

Genetic correlations among indicator traits for carcass composition measured in yearling beef bulls and finished feedlot steers

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Bergen, R., Miller, S. P. and Wilton, J. W. 2005. **Genetic correlations among indicator traits for carcass composition measured in yearling beef bulls and finished feedlot steers.** *Can. J. Anim. Sci.* **85**: 463–473. Genetic correlations were examined among 10 live growth and ultrasound traits measured in yearling beef bulls ($n = 2172$) and four carcass traits measured in cross-bred finished feedlot steers ($n = 1031$). Heritabilities ranged from 0.13 (bull ultrasound longissimus muscle width) to 0.83 (yearling bull hip height). Genetic correlations indicated that selecting yearling bulls for increased growth rate and hip height would lead to higher carcass weight, increased longissimus muscle area and reduced levels of carcass marbling in steers. Bull ultrasound fat depth was positively associated with both carcass fat depth and marbling score. Most ultrasound longissimus muscle size measurements in bulls were positively associated with each other and with carcass longissimus muscle area in steers, but the magnitude of the genetic correlation with carcass measurements depended on the bull longissimus muscle size trait in question. This suggests that longissimus muscle shape in bulls may be related to carcass weight, fat and muscle traits in steers. Results confirm that while ultrasound is a valuable tool for the genetic improvement of carcass traits in beef cattle, genetic correlations between live bull ultrasound and steer carcass traits less than unity suggest that selection would benefit from multiple trait evaluations in situations where reliable carcass data are available.

Key words: Ultrasound, beef carcass, heritability, genetic correlation

Bergen, R., Miller, S. P. et Wilton, J. W. 2005. **Corrélation génétique entre les paramètres de la composition de la carcasse mesurés chez les veaux de boucherie d'un an et les bouvillons engraisés en parquet.** *Can. J. Anim. Sci.* **85**: 463–473. Les auteurs ont examiné les corrélations génétiques entre 10 paramètres mesurés en vif ou aux ultrasons chez les veaux de boucherie d'un an ($n = 2172$) et quatre paramètres mesurés sur la carcasse de bouvillons hybrides engraisés en parquet ($n = 1031$). L'héritabilité des paramètres varie de 0,13 (épaisseur du *longissimus* des bovins établie aux ultrasons) à 0,83 (taille des veaux d'un an aux hanches). Les corrélations génétiques indiquent qu'en sélectionnant les bouvillons d'un an d'après un taux de croissance plus rapide et la hauteur aux hanches, on obtiendrait des carcasses plus lourdes, un *longissimus* d'une plus grande superficie et de la viande moins persillée. L'épaisseur du gras des bovins mesurée aux ultrasons présente une corrélation positive avec l'épaisseur du gras de la carcasse et le persillé. La plupart des mesures du *longissimus* obtenues aux ultrasons chez les bovins sont positivement corrélées les unes aux autres ainsi qu'avec la superficie de ce muscle dans la carcasse des bouvillons, mais l'importance de la corrélation génétique avec les mesures de la carcasse dépend du paramètre concerné des dimensions du *longissimus* chez l'animal adulte. On en déduit que la forme du muscle chez les bovins adultes pourrait dépendre de caractères régissant le poids de la carcasse, le gras et les muscles chez les bouvillons. Les résultats confirment que si l'analyse aux ultrasons a son utilité pour parvenir à une amélioration génétique des paramètres de la carcasse chez les bovins de boucherie, quand les corrélations génétiques entre les mesures prises sur l'animal vivant aux ultrasons et les paramètres de la carcasse des bouvillons ont une valeur inférieure à l'unité, la sélection profiterait d'une évaluation multifactorielle dans l'éventualité où on possède des données fiables sur la carcasse.

Mots clés: Ultrasons, carcasse des bovins, héritabilité, corrélation génétique

Previous research has shown that ultrasonic 12/13th rib fat depth and longissimus muscle area measurements are valuable predictors of carcass composition (Herring et al. 1994; Bergen et al. 1996; Williams et al. 1997; Realini et al. 2001; Greiner et al. 2003). These traits are heritable and are positively genetically correlated with the corresponding carcass traits (Moser et al. 1998; Crews and Kemp 2001, 2002; Devitt and Wilton 2001 and Crews et al. 2003), suggesting that selection based on ultrasonic fat depth and longissimus muscle area should be reflected in changes in the carcass composition of commercial progeny.

Recent research suggests that longissimus muscle depth and width measurements may be as valuable as traced longissimus

muscle area as predictors of carcass composition (Bergen et al. 2003, 2005). Estimates of carcass composition in yearling bulls may also benefit from live measurements of frame size and intramuscular fat percentage (Bergen et al. 2005). However, the genetic correlations between these alternative live measurements collected in yearling bulls with carcass measurements collected in commercial steer progeny have not been reported. This information would be useful in further assessing the potential value of linear ultrasonic longissimus muscle measurements to seedstock evaluation programs and in

Abbreviations: EPD, expected progeny difference; h^2 , heritability; r_g , genetic correlation.

developing approaches to optimally combine live seedstock and carcass data in an economic selection index.

The objective of this study was to determine the heritabilities of and genetic correlations among growth and ultrasound measurements collected in yearling beef bulls with carcass measurements collected from finished feedlot steers.

MATERIALS AND METHODS

Animals and Data

Growth and ultrasound data from yearling beef bulls and carcass data from finished crossbred feedlot steers were used in this study. Young beef bulls ($n = 2172$) were born between 1993 and 2002 in private seedstock herds and evaluated in post-weaning growth test and feed efficiency stations operated by Beef Improvement Ontario's Bull Evaluation Program. While bulls entering the test stations may have been pre-selected based on pre-weaning gain, an earlier study concluded that any bias resulting from this potential pre-selection was of minor importance (Schenkel et al. 2004a). There were 615 pre-weaning contemporary groups (herd of origin \times year) containing up to 25 bulls; 26% of observations were from pre-weaning contemporary groups containing at least 10 bulls. Because of these small groups, pre-weaning herd of origin effects would not be well estimated as a fixed effect. Consequently, pre-weaning herd of origin was fitted as a random effect in the genetic models for bull traits described below. Treating small contemporary groups as a random effect increases the effective number of progeny through the use of interclass information from relatives in other contemporary groups (Van Vleck 1987). Simulation study models using random contemporary groups produced estimated breeding values with higher accuracy, lower bias, and lower mean squared error than models with fixed contemporary groups, except when the best sires were represented in the worst contemporary groups (Visscher and Goddard 1993) or when unrealistically extreme preferential treatment was applied to progeny of superior sires (Oikawa and Sato 1997). Treating pre-weaning herd of origin as a random effect also allowed us to determine the effect of pre-weaning herd of origin on the phenotypic variance of yearling bull traits, which can be substantial for growth traits and longissimus muscle area (Schenkel et al. 2004b). There were 35 post-weaning contemporary groups (test station \times year \times start of test date), all of which contained at least 15 bulls. Schenkel et al. (2004b) described eligibility requirements, nutritional management and data collection protocols at the central test stations. Bulls had to be over 181 kg and under 291 d of age to enter a test station. Age range within a test group was restricted to 90 d. Following a 28-d adjustment period, bulls were fed a diet containing (dry matter basis) 15.0 to 15.8% crude protein, 64.1 to 66.8% total digestible nutrients and 9.7 to 10.1 MJ kg⁻¹ metabolizable energy for 140 (until 1995) or 112 d (after 1995). End of test weight, total post-weaning gain (end – start weight), hip height and ultrasound measurements were collected near 365 d of age. Ultrasonic 12/13th rib fat depth, longissimus muscle area and Method 1 and 2 longissimus muscle depth and width [described and illustrated in Bergen et al. (2003)] were measured from ultrasound images archived by Beef Improvement Ontario. In some cases, archived images could not be located

or recovered, resulting in 1488 ultrasound fat depth and longissimus size records. Ultrasound intramuscular fat estimates (Beef Quality Objective Measurement software; Critical Visions Incorporated, Atlanta, GA) were available for 1308 bulls tested from 1996 onwards. Animal management protocols were either approved by the University of Guelph Animal Care committee following Canadian Council on Animal Care (1993) guidelines or followed standard commercial bull test station management procedures established and supervised by Beef Improvement Ontario. Sire and dam breed compositions were used to calculate the breed composition and expected heterozygosity of each bull. Approximately 77% of bulls were fullblood (100% of breed composition contributed by a single breed), 16% were purebred (87.5 to 100% of breed composition contributed by a single breed) and 7% were crossbred (< 87.5% of breed composition contributed by a single breed). The main breeds represented in the present study were Angus, Charolais, Hereford, Simmental, Limousin, Blonde d'Aquitaine and Gelbvieh; no other breed accounted for more than 12.5% of the total breed composition of any bull.

Steers ($n = 1031$) were born between 1996 and 2002 as part of a long-term breeding project conducted by the University of Guelph at the Elora Beef Research Center, New Liskeard Agricultural Research Station and Agriculture and Agri-Food Canada's Kapuskasing Research Station. There were 39 pre-weaning contemporary groups (farm of birth \times year of birth \times season of birth) ranging in size from 7 to 53 steers. Over 96% of observations were from pre-weaning contemporary groups containing at least 10 steers, allowing steer pre-weaning contemporary group to be fitted as a fixed effect in subsequent genetic models. All steers were fed from weaning to harvest at the University of Guelph's Elora Beef Research Center. Steers were grouped into 62 post-weaning contemporary groups (experimental treatment \times year of slaughter \times season of slaughter) containing 5 to 58 head; 89% of observations were from post-weaning contemporary groups containing at least 10 steers. Many of the experimental treatments were comparisons of corn varieties or dietary energy levels. Consequently, steers were also classified into two "feedlot regime" groups according to whether they were fed a high grain diet from weaning to slaughter ($n = 499$) or were backgrounded on forage or limit fed grain diets prior to high grain finishing ($n = 532$). Steers were harvested at a federally inspected abattoir, and carcass weight, grade fat depth, traced longissimus muscle area and visual carcass marbling score were recorded for all steers. Experimental procedures were approved by the University of Guelph's Animal Care Committee and followed guidelines established by the Canadian Council on Animal Care (1993). Sire and dam breed compositions were used to calculate the breed composition and expected heterozygosity of each steer. All steers were crossbred, with predominantly Angus, Simmental and Charolais breeding. Simple statistics for live yearling bull growth and ultrasound traits and feedlot steer carcass traits are shown in Table 1.

Analyses

The degree of genetic connectedness was estimated by calculating the total number of direct genetic links (due to common sires and dams) between bull and steer post-weaning

groups (Roso et al. 2004). Subsequent genetic analyses were conducted in ASREML (Gilmour et al. 2000). Measurement at scan or slaughter age was used as a covariate in all animal models. Since Beef Improvement Ontario's Bull Evaluation Program controls both minimum start of test age and allowable age range in a given test group, scan age was regressed across post-weaning bull contemporary groups. However, since nutritional management (feedlot regime) affects slaughter age through its influence on rates of weight, fat and muscle deposition (Vaage et al. 1999; Block et al. 2001), adjusting all steers to a common slaughter age across feedlot regimes may be inappropriate. Consequently, slaughter age was regressed within feedlot regime for all steer traits. Breed effects were estimated by regressing the dependent variable on the percentage of total breed composition contributed by each breed.

The pedigree file used for all analyses contained 10 068 animals, and animals with records had an average of 4.1 recorded ancestors. Pair-wise analyses were performed between all traits to estimate (co)variance components and effects of age, contemporary group, feedlot regime, breed and expected heterozygosity using the following models: pairwise analyses between traits measured in bulls:

$$\begin{bmatrix} \mathbf{y}_{\text{Bull}_1} \\ \mathbf{y}_{\text{Bull}_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{Bull}_1} & 0 \\ 0 & \mathbf{X}_{\text{Bull}_2} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{Bull}_1} \\ \mathbf{b}_{\text{Bull}_2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{Bull}_1} & 0 \\ 0 & \mathbf{Z}_{\text{Bull}_2} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{Bull}_1} \\ \mathbf{a}_{\text{Bull}_2} \end{bmatrix} + \begin{bmatrix} \mathbf{W}_{\text{Bull}_1} & 0 \\ 0 & \mathbf{W}_{\text{Bull}_2} \end{bmatrix} \begin{bmatrix} \mathbf{h}_{\text{Bull}_1} \\ \mathbf{h}_{\text{Bull}_2} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{Bull}_1} \\ \mathbf{e}_{\text{Bull}_2} \end{bmatrix}$$

pairwise analyses between traits measured in steers:

$$\begin{bmatrix} \mathbf{y}_{\text{Steer}_1} \\ \mathbf{y}_{\text{Steer}_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{Steer}_1} & 0 \\ 0 & \mathbf{X}_{\text{Steer}_2} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{Steer}_1} \\ \mathbf{b}_{\text{Steer}_2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{Steer}_2} & 0 \\ 0 & \mathbf{Z}_{\text{Steer}_2} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{Steer}_1} \\ \mathbf{a}_{\text{Steer}_2} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{Steer}_1} \\ \mathbf{e}_{\text{Steer}_2} \end{bmatrix}$$

pairwise analyses between traits measured in bulls with traits measured in steers:

$$\begin{bmatrix} \mathbf{y}_{\text{Bull}_1} \\ \mathbf{y}_{\text{Steer}_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{Bull}_1} & 0 \\ 0 & \mathbf{X}_{\text{Steer}_2} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{Bull}_1} \\ \mathbf{b}_{\text{Steer}_1} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{Bull}_1} & 0 \\ 0 & \mathbf{Z}_{\text{Steer}_2} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{Bull}_1} \\ \mathbf{a}_{\text{Steer}_2} \end{bmatrix} + \begin{bmatrix} \mathbf{W}_{\text{Bull}_1} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} \mathbf{h}_{\text{Bull}_1} \\ 0 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{Bull}_1} \\ \mathbf{e}_{\text{Steer}_2} \end{bmatrix}$$

where \mathbf{y} is a vector of measurements for the traits, \mathbf{X} is a known incidence matrix of fixed classification and covariate effects influencing bull and steer traits, \mathbf{b} is a vector of fixed classification and covariate effects influencing bull (post-weaning contemporary group effect, and regressions on breed, expected breed heterozygosity, and scan age) and steer (pre- and post-weaning contemporary group and feedlot regime effects, and regressions on breed, expected breed heterozygosity, and slaughter age within feedlot regime) traits, \mathbf{Z} is a known incidence matrix of animals with observations for the traits, \mathbf{a} is a random vector of unknown animal additive genetic effects for the traits, \mathbf{W} is a known incidence matrix of pre-weaning contemporary group effects for bull traits, \mathbf{h} is a random vector of unknown pre-weaning contemporary group effects for bull traits, and \mathbf{e} is a random vector of unknown residual effects affecting the traits.

The expected mean of random effects was assumed to be zero, with (co)variance matrices

$$\text{Var} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{a_1} & \mathbf{A}\sigma_{a_{12}} \\ \mathbf{A}\sigma_{a_{12}} & \mathbf{A}\sigma^2_{a_2} \end{bmatrix}$$

where \mathbf{A} is the numerator relationship matrix, $\sigma^2_{a_1}$ is the additive genetic variance of trait 1, $\sigma^2_{a_2}$ is the additive genetic variance of trait 2, and $\sigma_{a_{12}}$ is the additive genetic covariance between traits 1 and 2,

$$\text{Var} \begin{bmatrix} \mathbf{h}_1 \\ \mathbf{h}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma^2_{h_1} & \mathbf{I}\sigma_{h_{12}} \\ \mathbf{I}\sigma_{h_{12}} & \mathbf{I}\sigma^2_{h_2} \end{bmatrix}$$

where \mathbf{I} is an identity matrix of order equal to the number of pre-weaning herd of origin bull contemporary groups, $\sigma^2_{h_1}$ is the herd of origin variance of bull trait 1, $\sigma^2_{h_2}$ is the herd of origin variance of bull trait 2, and $\sigma_{h_{12}}$ is the herd of origin covariance between bull traits 1 and 2,

$$\text{Var}(\mathbf{e}) = \begin{bmatrix} \mathbf{I}\sigma^2_{e_1} & \mathbf{I}\sigma_{e_{12}} \\ \mathbf{I}\sigma_{e_{12}} & \mathbf{I}\sigma^2_{e_2} \end{bmatrix}$$

where \mathbf{I} is an identity matrix of order equal to the number of observations, $\sigma^2_{e_1}$ is the residual variance of trait 1, $\sigma^2_{e_2}$ is the residual variance of trait 2, and $\sigma_{e_{12}}$ is the residual covariance between traits 1 and 2 measured the same gender of animal. Since live bull and steer carcass data were not available for the same animal, bivariate models involving both bull and steer traits assumed

$$\text{Var}(\mathbf{e}) = \begin{bmatrix} \mathbf{I}\sigma^2_{e_1} & 0 \\ 0 & \mathbf{I}\sigma^2_{e_2} \end{bmatrix}$$

After accounting for the fixed breed effect in the animal model, homogeneous genetic, herd of origin and residual (co)variance was assumed across all breeds, and all unknown sires and dams were assumed to originate from the same non-inbred base population regardless of breed.

Table 1. Summary statistics for traits measured in live yearling beef bulls and finished feedlot steers

Trait	Number of records	Mean	Standard deviation	Minimum	Maximum	Coefficient of variation
<i>Live yearling bull growth and ultrasound traits</i>						
Scan age (d)	2172	375	28	285	448	7.5
Yearling weight (kg)	2105	561.2	62.8	336.4	785.4	11.2
Post-weaning gain (kg)	2105	217.4	32.6	112.1	325.3	15.0
Hip height (cm)	2109	116.4	4.1	100.3	132.3	3.5
Subcutaneous fat depth (mm)	1488	4.8	2.5	0	18.4	52.8
Intramuscular fat content (%)	1308	3.42	0.97	1.02	8.22	28.4
Longissimus muscle area (cm ²)	1488	94.0	10.6	56.2	125.8	11.3
Method 1 longissimus muscle depth ^z (mm)	1488	70.4	6.5	49.3	95.3	9.2
Method 1 longissimus muscle width ^z (mm)	1488	157.9	7.6	115.1	178.1	4.8
Method 2 longissimus muscle depth ^z (mm)	1488	81.1	6.7	61.1	102.4	8.3
Method 2 longissimus muscle width ^z (mm)	1488	116.8	7.9	87.6	141.5	6.8
<i>Finished feedlot steer carcass traits</i>						
Slaughter age (d)	1031	453	74.4	292	758	16.4
Hot carcass weight (kg)	1031	349.5	58.5	207	583	16.7
Grade fat depth (mm)	1029	8.8	2.1	1	18	24.1
Longissimus muscle area (cm ²)	1027	87.0	12.9	43.2	138.2	14.8
Visual marbling score ^y	1023	5.1	0.7	3	7.5	13.7

^zDescribed and illustrated in Bergen et al. (2003).

^y≤ 3.0 = devoid, 3.1 to 4.0 = traces, 4.1 to 5.9 = slight, 6.0 to 7.0 = small to moderate, ≥ 7.0 = slightly abundant to abundant.

For summary purposes, heterosis and breed effects as well as phenotypic, additive genetic and pre-weaning bull contemporary group variances were calculated as the average solution from the 13 pair-wise analyses performed for each trait. Breed effects were expressed relative to the Charolais breed, which was constrained to zero.

RESULTS AND DISCUSSION

Genetic Connectedness

Direct genetic ties (i.e., through common sires or dams) connected all bull and steer post-weaning contemporary groups; no post-weaning contemporary group was genetically isolated. Each bull post-weaning contemporary group had an average of 356 (ranging from 44 to 888) direct genetic ties to bulls or steers in other contemporary groups. Each steer post-weaning contemporary group had over 300 direct genetic ties to bulls or steers in other contemporary groups. The steers were the progeny of 76 sires, 47 of which had their own ultrasound records or at least three intact male progeny with ultrasound records.

Pre-weaning Herd of Origin, Feedlot Regime, Heterosis and Breed Solutions

Pre-weaning bull contemporary group accounted for less than 10% of the phenotypic variation for most traits, with the exception of yearling weight (Table 2). Consequently, while results obtained for yearling weight in the present study are shown, they will not be discussed in detail. Schenkel et al. (2004b) reported similar results suggesting that pre-test herd of origin effects continue to influence yearling bull performance at the end of a 112 or 140 d post-weaning growth evaluation period in centralized bull test stations using an initial 28 d warm-up period.

Slaughter age varied between the different feedlot regimes. Steers fed high grain diets from weaning were slaughtered at

426 ± 62 d of age, while steers backgrounded prior to high grain finishing were slaughtered at 478 ± 76 d. The magnitude of the slaughter age adjustment also varied between feedlot regimes (Table 3). Carcass weight increased at a greater rate ($P < 0.10$) in calves that were backgrounded prior to high grain finishing than in calves fed a high grain diet from weaning until slaughter. The opposite trend applied to marbling score ($P < 0.05$). Other studies have shown higher rates of gain. Vaage et al. (1998) reported that high grain fed (vs. backgrounded) steers had average daily growth rates of 1.62 (vs. 1.03) kg liveweight, 0.04 (vs. 0.02) mm 12/13th rib ultrasound fat depth, and 0.22 (vs. 0.11) cm² longissimus muscle area over the entire weaning to slaughter feeding period. However, figures indicated that diet differences became very slight late in the feeding period (Vaage et al. 1999). Block et al. (2001) reported that steers backgrounded for 70 (vs. 126) d averaged daily growth rates of 1.82 (vs. 1.90) kg liveweight, 0.06 (vs. 0.07) mm for 12/13th rib ultrasound fat depth, and 0.23 (vs. 0.15) cm² for 12/13th rib ultrasound longissimus muscle area during the finishing period. The general effects of backgrounding vs. high grain finishing on performance late in the feeding period appear to be in agreement among these studies. It must also be noted that the age adjustment factors obtained in the present study were calculated based only on a regression of carcass measurements on slaughter age rather than repeated ultrasound measurements over time, and do not reflect overall growth during the entire feeding period.

In general, heterosis was higher for size traits than for ultrasound and carcass traits. Heterosis estimates expressed as a percentage of the phenotypic mean ranged from 0.19% (yearling bull ultrasound Method 1 longissimus muscle width) to 5.62% (yearling bull post-weaning gain; Table 3). However, heterosis estimates were significant ($P < 0.05$) only for live bull and steer carcass weight traits and for live yearling bull ultrasound Method 2 longissimus muscle depth

Table 2. Estimates^z of phenotypic variance, pre-weaning contemporary group by phenotypic variance ratio and heritabilities (\pm standard error) for traits evaluated in live yearling beef bulls and finished feedlot steers on an age-constant basis

	Phenotypic variance	Pre-weaning contemporary group by phenotypic variance ratio	Heritability
<i>Live yearling bull growth and ultrasound traits</i>			
Yearling weight	2050.77 \pm 74.79	0.21 \pm 0.03	0.50 \pm 0.07
Post-weaning gain	593.18 \pm 20.08	0.08 \pm 0.02	0.47 \pm 0.07
Hip height	11.14 \pm 0.39	0.09 \pm 0.02	0.83 \pm 0.07
Subcutaneous fat depth	3.14 \pm 0.13	0.12 \pm 0.03	0.31 \pm 0.08
Intramuscular fat content	0.50 \pm 0.02	0.07 \pm 0.03	0.29 \pm 0.09
Longissimus muscle area	68.37 \pm 2.70	0.08 \pm 0.02	0.36 \pm 0.08
Method 1 longissimus muscle depth ^y	28.90 \pm 1.12	0.06 \pm 0.02	0.31 \pm 0.08
Method 1 longissimus muscle width ^y	33.76 \pm 1.29	0.02 \pm 0.02	0.25 \pm 0.08
Method 2 longissimus muscle depth ^y	33.64 \pm 1.30	0.07 \pm 0.03	0.25 \pm 0.08
Method 2 longissimus muscle width ^y	41.99 \pm 1.57	0.01 \pm 0.02	0.13 \pm 0.07
<i>Finished feedlot steer carcass traits</i>			
Hot carcass weight	1014.54 \pm 56.67		0.58 \pm 0.10
Grade fat depth	3.62 \pm 0.18		0.23 \pm 0.08
Longissimus muscle area	88.47 \pm 4.50		0.35 \pm 0.09
Marbling score ^x	0.34 \pm 0.02		0.43 \pm 0.09

^zResults represent the average solution from all bivariate models involving the trait in question.

^yDescribed and illustrated in Bergen et al. (2003).

^x \leq 3.0 = devoid, 3.1 to 4.0 = traces, 4.1 to 5.9 = slight, 6.0 to 7.0 = small to moderate, \geq 7.0 = slightly abundant to abundant.

and steer carcass longissimus muscle area ($P < 0.10$). Given the low numbers of crossbred bulls included in the present study, the heterosis estimates calculated for bull traits should be viewed with caution. Of the traits measured in this study, Marshall (1994) reported average heterosis estimates (calculated from literature values) ranging from 3.8% (marbling score) to 10.1% (carcass fat depth).

Breed solutions followed expected trends (Table 3). Charolais and Simmental bulls were larger than all other breeds. Ultrasound subcutaneous fat depth and intramuscular fat levels were higher for Angus and Hereford, intermediate for Charolais, Simmental and Gelbvieh, and lowest for Limousin and Blonde d'Aquitaine bulls. The opposite trend was observed for ultrasound longissimus muscle size traits (Table 3). Schenkel et al. (2004b) reported similar results in a larger data set. Continental (Charolais, Simmental, Limousin, Blonde d'Aquitaine and Gelbvieh) steers had heavier carcasses with less fat depth and greater longissimus muscle area than British (Angus and Hereford) steers (Table 3). Angus steers had higher carcass marbling scores than other breeds. These results agree with literature estimates (Marshall 1994; Wheeler et al. 2004, 2005).

Genetic Parameters

Live Bull Growth and Ultrasound Traits

The heritability of post-weaning gain in the present study ($h^2 = 0.47$) compared well with values of 0.46 and 0.35 reported by Devitt and Wilton (2001) and Schenkel et al. (2004b), respectively. The high heritability of hip height obtained in the present study ($h^2 = 0.83$; Table 3) was in general agreement with previous studies of yearling beef bulls ($h^2 = 0.55$; Schenkel et al. 2004b) and beef cows ($h^2 = 0.68$; Arango et al. 2002).

The heritability of 0.31 obtained for ultrasound fat depth in the present study (Table 3) agreed with recent estimates, which range from 0.11 (Moser et al. 1998) to 0.53 (Crews et

al. 2003). Similarly, the heritability estimate for ultrasound intramuscular fat percentage (0.29) found in the present study agreed with literature values obtained using the same image interpretation software. Devitt and Wilton (2001), Crews et al. (2003) and Schenkel et al. (2004b) obtained respective heritability estimates of 0.23, 0.47, and 0.14 for this trait.

The heritability of ultrasound longissimus muscle area obtained in the present study ($h^2 = 0.36$) was similar to published heritability estimates for this trait, which range from 0.37 (Crews et al. 2003) to 0.61 (Crews and Kemp 2001). Recent reports suggest that longissimus muscle depth and width measurements may predict carcass lean meat yield as effectively as traced longissimus muscle area (Bergen et al. 2003, 2005). However, the genetic parameters of these linear longissimus muscle size measurements have not been studied previously in beef cattle. The heritabilities of longissimus muscle Method 1 depth and width and Method 2 longissimus muscle depth ($h^2 = 0.31$, 0.25 and 0.25, respectively) are similar to that of longissimus muscle area, suggesting that selection for any of these longissimus muscle size traits should be effective. However, Method 2 longissimus muscle width appears to be less heritable ($h^2 = 0.13$) than other longissimus muscle measurements and would respond less quickly to selection. Obtaining accurate longissimus muscle width measurements may be somewhat more problematic than for depth measurements, and this would negatively impact heritability estimates. Longissimus muscle width measurements are based on muscle interfaces that are parallel with the direction of travel of the ultrasound wave. In contrast, the muscle boundaries used for depth measurements are more perpendicular to the ultrasound wave and therefore produce a stronger echo and sharper image. Furthermore, obtaining a sufficiently accurate Method 2 width measurement may be difficult if the exact boundaries of the "acorn" fat landmark are difficult to discern. Fernandes et al. (2004) also reported that age-constant

Table 3. Age covariate, heterosis and breed solutions^z for traits measured in live yearling beef bulls and finished feedlot steers

Live yearling bull traits	Scan age	Heterosis (%)	Angus	Hereford	Simmental	Limousin	Blonde d ^t	
							Aquitaine	Gelbvieh
Yearling weight (kg)	1.15 ± 0.05**	4.28 ± 1.11**	-29.49	-41.96	-0.59	-62.85	-27.27	-32.54
Post-weaning gain (kg)	0.02 ± 0.03	5.62 ± 1.33**	-8.55	-21.40	-6.66	-27.44	-18.41	-14.04
Hip height (cm)	0.05 ± 0.003**	0.60 ± 0.40	-5.17	-3.67	-0.04	-2.26	-0.83	-3.91
Subcutaneous fat depth (mm)	0.012 ± 0.0005**	5.21 ± 6.27	0.32	0.33	0.01	-0.01	-0.13	-0.01
Intramuscular fat content (%)	0.001 ± 0.001	-3.44 ± 3.58	1.10	0.68	0.11	-0.16	-0.22	0.18
Longissimus muscle area (cm ²)	0.08 ± 0.01**	1.85 ± 1.49	-12.65	-16.53	-1.22	3.63	8.11	-2.57
Method 1 longissimus muscle depth (mm) ^b	0.04 ± 0.01**	2.04 ± 1.29	-5.73	-8.87	-1.63	1.74	3.54	-1.46
Method 1 longissimus muscle width (mm) ^y	0.04 ± 0.01**	0.19 ± 0.61	-7.69	-8.02	0.97	2.72	3.78	-1.46
Method 2 longissimus muscle depth (mm) ^y	0.05 ± 0.01**	2.14 ± 1.20*	-3.71	-8.37	-0.78	1.23	3.03	-0.79
Method 2 longissimus muscle width (mm) ^y	0.01 ± 0.01	-1.30 ± 0.89	-9.17	-7.30	-1.75	2.23	3.67	-2.43
<i>Finished feedlot steer carcass traits</i>								
	Slaughter age							
	HG ^x	BG ^x						
Hot carcass weight (kg)	0.69 ± 0.05 ^b	0.79 ± 0.04 ^a	-57.74	-73.06	-35.94	-28.04	-6.87	-62.20
Grade fat depth (mm)	0.012 ± 0.003	0.017 ± 0.003	1.21	1.68	0.11	0.66	-0.21	0.27
Longissimus muscle area (cm ²)	0.10 ± 0.01	0.12 ± 0.01	-13.54	-20.17	-4.46	8.06	10.48	-7.32
Visual marbling score ^w	0.0061 ± 0.0009 ^b	0.0039 ± 0.0008 ^a	0.66	-0.09	0.12	-0.15	0.22	-0.09

** Value differs significantly from zero ($P \leq 0.05$).

* Value differs significantly from zero ($P \leq 0.10$).

^{a,b} Values in the same row with different letters differ ($P < 0.10$).

^zResults represent average solutions from bivariate models involving each trait, expressed relative to the Charolais breed solution.

^ydescribed and illustrated in Bergen et al. (2003).

^wHG, steers fed a high grain diet from weaning to slaughter; BG, steers backgrounded prior to high grain finishing.

^x3.0 = devoid, 3.1 to 4.0 = traces, 4.1 to 5.9 = slight, 6.0 to 7.0 = small to moderate, ≥ 7.0 = slightly abundant to abundant.

loin depth was more heritable than loin width in sheep ($h^2 = 0.38$ and 0.30 , respectively).

Carcass Traits

The heritability estimate obtained for carcass weight in the present study ($h^2 = 0.58$) agreed with recent literature values, which range from 0.15 to 0.71 (Minick et al. 2004). The heritability obtained for carcass fat depth ($h^2 = 0.23$) in the present study was similar to other literature estimates which range from 0.10 (Minick et al. 2004) to 0.46 (Crews and Kemp 2001, 2002). The heritability of longissimus muscle area (0.35) in the present study was also similar to literature estimates, which range from 0.18 to 0.62 (Minick et al. 2004). Similarly, the heritability estimate for carcass marbling score in the present study was 0.43; literature estimates for carcass marbling score range from 0.26 (Minick et al. 2004) to 0.55 (Crews and Kemp 2001, 2002).

Correlations among Live Bull and Steer Carcass Traits

Correlations among bull pre-weaning herd of origin and residual effects are shown in Table 4. These results are shown for completeness, but are not discussed since the primary focus of the present study pertains to the genetic correlations shown in Table 5.

Positive genetic correlations ($P \leq 0.10$) were observed among growth and size traits in both bulls and steers (Table 5). In the present study, yearling bull weight and hip height were positively correlated with carcass weight ($r_g = 0.68$ and 0.51 , respectively) and carcass longissimus muscle area ($r_g = 0.62$ and 0.40 , respectively) and negatively correlated with carcass marbling score ($r_g = -0.58$ and -0.42 , respectively). Literature estimates for the genetic correlation between live and carcass weight range from 0.53 (yearling bull post-weaning average daily gain; Devitt and Wilton 2001) to 0.82 (yearling weight; Crews and Kemp 2001, 2002). Genetic correlations between yearling bull weight, post-weaning gain and hip height with carcass fat depth in steers were not significant ($P > 0.10$) in the present study ($r_g = 0.11$, -0.15 and 0.20 , respectively). Devitt and Wilton (2001) reported a genetic correlation of -0.40 of between postweaning average daily gain and carcass fat depth. These results suggest that selection for increased growth rate and mature size would lead to increased carcass size and longissimus muscle area, reduced marbling score and somewhat less change in fat depth.

Yearling bull ultrasound 12/13th rib subcutaneous fat depth was strongly correlated (Table 5) with both steer carcass fat depth ($r_g = 0.78$) and steer carcass marbling score ($r_g = 0.73$). Previous studies have shown that live ultrasound fat depth in bulls has a positive genetic correlation with age-constant carcass fat depth in slaughter progeny (estimates range from $r_g = 0.23$ (Crews and Kemp 2001, 2002) to $r_g = 0.88$ (Devitt and Wilton 2001)). The genetic relationship between bull ultrasound fat depth with steer carcass marbling score is less well established; estimates range from -0.27 (Crews and Kemp 2002) to 0.54 (Devitt and Wilton 2001). Ultrasound estimates of intramuscular fat content obtained from yearling bulls had a non-significant ($P > 0.10$) positive correlation with steer

carcass fat depth ($r_g = 0.49$) in the present study; Devitt and Wilton (2001) obtained a value of 0.08. The bivariate analysis between ultrasound intramuscular fat percentage and carcass marbling score failed to converge in the present study. There are several possible reasons for this unexpected result. First, ultrasound intramuscular fat percentage data were available for 2 fewer years than the other growth and ultrasound traits, so there may have been insufficient data (1308 bull ultrasound intramuscular fat percentage records and 1023 steer carcass marbling records) to estimate the correlation. This explanation is unlikely since other bivariate models involving either ultrasound intramuscular fat or carcass marbling score did converge. Second, likelihood response surface may have been relatively flat with a correlation so close to the edge of the allowable parameter space (i.e., 1.00) that it could not be reliably estimated. Literature estimates for the genetic correlation between live ultrasound intramuscular fat percentage and carcass marbling score range from 0.74 [Crews et al. (2003) using 3389 bull ultrasound intramuscular fat percentage records and 7254 carcass marbling records] to 0.80 [Devitt and Wilton (2001) using 3450 bull ultrasound intramuscular fat percentage records and 843 steer carcass marbling records]. The convergence problem encountered in the present study was not investigated further, as the primary intention of this research was to examine indicator traits for carcass composition rather than carcass quality. Regardless, accumulating evidence suggests that while intensive selection for reduced fat depth in yearling bulls will reduce carcass fat trim, it may also reduce marbling score. Conversely, selection solely for increased ultrasound intramuscular fat percentage in yearling bulls may lead to increases in both carcass marbling and subcutaneous fat depth in commercial cattle. This finding underscores the potential challenge associated with divergent selection for improved beef carcass composition and quality traits.

Correlations among longissimus muscle size traits were mostly positive but ranged considerably in magnitude. The genetic correlation between live ultrasound and carcass longissimus muscle area ($r_g = 0.59$) obtained in the present study was slightly lower than literature estimates, which range from 0.66 (Moser et al. 1998; Devitt and Wilton 2001) to 0.80 (Crews et al. 2003). Linear longissimus muscle Method 1 depth and width were positively correlated with steer carcass longissimus muscle area ($r_g = 0.68$ and 1.00 , respectively) and bull ultrasound longissimus muscle area ($r_g = 0.91$ and 0.81 , respectively). Longissimus muscle Method 2 depth was positively correlated with bull ultrasound longissimus muscle area ($r_g = 0.80$) but was not correlated with steer carcass longissimus muscle area (-0.17 ; $P > 0.10$). Method 2 longissimus muscle width had a weaker correlation with ultrasound longissimus muscle area ($r = 0.31$; $P > 0.10$), and bivariate models involving this trait with carcass longissimus muscle area and marbling score failed to converge. This may have been due to insufficient data, given the low heritability of the ultrasound trait.

Significant negative correlations were observed between ultrasound longissimus muscle area and Method 1 width measurements with ultrasound intramuscular fat measurements

Table 4. Estimates² of age-constant pre-weaning herd of origin (above diagonal) and residual (below diagonal) correlations (\pm standard error) among growth and live ultrasound traits evaluated in yearling beef bulls and steer carcass traits

Live yearling bull growth and ultrasound traits	Trait abbreviation													
	YW	PG	HH	UF	UM	UL	DI	W1	D2	W2	CW	CF	CL	
Yearling weight (YW)	0.67 \pm 0.07	0.02 \pm 0.15	0.62 \pm 0.09	0.48 \pm 0.14	-0.03 \pm 0.19	0.61 \pm 0.12	0.74 \pm 0.15	0.85 \pm 0.43	0.48 \pm 0.15	0.69 \pm 0.10				
Post-weaning gain (PG)		0.61 \pm 0.20	-0.16 \pm 0.21	-0.03 \pm 0.21	-0.44 \pm 0.26	-0.01 \pm 0.23	0.11 \pm 0.25	-0.16 \pm 0.50	0.14 \pm 0.24	0.68 \pm 0.79				
Hip height (HH)			0.61 \pm 0.23	0.16 \pm 0.20	0.33 \pm 0.25	0.11 \pm 0.22	0.36 \pm 0.23	-0.17 \pm 0.43	0.18 \pm 0.23	0.09 \pm 0.60				
Subcutaneous fat depth (UF)			0.13 \pm 0.25	0.13 \pm 0.25	0.13 \pm 0.25	0.71 \pm 0.18	0.76 \pm 0.19	0.58 \pm 0.49	0.61 \pm 0.19	0.31 \pm 0.89				
Intramuscular fat content (UM)			-0.04 \pm 0.11	0.14 \pm 0.10	0.14 \pm 0.10	0.44 \pm 0.27	0.02 \pm 0.32	0.66 \pm 0.46	0.00 \pm 0.30	0.45 \pm 0.98				
Longissimus muscle area (UL)			0.68 \pm 0.34	0.04 \pm 0.09	0.10 \pm 0.10	NC	0.76 \pm 0.28		0.86 \pm 0.09	NC				
Longissimus muscle Method 1 depth (D1) ^z			0.54 \pm 0.29	0.06 \pm 0.09	0.01 \pm 0.09	0.72 \pm 0.04	0.94 \pm 0.44	1.00 \pm 0.09	NC	NC				
Longissimus muscle Method 1 width (W1) ^z			0.56 \pm 0.30	-0.10 \pm 0.08	0.17 \pm 0.09	0.52 \pm 0.06	0.16 \pm 0.08	0.15 \pm 0.45	0.33 \pm 0.99					
Longissimus muscle Method 2 depth (D2) ^z			0.40 \pm 0.26	0.12 \pm 0.08	0.07 \pm 0.09	0.70 \pm 0.04	0.60 \pm 0.05	0.15 \pm 0.07	0.94 \pm 0.43					
Longissimus muscle Method 2 width (W2) ^z			0.03 \pm 0.10	0.01 \pm 0.08	0.03 \pm 0.19	-0.20 \pm 0.07	-0.04 \pm 0.08	0.28 \pm 0.07	0.07 \pm 0.07	0.54 \pm 0.05	0.00 \pm 0.07			
<i>Steer carcass traits</i>														
Carcass grade fat depth (CF)											0.21 \pm 0.10			
Carcass longissimus muscle area (CL)											0.58 \pm 0.08	0.08 \pm 0.09		
Carcass marbling score (CM)											0.33 \pm 0.13	0.15 \pm 0.09	0.26 \pm 0.10	

^zDescribed and illustrated in Bergen et al. (2003).

collected in yearling bulls ($r_g = -0.49$ and -0.79 , respectively). Method 1 ultrasound longissimus muscle Method 1 width was also negatively correlated ($P < 0.10$) with carcass marbling scores from finished steers ($r_g = -0.84$). These genetic correlations suggest that the impact of selection for increased carcass lean content on carcass quality may depend on the longissimus muscle trait used. Closer examination of the genetic correlations raises additional possibilities in this regard. It was initially anticipated that the various ultrasound longissimus muscle size measurements would have strong, positive genetic correlations with each other, and would have similar genetic correlations with carcass traits. This expectation was clearly not realized. Results shown in Table 5 suggest that while selecting yearling bulls for (or against) ultrasound longissimus muscle depth, width or area should be effective, the magnitude and direction of correlated changes in steer carcass traits may depend on the ultrasound longissimus muscle size trait in question. For example, results of the present study indicate that selection for increased ultrasound longissimus muscle area will tend ($P > 0.10$) to decrease steer carcass fat and marbling score ($r_g = -0.11$ and -0.30 , respectively), tend to increase carcass weight ($r_g = 0.22$; $P > 0.10$) and increase longissimus muscle area ($r_g = 0.59$; $P < 0.10$). In contrast, selection for increased ultrasound longissimus Method 1 depth may lead to similar changes in marbling score ($r_g = -0.30$; $P > 0.10$), slightly greater changes in carcass fat depth ($r_g = -0.34$; $P > 0.10$) and longissimus muscle area ($r_g = 0.68$; $P < 0.10$), and little or no change in carcass weight ($r_g = 0.01$; $P > 0.10$). Differences in the genetic correlation between carcass marbling score and longissimus muscle area (-0.30) vs. Method 1 longissimus muscle width (-0.84) hint that longissimus muscle shape (i.e., depth and width) may be as important as longissimus muscle area. Fernandes et al. (2004) reported that while fat depth was negatively associated with ultrasound loin muscle depth ($r_g = -0.17$), it was positively associated with loin muscle width ($r_g = 0.23$) in sheep. Genetic correlations among ultrasound longissimus muscle size measurements less than unity suggest that longissimus muscle shape may be amenable to selection. However, further research is strongly encouraged to confirm or invalidate these results. This should be fairly simple and economical provided that seedstock ultrasound images collected in previous studies (Moser et al. 1998; Crews and Kemp 2001, 2002; Crews et al. 2003) were archived.

The common finding that genetic correlations between corresponding live yearling bull growth and ultrasound traits and steer carcass traits are less than unity is not surprising for several reasons. First, the nutritional environment in which the animals are raised differs. Seedstock bulls are commonly raised on diets designed to restrict growth in order to prevent over-fatening, while feedlot steer diets are designed to maximize growth and fat deposition. In addition, the reduction of testosterone through castration may prevent steers from attaining their genetic potential for growth and muscle deposition. Finally, bull ultrasound measurements and steer carcass measurements are collected when the animals are at different stages of physiological maturity. Consequently, yearling bull and steer carcass traits must be treated as separate but correlated traits when both sources of information are incorporated into a genetic evaluation to improve carcass merit (Crews et al. 2004).

Table 5. Estimates^z of age-constant additive genetic (above diagonal) and phenotypic (below diagonal) correlations (\pm standard error) among growth and ultrasound traits evaluated in beef bulls and steer carcass traits. Significant correlations (t-test) are shown in bold

	Trait abbreviation													
	YW	PG	HH	UF	UM	UL	D1	W1	D2	W2	CW	CF	CL	CM
Bull growth and ultrasound traits														
Yearling weight (YW)		0.61 \pm 0.07	0.69 \pm 0.05	0.12 \pm 0.14	0.08 \pm 0.16	0.37 \pm 0.11	0.31 \pm 0.12	0.22 \pm 0.15	0.39 \pm 0.14	0.27 \pm 0.20	0.68 \pm 0.19	0.11 \pm 0.31	0.62 \pm 0.22	-0.58 \pm 0.22
Post-weaning gain (PG)	0.54 \pm 0.02		0.32 \pm 0.08	0.18 \pm 0.15	0.10 \pm 0.17	0.24 \pm 0.13	0.22 \pm 0.15	0.22 \pm 0.16	0.32 \pm 0.16	0.11 \pm 0.22	0.36 \pm 0.22	-0.15 \pm 0.30	0.36 \pm 0.25	-0.34 \pm 0.25
Hip height (HH)	0.62 \pm 0.02	0.30 \pm 0.02		0.01 \pm 0.12	0.05 \pm 0.13	0.04 \pm 0.11	-0.06 \pm 0.12	0.10 \pm 0.13	-0.05 \pm 0.14	0.35 \pm 0.18	0.51 \pm 0.18	0.20 \pm 0.27	0.40 \pm 0.22	-0.42 \pm 0.21
Subcutaneous fat depth (UF)	0.22 \pm 0.03	0.12 \pm 0.03	0.05 \pm 0.03		0.26 \pm 0.21	-0.02 \pm 0.18	0.26 \pm 0.19	0.13 \pm 0.22	0.01 \pm 0.22	0.00 \pm 0.28	-0.19 \pm 0.31	0.78 \pm 0.37	0.17 \pm 0.36	0.73 \pm 0.29
Intramuscular fat content (UM)	0.01 \pm 0.03	-0.02 \pm 0.03	0.02 \pm 0.03	0.18 \pm 0.03		-0.49 \pm 0.21	-0.17 \pm 0.22	-0.79 \pm 0.27	-0.26 \pm 0.23	-0.28 \pm 0.31	-0.23 \pm 0.29	0.49 \pm 0.35	-0.03 \pm 0.34	NC ^y
Longissimus muscle area (UL)	0.46 \pm 0.02	0.25 \pm 0.03	0.17 \pm 0.03	0.09 \pm 0.03	-0.06 \pm 0.03	0.60 \pm 0.02	0.91 \pm 0.04	0.81 \pm 0.11	0.80 \pm 0.08	0.31 \pm 0.22	0.22 \pm 0.29	-0.11 \pm 0.36	0.59 \pm 0.32	-0.30 \pm 0.31
Longissimus muscle Method 1 depth (D1) ^x	0.39 \pm 0.02	0.20 \pm 0.03	0.11 \pm 0.03	0.18 \pm 0.03	-0.04 \pm 0.03	0.80 \pm 0.01	0.52 \pm 0.18	0.74 \pm 0.11	0.74 \pm 0.11	0.10 \pm 0.25	0.01 \pm 0.32	-0.34 \pm 0.40	0.68 \pm 0.35	-0.30 \pm 0.36
Longissimus muscle Method 1 width (W1) ^x	0.30 \pm 0.03	0.15 \pm 0.03	0.16 \pm 0.03	0.00 \pm 0.03	-0.05 \pm 0.03	0.60 \pm 0.02	0.28 \pm 0.02	0.44 \pm 0.21	0.44 \pm 0.21	0.67 \pm 0.19	0.83 \pm 0.28	0.08 \pm 0.44	1.00 \pm 0.32	-0.84 \pm 0.31
Longissimus muscle Method 2 depth (D2) ^x	0.35 \pm 0.02	0.20 \pm 0.03	0.08 \pm 0.03	0.14 \pm 0.03	-0.02 \pm 0.03	0.73 \pm 0.01	0.67 \pm 0.02	0.22 \pm 0.03	-0.19 \pm 0.30	-0.19 \pm 0.32	-0.22 \pm 0.32	-0.41 \pm 0.40	-0.17 \pm 0.38	-0.06 \pm 0.37
Longissimus muscle Method 2 width (W2) ^x	0.11 \pm 0.03	0.05 \pm 0.03	0.12 \pm 0.03	-0.13 \pm 0.03	-0.08 \pm 0.03	0.29 \pm 0.02	0.09 \pm 0.03	0.56 \pm 0.02	-0.02 \pm 0.03	0.79 \pm 0.38	-0.62 \pm 0.57	NC ^y	NC ^y	NC ^y
Steer carcass traits														
Hot carcass weight (CW)												0.18 \pm 0.20	0.50 \pm 0.13	0.26 \pm 0.16
Carcass grade fat depth (CF)											0.19 \pm 0.04		-0.41 \pm 0.21	0.13 \pm 0.21
Carcass longissimus muscle area (CL)											0.53 \pm 0.03	-0.07 \pm 0.04	-0.49 \pm 0.19	
Carcass marbling score (CM)											0.04 \pm 0.04	0.14 \pm 0.04	-0.01 \pm 0.04	

^zResults represent the average solution from all bivariate models involving the trait in question.

^yBivariate model did not converge.

^xDescribed and illustrated in Bergen et al. (2003).

Genetic correlations among live seedstock ultrasound and carcass traits have also been studied extensively in Australia (Reverter et al. 2000). However, the seedstock bulls and heifers used in the Australian study were considerably older (approximately 490 d) than the bulls used in the present study. Differences in physiological maturity between 12 and 16 mo may mean that growth and ultrasound traits evaluated in Australian and North American seedstock cattle are not genetically equivalent, and comparing genetic parameters between them may be of questionable value. Crews and Kemp (2001) found that growth and ultrasound measurements collected at 12 and 14 mo were highly genetically correlated (0.95 for both ultrasound 12/13th rib fat depth and longissimus muscle area and 0.98 for liveweight). Whether this can be extrapolated to 16 mo may depend on the breed types and nutritional management of the cattle in question. However, comparisons of live ultrasound and carcass traits between North American and Australian are further compounded by the fact that carcass traits are commonly evaluated on a carcass weight constant basis in Australia, and on a slaughter age constant basis in North America. This raises the question of how alternative slaughter endpoint adjustments may impact genetic evaluations for carcass traits. This will be the subject of future research.

CONCLUSIONS

Live growth and ultrasound measurements collected in yearling bulls are genetically related to the corresponding carcass measurements adjusted to a constant slaughter age. The findings of this study provide further evidence of the potential value of ultrasound technology in beef cattle breeding programs, and suggest that longissimus muscle shape may have important correlations with steer carcass yield and quality grade. More importantly, these findings provide the basis for further studies to quantify the impact of ultrasound-based selection on carcass lean content at commercially relevant slaughter endpoints.

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Arango, J. A., Cundiff, L. V. and Van Vleck, L. D. 2002. Genetic parameters for weight, weight adjusted for body condition score, height, and body condition score in beef cows. *J. Anim. Sci.* **80**: 3112–3122.

Bergen, R. D., McKinnon, J. J., Christensen, D. A. and Kohle, N. 1996. Prediction of lean yield on yearling bulls using real-time ultrasound. *Can. J. Anim. Sci.* **76**: 305–311.

Bergen, R., Crews, D. H., Jr., Miller, S. P. and McKinnon, J. J. 2003. Predicting lean meat yield in beef cattle using ultrasonic muscle depth and width measurements. *Can. J. Anim. Sci.* **83**: 429–434.

Bergen, R., Miller, S. P., Mandell, I. B. and Robertson, W. M. 2005. Use of live ultrasound, weight and linear measurements to predict carcass composition of young beef bulls. *Can. J. Anim. Sci.* **85**: 23–35.

Block, H. C., McKinnon, J. J., Mustafa, A. F. and Christensen, D. A. 2001. Manipulation of cattle growth to target carcass quality. *J. Anim. Sci.* **79**: 133–140.

Canadian Council on Animal Care. 1993. Guide to the care and use of experimental animals. CCAC, Ottawa, ON.

Cannell, R. C., Belk, K. E., Tatum, J. D., Wise, J. W., Chapman, P. L., Scanga, J. A. and Smith, G. C. 2002. Online evaluation of a commercial video image analysis system (Computer Vision System) to predict beef carcass red meat yield and for augmenting the assignment of USDA yield grades. *J. Anim. Sci.* **80**: 1195–1201.

Crews, D. H., Jr. and Kemp, R. A. 2001. Genetic parameters for ultrasound and carcass measures of yield and quality among replacement and slaughter beef cattle. *J. Anim. Sci.* **79**: 3008–3020.

Crews, D. H., Jr. and Kemp, R. A. 2002. Genetic evaluation of carcass yield using ultrasound measures on young replacement beef cattle. *J. Anim. Sci.* **80**: 1809–1818.

Crews, D. H., Jr., Pollak, E. J., Weaver, R. L., Quaas, R. L. and Lipsey, R. J. 2003. Genetic parameters for carcass traits and their live animal indicators in Simmental cattle. *J. Anim. Sci.* **81**: 1427–1433.

Crews, D. H., Jr., Pollak, E. J. and Quaas, R. L. 2004. Evaluation of Simmental carcass EPD estimated using live and carcass data. *J. Anim. Sci.* **82**: 661–667.

Devitt, C. J. and Wilton, J. W. 2001. Genetic correlation estimates between ultrasound measurements on yearling bulls and carcass measurements on finished steers. *J. Anim. Sci.* **79**: 2790–2797.

Fernandes, T. L., Wilton, J. W. and Tosh, J. J. 2004. Estimates of genetic parameters for ultrasound-measured carcass traits in sheep. *Can. J. Anim. Sci.* **84**: 361–365.

Gilmour, A. R., Cullis, B. R., Welham, S. J. and Thompson, R. 2000. ASREML reference manual. New South Wales Agriculture, Orange, Australia.

Greiner, S. P., Rouse, G. H., Wilson, D. E., Cundiff, L. V. and Wheeler, T. E. 2003. Accuracy of predicting weight and percentage of beef carcass retail product using ultrasound and live animal measures. *J. Anim. Sci.* **81**: 466–473.

Herring, W. O., Williams, S. E., Bertrand, J. K., Benyshek, L. L. and Miller, D. C. 1994. Comparison of live and carcass equations predicting percentage of cutability, retail product weight, and trimmable fat in beef cattle. *J. Anim. Sci.* **72**: 1107–1118.

Marshall, D. M. 1994. Breed differences and genetic parameters for body composition traits in beef cattle. *J. Anim. Sci.* **72**: 2745–2755.

Minick, J. A., Dikeman, M. E., Pollak, E. J. and Wilson, D. E. 2004. Heritability and correlation estimates of Warner-Bratzler shear force and carcass traits from Angus-, Charolais-, Hereford-, and Simmental-sired cattle. *Can. J. Anim. Sci.* **84**: 599–609.

Moser, D. W., Bertrand, J. K., Misztal, I., Kriese, L. A. and Benyshek, L. L. 1998. Genetic parameter estimates for carcass and yearling ultrasound measurements in Brangus cattle. *J. Anim. Sci.* **76**: 2542–2548.

Oikawa, T. and Sato, K. 1997. Treating small herds as fixed or random in an animal model. *J. Anim. Breed. Genet.* **114**: 177–183.

- Realini, C. E., Williams, R. E., Pringle, T. D. and Bertrand, J. K. 2001.** Gluteus medius and rump fat depths as additional live animal ultrasound measurements for predicting retail product and trimmable fat in beef carcasses. *J. Anim. Sci.* **79**: 1378–1385.
- Reverter, A., Johnston, D. J., Graser, H.-U., Wolcott, M. L. and Upton, W. H. 2000.** Genetic analyses of live-animal ultrasound and abattoir carcass traits in Australian Angus and Hereford cattle. *J. Anim. Sci.* **78**: 1786–1795.
- Roso, V. R., Schenkel, F. S. and Miller, S. P. 2004.** Degree of connectedness among groups of centrally tested beef bulls. *Can. J. Anim. Sci.* **84**: 37–47.
- Schenkel, F. S., Miller, S. P. and Wilton, J. W. 2004a.** Herd of origin effect on weight gain of station-tested beef bulls. *Livest. Prod. Sci.* **86**: 93–103.
- Schenkel, F. S., Miller, S. P. and Wilton, J. W. 2004b.** Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. *Can. J. Anim. Sci.* **84**: 177–178.
- Vaage, A. S., McCartney, D. H., McKinnon, J. J. and Bergen, R. D. 1998.** Effect of prolonged backgrounding on growth performance and carcass composition of crossbred beef steers. *Can. J. Anim. Sci.* **78**: 359–367.
- Van Vleck, L. D., Pollak, E. J. and Oltenacu, E. A. B. 1987.** Genetics for the animal sciences. W.H. Freeman and Company, New York, NY.
- Van Vleck, L. D. 1987.** Contemporary groups for genetic evaluations. *J. Dairy Sci.* **70**: 2456–2464.
- Visscher, P. M. and Goddard, M. E. 1993.** Fixed and random contemporary groups. *J. Dairy Sci.* **76**: 1444–1454.
- Wheeler, T. L., Cundiff, L. V., Shackelford, S. D. and Koohmaraie, M. 2004.** Characterization of biological types of cattle (Cycle VI): Carcass, yield and longissimus palatability traits. *J. Anim. Sci.* **82**: 1177–1189.
- Wheeler, T. L., Cundiff, L. V., Shackelford, S. D. and Koohmaraie, M. 2005.** Characterization of biological types of cattle (Cycle VII): Carcass, yield and longissimus palatability traits. *J. Anim. Sci.* **83**: 196–207.
- Williams, R. E., Bertrand, J. L., Williams, S. E. and Benyshek, L. L. 1997.** Biceps femoris and rump fat as additional ultrasound measurements for predicting retail product and trimmable fat in beef carcasses. *J. Anim. Sci.* **75**: 7–13.

