers fed for harvest and seedstock managed as replacement animals, it seems most likely that the greater heritability of fat depth measured ultrasonically may arise from the introduction of additional error in the carcass trait associated with harvest. However, average estimates from earlier studies reviewed by Bertrand et al. (2001) suggest heritability of the carcass measurements may be greater than the corresponding measurements of subcutaneous fat made using ultrasound.

As with IMF and aside from the 0.66 ± 0.15 estimate for heifers and steers, ultrasonic measurement of SQF appears to result in observation of the same phenotype irrespective of gender. Other estimates of the genetic correlation across genders for fat depth were marginally smaller, averaging approximately 0.7 (Reverter et al., 2000; Crews et al., 2003; Meyer, 2007). Contrary to these references and Kemp et al. (2002), the present data seeming suggest that FD and SQF of seedstock replacement animals measured ultrasonically are different traits. Obviously, part of this difference can result from use of 2 anatomically different measures of subcutaneous fat in SQF as opposed to the use of only 1 of those measures for FD. However, even this more pessimistic present result is interpreted to indicate considerable value derived from measurement made with ultrasound in identifying genetic differences in carcass fat depth. Given the similar magnitude of genetic correlations for fat depths of bulls and heifers with carcass fat depth, records from both sexes are expected to contribute approximately equally to the prediction of breeding value for carcass fat depth.

Shown in Table 4 are estimates of genetic (co)variances and parameters derived from them for CWT, live weight at scanning, cLMA, and uLMA. Carcass weight had greater estimated heritability than scan weights. The relatively smaller genetic correlations of weight taken at scanning and carcass weight indicate that, as expected, these are likely not the same trait. However, weight taken at scanning remains a reasonable indicator of carcass weight. If it were so desired, the weight collected at scanning could be replaced

with 365-d weight with little loss of information in these analyses (*result not shown*) and potential to predict breeding values of many more animals for longissimus muscle area and carcass weight. This conclusion is also supported by the 0.81 estimate of Kemp et al. (2002) for the genetic correlation between yearling weight and carcass weight. However, these predicted breeding values would have low accuracy.

Carcass longissimus muscle area was more highly heritable than uLMA of heifers and steers, but not bulls. However, in general, the literature seems to indicate no major differences in heritability of longissimus muscle area measured on carcasses or ultrasonically (Reverter et al., 2000; Crews et al., 2003; Meyer, 2007), the substantially greater estimate from carcass data of Kemp (2002) notwithstanding. The substantial genetic correlations of: CWT with cLMA, scan weights with CWT, and cLMA with uLMA confirm the utility of the *a priori* envisioned joint analysis based on the findings of Wilson et al. (1993), Hassen et al. (1998), and Sapp et al. (2002).

The present results support the hypothesis that longissimus muscle area measured with ultrasound is the same trait, irrespective of gender. Support for this hypothesis is also found in the work of Reverter et al. (2000) and Crews et al. (2003). Countervailing evidence suggesting gender-specific trait definitions comes from Kemp et al. (2002) and Meyer (2007). Further, the presently estimated genetic correlations between uLMA of heifers and steers indicate that they may be the same trait as that recorded from carcasses of steers. However, Meyer (2007) estimated the genetic correlation between uLMA of heifers and steers combined and cLMA from steers to be 0.69±0.04. The somewhat lower genetic correlation between uLMA of bulls and cLMA of steers in the present study indicates potential for these being slightly different traits. These data suggest that ultrasound imagery of heifers has 13% greater value in prediction of cLMA than scans of bulls and scans of steers are also 6% more valuable than scans of bulls. Similarly, results from Meyer (2007) may be interpreted to suggest 9% greater value of scans of heifers and steers relative to scans of bulls. Devitt and Wilton (2001) and Meyer (2007) estimated the genetic correlation between uLMA of bulls longissimus muscle area and cLMA from steers to be 0.66±0.07 and 0.59±0.07, respectively. Certainly, uLMA measurements from seedstock are very useful indicators of cLMA of steers fed for harvest.

Measures of genetic trend (Figure 1) from data collected post-harvest and using ultrasound to the joint analyses were qualitatively similar to those from the analyses using only data collected with ultrasound. As expected from the less than unit genetic correlations between carcass traits and the respective indicator traits, the genetic trends from the combined analyses were reduced relative to those obtained from the ultrasound data alone. Genetic trends estimated from the carcass data alone were somewhat more disparate.

Using parameter estimates derived above, the prototype NCE altered the ranking of sires somewhat relative to the separate NCE conducted previously by AAA. For high impact sires, rank correlations between new and previous analyses of carcass data were 0.91, 0.90, 0.84, and 0.79 for MRB, FD, CWT, and cLMA, respectively. Also for the high

impact sires, rank correlations between evaluations of MRB, FD, and cLMA from the new analyses and previous evaluations from measurements of IMF, SQF and uLMA were 0.84, 0.79, and 0.89, respectively. Differences in ranks may be due in part to model enhancements, such as analysis of carcass data under an animal model in which dam pedigrees were included if available. Also, ultrasound steer data had been previously included in the carcass evaluation after adjustments to a carcass-trait basis.

Implications

This work supports a unified national cattle evaluation leading to publication of EPD for carcass traits using measurements from harvested animals and ultrasonic imagery of seedstock in a combined analysis. Unified national cattle evaluations for carcass merit resolve breeder confusion created by inconsistency of results when separate evaluations are reported for conceptually similar traits measured in different ways. The accuracy of selection decisions to change carcass attributes may be improved as a result. For all traits, ultrasonic imagery of bulls, heifers, and steers provides substantial value to prediction of breeding value for carcass merit. Gender-specific relationships of carcass measures with ultrasonic measures are indicated for intramuscular fat content and longissimus muscle area, but not for weight or subcutaneous fat depth.

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Table 1. Means and phenotypic standard deviations for carcass traits of steers and their ultrasonically measured indicators from live steers, heifers, and bulls.

Sex	Trait	Mean	SD
Steer	Carcass		
	Fat depth, cm	1.42	0.38
	Longissimus muscle area, cm^2	80.6	7.1
	Marbling score	6.02	0.78
	Weight, kg	355	27
	Ultrasound		
	Subcutaneous fat depth, cm	0.98	0.22
	Longissimus muscle area, cm^2	78.7	7.7
	intramuscular fat content, %	4.74	0.97
	Scan weight, kg	505	41
Heifer	Ultrasound		
	Subcutaneous fat depth, cm	0.66	0.16
	Longissimus muscle area, cm^2	63.2	6.5
	intramuscular fat content, %	4.46	0.76
	Scan weight, kg	396	27
Bull	Ultrasound		
	Subcutaneous fat depth, cm	0.75	0.18
	Longissimus muscle area, cm^2	81.3	7.1
	intramuscular fat content, %	3.73	0.47
	Scan weight, kg	571	34

Table 2. Estimates of additive genetic variance and heritability ($h^2 \pm SE$) for marbling score and sex-specific intramuscular fat content (IMF) measured using ultrasound (on diagonal), genetic covariances among traits (above diagonal), and genetic correlations ($r_g \pm SE$) derived from them (below diagonal).

Trait	MRB	IMF_b	IMF_h	IMF_s
Marbling score (MRB)	0.3456 0.445±0.025	0.1620	0.1676	0.2482
Bull IMF (IMF_b)	0.656±0.049	0.1764 0.375±0.028	0.2059	0.1911
Heifer IMF (IMF_h)	0.517±0.061	0.889±0.022	0.3040 0.401±0.033	0.2640
Steer IMF (IMF_s)	0.837±0.116	0.902±0.111	0.949±0.081	0.2545 0.262±0.086

Table 3. Estimates of additive genetic variance and heritability ($h^2 \pm SE$) for fat depth of steer carcasses and subcutaneous fat depth of live animals measured using ultrasound (on diagonal), genetic covariances among traits (above diagonal), and genetic correlations ($r_g \pm SE$) derived from them (below diagonal).

Trait	FD	SQF_b	SQF_h	SQF_s
Carcass fat depth (FD)	0.0486 0.337±0.023	0.01291	0.01314	0.02231
Bull scanned fat depth (SQF_b)	0.534±0.060	0.0120 0.392±0.031	0.01043	0.01025
Heifer scanned fat depth (SQF_h)	0.552±0.058	0.881±0.023	0.0117 0.463±0.037	0.00801
Steer scanned fat depth (SQF_s)	0.904±0.111	0.835±0.122	0.663±0.149	0.0125 0.258±0.083

Table 4. Estimates of additive genetic variance and heritability ($h^2 \pm SE$) for weight and longissimus muscle area of steer carcasses and weight at scanning and longissimus muscle area of live animals measured using ultrasound (on diagonal), genetic covariances among traits (above diagonal), and genetic correlations ($r_g \pm SE$) derived from them (below diagonal).

| Trait	CWT	cLMA	SWT_b	SWT_h	SWT_s	$uLMA_b$	$uLMA_h$	$uLMA_s$
Carcass weight (CWT)	65.7 0.397±0.024	6.75	30.1	23.4	48.4	2.67	2.05	5.80
Carcass longissimus muscle area (cLMA)	0.507±0.038	2.70 0.332±0.022	1.47	1.69	2.98	1.67	1.74	1.85
Bull scan weight (SWT_b)	0.460±0.070	0.111±0.081	65.0 0.255±0.026	51.1	60.2	4.28	2.40	2.10
Heifer scan weight (SWT_h)	0.400±0.074	0.142±0.080	0.877±0.028	52.2 0.312±0.031	25.4	2.13	3.53	4.42
Steer scan weight (SWT_s)	0.599±0.175	0.182±0.223	0.751±0.156	0.353±0.234	99.2 0.274±0.094	0.48	2.00	5.67
Bull scanned longissimus muscle area ($uLMA_b$)	0.204±0.074	0.631±0.057	0.329±0.065	.0183±0.075	0.030±0.238	2.60 0.328±0.029	1.84	1.98
Heifer scanned longissimus muscle area ($uLMA_h$)	0.185±0.080	0.776±0.048	0.218±0.078	0.357±0.066	0.147±0.231	0.835±0.034	1.87 0.276±0.027	1.69
Steer scanned longissimus muscle area ($uLMA_s$)	0.571±0.221	0.899±0.182	0.208±0.297	0.488±0.235	0.454±0.245	0.982±.0114	0.987±0.115	1.57 0.178±0.064
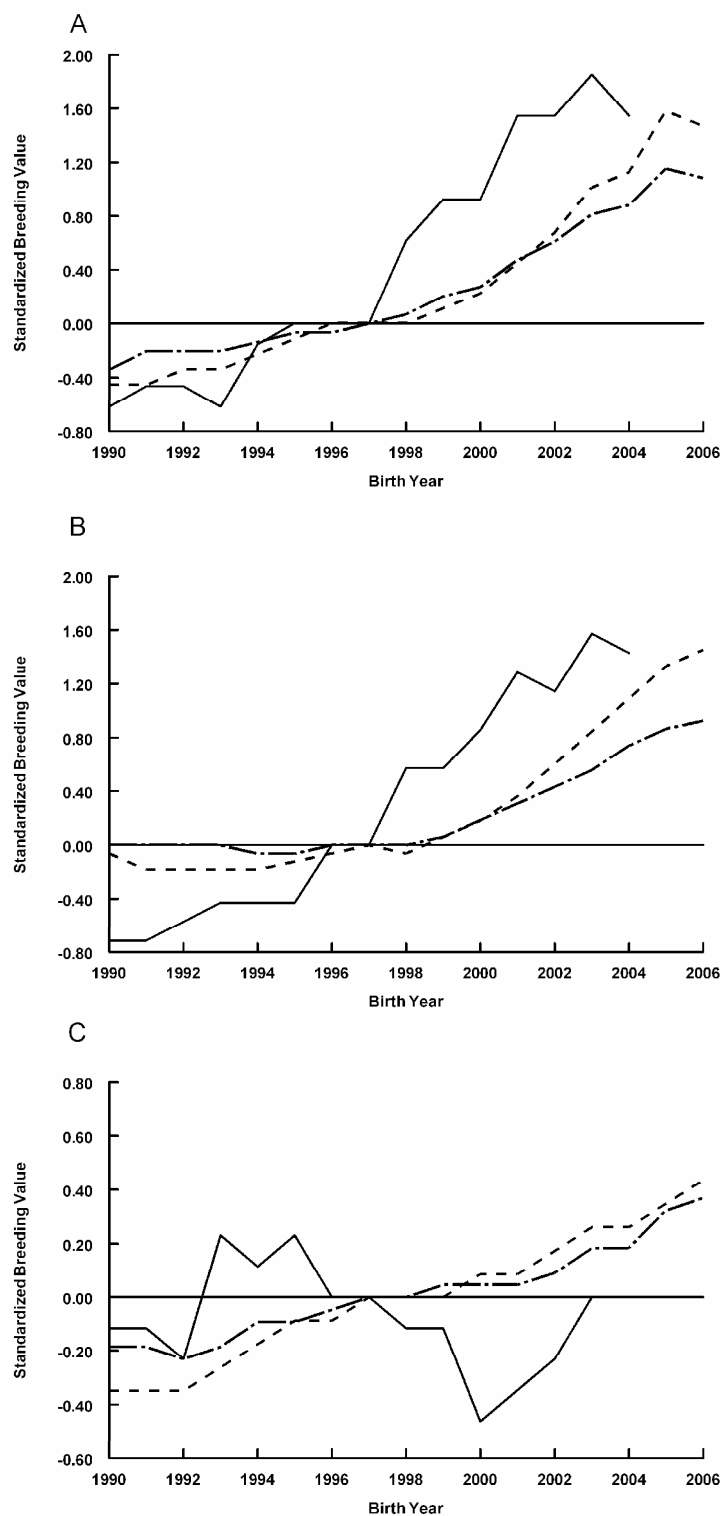
Figure 1. Standardized genetic trends in marbling score or intramuscular fat content (A), longissimus muscle area (B), and subcutaneous fat depth (C) as estimated from previous national cattle evaluation analyses of carcass (solid lines) and ultrasound data (dashed lines), and proposed national cattle evaluation analyses of carcass traits using the merged carcass and ultrasound data bases (dash-dot lines).