Genetic analysis of carcass traits of steers adjusted to age, weight, or fat thickness slaughter endpoints[1]

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ABSTRACT: Carcass measurements from 1,664 steers from the Germ Plasm Utilization project at U.S. Meat Animal Research Center were used to estimate heritabilities (h^2) of, and genetic correlations (r_g) among, 14 carcass traits adjusted to different endpoints (age, carcass weight, and fat thickness): HCW (kg), dressing percent (DP), adjusted fat thickness (AFT, cm), LM area (LMA, cm^2), KPH (%), marbling score (MS), yield grade (YG), predicted percentage of retail product (PRP), retail product weight (RPW, kg), fat weight (FW, kg), bone weight (BNW, kg), actual percentage retail product (RPP), fat percent (FP), and bone percent. Fixed effects in the model included breed group, feed energy level, dam age, birth year, significant ($P < 0.05$) interactions, covariate for days on feed, and the appropriate covariate for endpoint nested (except age) within breed group. Random effects in the model were additive genetic effect of animal and total maternal effect of dam. Parameters were estimated by REML. For some traits, estimates of h^2 and phenotypic variance changed with different endpoints. Estimates of h^2 for HCW, DP, RPW, and BNW at constant age, weight, or fat thickness were 0.27, —, and 0.41; 0.19, 0.26, and 0.18; 0.42, 0.32, and 0.50; and 0.43, 0.32, and 0.48, respectively. Magnitude and/or sign of r_g also changed across endpoints for 54 of the 91 trait pairs. Estimates for HCW-LMA, AFT-RPW, LMA-YG, LMA-PRP, LMA-FW, LMA-RPP, and LMA-FP at constant age, weight, or fat thickness were 0.32, —, and 0.51; −0.26, −0.77, and —; −0.71, −0.89, and −0.66; 0.68, 0.85, and 0.63; −0.16, −0.51, and 0.22; 0.47, 0.57, and 0.27; and −0.44, −0.43, and −0.18, respectively. Fat thickness was highly correlated with YG (0.86 and 0.85 for common age and weight) and PRP (−0.85 and −0.82 for common age and weight), indicating that selection for decreased fat thickness would improve YG and PRP. Carcass quality, however, would be affected negatively because of moderate r_g (0.34 and 0.35 for common age and weight) between MS and AFT. Estimates of h^2 and phenotypic variance indicate that enough genetic variation exists to change measures of carcass merit by direct selection. For some carcass traits, however, magnitude of change would depend on effect of endpoint on h^2 and phenotypic variance. Correlated responses to selection would differ depending on endpoint.

Key Words: Beef Cattle, Carcass Traits, Heritability, Genetic Correlation, Slaughter Endpoints

Introduction

The expression of genetic and environmental differences for carcass traits may be modified by age, weight, and fat thickness slaughter endpoints (Koch et al., 1995). Choice of endpoint has not been consistent in genetic evaluation programs conducted by different breed associations in the United States. The chosen endpoint should be determined by expected response to alternative selection criteria (e.g., increased retail product and increased marbling). Few studies (Cundiff et al., 1969; Lee et al., 2000; Devitt and Wilton et al., 2001; Shanks et al., 2001) have compared estimates of heritability and genetic correlations for carcass traits adjusted to different slaughter endpoints. Results from those few studies were inconsistent, although some studies revealed that heritability and genetic correlations estimates were sensitive to the covariate included

in the model as the endpoint. Greater expected response to selection for retail product weight has been reported (Koch et al., 1982) at a constant age vs. at a constant weight. Ríos-Utrera (2004), from a review of estimates of heritability and genetic correlations for carcass traits of cattle published from 1962 to 2004, concluded that most estimates of heritability and genetic correlations were on an age-constant basis and that the effect of different endpoints on estimates of heritability and genetic correlations for several carcass traits had not been studied. The objective of this study was to estimate genetic variance and heritabilities (h^2) of, and genetic correlations (r_g) among, carcass traits of steers adjusted to constant age, carcass weight, or fat thickness endpoints.

Materials and Methods

Populations

The purebred and composite steers with carcass measurements included in this analysis were from the Germ Plasm Utilization project at the U.S. Meat Animal Research Center (**MARC**), Clay Center, NE, and were the unselected progeny of 21 Red Poll, 22 Hereford, 23 Angus, 24 Limousin, 26 Braunvieh, 27 Pinzgauer, 27 Gelbvieh, 19 Simmental, 25 Charolais, 39 MARC I (¼ Limousin, ¼ Braunvieh, ¼ Charolais, ⅛ Hereford, ⅛ Angus), 30 MARC II (¼ Hereford, ¼ Angus, ¼ Gelbvieh, ¼ Simmental), and 24 MARC III (¼ Pinzgauer, ¼ Red Poll, ¼ Hereford, ¼ Angus) sires. These steers were born from 1988 to 1991 to dams of these breeds, which were 2 yr old or older.

Feeding and Management

From 1989 through 1991, steers were weaned at an average age of approximately 150 d on September 7 or 11. In 1988, steers were weaned on August 18 at an average age of 127 d. After weaning, steers were started on a diet of 2.65 Mcal of ME/kg and 15.4% CP (DM basis). Later, steers were kept on a backgrounding diet (2.69 Mcal of ME/kg and 12.88% CP; DM basis) for different periods in different years before changing to finishing diets. At an average age of 203 d over the 4 yr, animals were weighed and were assigned to one of two finishing diets (treatments) on a random basis stratified by weight. Dietary energy density was the basis for the two finishing diets. Feed Level 1 was 2.82 Mcal of ME/kg and 11.50% CP (DM basis). Feed Level 2 was 3.07 Mcal of ME/kg and 11.50% CP (DM basis). Gregory et al. (1995) provided detailed information on feeding and management after weaning.

Slaughter and Processing Procedures

Animals were serially slaughtered at four dates each year with 20, 21, or 22 d between slaughter dates and 63 d between first and fourth slaughter dates. Initial slaughter date was between May 21 and 26 for the 4 yr. Days from initial weight (203 d) to final weight averaged 204, 224, 245, and 267 d for the four slaughter groups. Mean days fed was 235, and mean slaughter age was 438 d. Steers were assigned to slaughter groups on a random basis stratified by weight based on the last weight taken before the start of the serial slaughter schedule. The final weight was a single full weight taken starting at 0700 in the morning, with overnight access to feed and water. All steers were weighed at each slaughter date. The average weight of steers slaughtered at each of the first three slaughter dates was approximately the same as the average weight of steers remaining in a pen. Steers were slaughtered in a commercial facility. Following a 24-h chill period, data on fat thickness at the 12th rib, perirenal fat percent, and LM area were obtained. The right side of each carcass was returned to the MARC to obtain carcass cutout and chemical composition data. For animals born from 1988 through 1990, limitations on processing capability forced random sampling of sides for detailed cutout and sensory data. Cutout data were not obtained on 65 carcasses in those 3 yr. Carcasses were processed into wholesale cuts of round, loin, rib, chuck, plate, flank, and brisket plus shank. Each wholesale cut was processed further by cutting into boneless steaks, roasts, lean trim, and fat trim to 8-mm fat trim, except that the dorsal and lateral vertebral processes in the short loin and dorsal vertebral processes and ribs were left in standing rib roasts. Lean trim was targeted to contain 20% fat and was adjusted to 20% based on chemical analysis of the lean trim. Further processing removed all s.c. and accessible intermuscular fat (0-mm fat trim) from any surface. The remaining bone was removed from the short loin and from the standing rib roasts. The 9th-10th-11th rib cut was removed and processed by procedures described for wholesale cuts and kept separate from the remainder of the rib. Soft tissue (lean and fat) from the 9th-10th-11th rib cut was ground and sampled for determination of water and fat. Retail product included trimmed (0-mm fat trim) steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of the lean trim. Lean trim was ground and sampled for water and fat determinations to provide a basis for adjusting retail product to 80% lean and 20% fat in the lean trim. Carcass fat was calculated as the sum of the physically removed perirenal, s.c., and accessible intermuscular fat from the lean trim based on chemical analysis. Carcass bone included all the bone from the carcass.

Carcass Traits Evaluated

Genetic parameters were estimated for 14 carcass traits: HCW (kg), dressing percent (**DP**; [HCW/final live weight] × 100), fat thickness measured at the 12th rib and adjusted to reflect unusual distribution of fat on other parts of the carcass (**AFT**, cm), LM area at the 12th rib (**LMA**, cm^2), KPH as a percentage of carcass

Table 1. Descriptive statistics for carcass traits of purebred and composite steers

Carcass trait	No.	Mean	SD	CV	Minimum	Maximum
HCW, kg	1,663	334.50	40.36	12.07	218.18	489.43
Dressing percent	1,663	60.64	2.38	3.93	43.01	78.27
Adjusted fat thickness, cm	1,663	0.65	0.44	67.98	0.03	2.54
LM area, cm^2	1,663	78.64	10.37	13.19	50.32	117.42
KPH, %	1,664	2.78	0.69	24.95	0.50	5.00
Marbling score[a]	1,664	4.95	0.71	14.27	2.90	9.50
Yield grade	1,661	2.60	0.82	31.64	0.28	5.76
Predicted retail product, %	1,661	64.95	3.33	5.13	52.13	74.22
Retail product weight, kg	1,599	209.55	27.76	13.25	136.16	301.06
Fat weight, kg	1,599	59.89	21.70	36.24	3.99	146.70
Bone weight, kg	1,599	48.29	6.40	13.25	33.32	71.00
Actual retail product, %	1,599	66.05	5.20	7.87	51.20	81.76
Fat, %	1,599	18.71	6.00	32.09	1.31	36.43
Bone, %	1,599	15.24	1.41	9.27	11.82	22.61

[a]2 = practically devoid, 9 = moderately abundant.

weight, marbling score (**MS**), yield grade (**YG**), predicted percentage of retail product (**PRP**), retail product weight (**RPW**, kg; 0-mm fat trim), fat weight (**FW**, kg; 0-mm fat trim), bone weight (**BNW**, kg; 0-mm fat trim), and actual retail product (**RPP**), fat (**FP**), and bone (**BP**) as percentages of carcass weight. Marbling was evaluated at the 12th-rib interface and scored on a 10-point scale within each of eight categories, which were converted to numeric scores (BIF, 2002). Estimation of YG (BIF, 2002) was as follows: YG = 2.5 + (0.98 × AFT, cm) + (0.2 × KPH, %) + (0.0084 × HCW, kg) − (0.05 × LMA, cm^2). The percentage of total retail product trimmed to zero surface fat was predicted as proposed by Dikeman et al. (1998) using traits in the USDA yield grade system: PRP = 65.69 − (3.91 × AFT, cm) − (1.29 × KPH, %) − (0.029 × HCW, kg) + (0.19 × LMA, cm^2).

Endpoints Evaluated

Carcass traits adjusted to different endpoints (age, carcass weight, or fat thickness) are biologically different; thus, they should be regarded as distinct traits. At a common age endpoint, variation in the weight of different tissues reflects variation in accretion rates of those tissues (e.g., carcass weight, retail product, fat trim, and bone). Adjustment to a common carcass weight focuses on variation in carcass composition. At a constant carcass weight, RPP, FP, and BP are perfectly correlated with RPW, FW, and BNW, respectively, and reflect variation in carcass composition independent of carcass weight. Dinkel et al. (1965) advanced the argument that use of carcass weight as a covariate was more appropriate than use of percents or ratios (e.g., retail product weight/carcass weight) because ratios were forced to be negatively correlated with their denominator. Adjustment to a common fat thickness endpoint is appropriate if the objective is to select for a trait independent of fat thickness. For example, selection for marbling adjusted for fat thickness would be expected to improve marbling with little or no change in fat thickness. Similarly, response to selection for weight (or

percentage) of retail product adjusted for fat thickness would be expected to result from changes in proportion of muscle and fat deposits at sites other than those associated with fat thickness.

Statistical Analyses of Data

Preliminary Analyses. Simple descriptive statistics are in Table 1. Number of records for the carcass traits evaluated ranged from 1,599 to 1,664. Before estimation of genetic parameters, preliminary statistical analyses for each carcass trait by endpoint were performed to determine fixed effects that were important sources of variation using the Mixed procedure of SAS (Littell et al., 1996). Fixed effects included in the full model were breed group, year of birth, age of dam, energy level of treatment, all possible two-way interactions among these main effects, linear effect of number of days on feed, and linear effect of endpoint (fat thickness, slaughter age, or carcass weight) nested within breed group. The random effects in the full model, other than the error term, were sires nested within breed group. Sequential analyses were run by removing from the full model those interactions and covariates that were not significant at $P \le 0.05$. An interaction effect remained in the model if significant for at least one carcass trait within endpoint. The effects of linear slaughter age nested within breed group were not significant in preliminary analyses; therefore, only the simple linear effect of slaughter age was included as a covariate in the final model. Slaughter age and days on feed are confounded to some extent, which may have partially caused the failure to detect differences in slaughter age within breed groups. Consequently, the final model included all main effects, significant interactions, covariate for number of days on feed, and a second covariate, fat thickness, carcass weight (nested within breed), or slaughter age. Days on feed and slaughter age were included simultaneously in the age constant analysis to draw inference to field data analyses computed within contemporary groups (animals in contemporary groups

are, by definition, fed and slaughtered at the same time). At a common age, significant interactions for at least one carcass trait were breed group × energy level, breed group × year of birth, energy level × year of birth, and age of dam × year of birth. At constant weight nested within breed group, the model included the same two-way interactions as those for carcass traits adjusted to common age, except for age of dam × year of birth. The model for carcass traits adjusted to a common fat thickness nested within breed group included the same interactions as for carcass traits adjusted to common age and also breed group × age of dam.

Univariate Analyses with REML. Components of variance and h^2 for each carcass trait were estimated for a single-trait animal model by derivative-free REML (Smith and Graser, 1986) with a simplex algorithm using the MTDFREML programs (Boldman et al., 1995). The statistical model to analyze each carcass trait included all of the fixed effects mentioned above as well as additive genetic effects of the animals and the total maternal effects of dams of the animals as random effects. In preceding analyses, maternal genetic effects were tested and deleted from the model for all carcass traits evaluated in this study; therefore, this particular effect was not included alone in the model. The total maternal effect of the dam accounts jointly for the genetic and the permanent environmental effects of the dam and was considered as an additional uncorrelated random effect. Starting values of the genetic and environmental variances used were based on those available in the scientific literature. Local convergence was declared when the variance of the simplex was less than 10^{-9}, after which several restarts were made until convergence at a global maximum was declared when −2(log likelihood) did not change to the second decimal. Approximate standard errors for estimates of genetic parameters for a single trait were estimated using the average information matrix (Johnson and Thompson, 1995), and the delta method (e.g., Dodenhoff et al., 1998). Using matrix notation, the model can be represented as $y = X\beta + Z_a a + Z_d d + e$, where y is the vector of measurements for a particular carcass trait, β is the vector of fixed effects, a is the vector of additive genetic effects of the animals, d is the vector of total maternal effects of dams of the animals, X is a known incidence matrix relating observations to fixed effects in vector β, Z_a is a known incidence matrix relating observations to random additive genetic effects in vector a, Z_d is a known incidence matrix relating observations to random maternal effects in vector d, and e is an unknown vector of random temporary environmental effects. Expected values and covariances for random effects in the model were assumed to be as follows:

$$E\begin{bmatrix} a \\ d \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \text{ and } V\begin{bmatrix} a \\ d \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 \\ 0 & \mathbf{I}_d\sigma_d^2 & 0 \\ 0 & 0 & \mathbf{I}_N\sigma_e^2 \end{bmatrix}$$

where A is the matrix of Wright's additive numerator relationships among all animals in the pedigree, σ_a^2 is the direct additive genetic variance, σ_d^2 is the variance of total maternal (dam) effects, σ_e^2 is the temporary environmental variance, and I_d and I_N are identity matrices with orders the number of dams and total observations, respectively. Ancestors were traced back three generations to generate a pedigree of 5,463 animals, including parents and ancestors without records.

Bivariate Analyses with REML. Two-trait analyses with the same fixed effects for each endpoint were conducted to estimate genetic and environmental correlations between all possible pairs (91) of traits that resulted from the fourteen carcass traits. Analyses were with MTDFREML (Boldman et al., 1995). The same convergence criterion used in single-trait analyses was also used for two-trait analyses, except that local convergence was declared when the variance of the simplex was less than 10^{-6}. Estimates of variance components obtained from single-trait analyses were used as starting values for two-trait analyses with covariances initially set to guessed intermediate values. Standard errors of parameter estimates obtained from two-trait analyses could not be computed when there were missing observations. The number of observations for each trait could be different for any reason, so that standard errors could not be computed from two-trait analyses where a pair of traits had different number of observations (Table 1). To obtain estimates of standard errors for the two-trait analyses, data were edited to include only steers that had both traits included in an analysis. Such standard errors should be considered as conservative estimates because less information was used to obtain them than to obtain the corresponding estimates of genetic parameters from all of the data.

Results and Discussion

Effect of Endpoint on Estimates of Variance Components

Variance of Total Maternal Effects. Estimates of fractions of phenotypic variance due to total maternal effects of the dam and due to temporary environmental effects associated with the animal as well as corresponding standard errors for carcass traits of steers adjusted to slaughter age, fat thickness, or carcass weight endpoints are summarized in Table 2. In general, total maternal effects of the dam accounted for only small fractions of the total variance for carcass traits. At constant slaughter age, estimates of fractions of variance due to total maternal effects ranged from 0.00 for DP to 0.19 for AFT. The range for estimates of fractions of variance due to total maternal effects was from 0.00 for DP and RPW to 0.17 for FP at constant fat thickness. With carcass weight held constant, estimates of fractions of total maternal effects ranged from 0.00 for DP to 0.18 for AFT. Total maternal effects explained 9% of total variance for HCW on an age-constant basis but

Table 2. Estimates (±SE) of fraction of phenotypic variance due to total maternal effects (d^2) of the dam of the animal, and to temporary environmental effects (e^2) of the animal for carcass traits of steers adjusted to constant age, fat thickness, and carcass weight endpoints

Carcass trait	Age constant		Fat thickness constant		Carcass weight constant	
	d^2	e^2	d^2	e^2	d^2	e^2
HCW, kg	0.09 ± 0.05	0.64 ± 0.08	0.02 ± 0.05	0.57 ± 0.09	—	—
Dressing percent	0.00 ± 0.05	0.81 ± 0.07	0.00 ± 0.05	0.82 ± 0.08	0.00 ± 0.05	0.74 ± 0.08
Adjusted fat thickness, cm	0.19 ± 0.05	0.61 ± 0.07	—	—	0.18 ± 0.05	0.61 ± 0.07
LM area, cm^2	0.08 ± 0.05	0.68 ± 0.07	0.06 ± 0.05	0.69 ± 0.08	0.11 ± 0.05	0.64 ± 0.07
Kidney, pelvic, and heart fat, %	0.03 ± 0.05	0.74 ± 0.08	0.04 ± 0.05	0.70 ± 0.08	0.03 ± 0.05	0.74 ± 0.08
Marbling score[a]	0.06 ± 0.05	0.54 ± 0.08	0.04 ± 0.05	0.61 ± 0.08	0.04 ± 0.05	0.55 ± 0.08
Yield grade	0.13 ± 0.05	0.57 ± 0.07	0.10 ± 0.05	0.66 ± 0.07	0.12 ± 0.05	0.58 ± 0.07
Predicted retail product, %	0.11 ± 0.05	0.59 ± 0.07	0.08 ± 0.05	0.68 ± 0.07	0.10 ± 0.05	0.60 ± 0.08
Retail product weight, kg	0.04 ± 0.05	0.54 ± 0.08	0.00 ± 0.05	0.50 ± 0.09	0.16 ± 0.05	0.52 ± 0.08
Fat weight, kg	0.18 ± 0.05	0.54 ± 0.08	0.12 ± 0.05	0.59 ± 0.08	0.17 ± 0.05	0.48 ± 0.08
Bone weight, kg	0.11 ± 0.05	0.47 ± 0.08	0.05 ± 0.05	0.47 ± 0.09	0.09 ± 0.05	0.59 ± 0.08
Actual retail product, %	0.17 ± 0.05	0.41 ± 0.08	0.11 ± 0.05	0.48 ± 0.08	0.15 ± 0.05	0.41 ± 0.08
Fat, %	0.18 ± 0.05	0.51 ± 0.07	0.17 ± 0.05	0.57 ± 0.08	0.17 ± 0.05	0.48 ± 0.07
Bone, %	0.05 ± 0.05	0.67 ± 0.08	0.06 ± 0.05	0.59 ± 0.08	0.09 ± 0.05	0.58 ± 0.08

[a]2 = practically devoid, 9 = moderately abundant.

only 2% on a fat thickness-constant basis. Similarly, total maternal effects accounted for 11% of total variance for BNW with a constant slaughter age, but only 5% with a constant fat thickness. With a covariate for fat thickness in the model, total maternal effects were negligible (0%) for RPW, whereas maternal effects accounted for 16% of total variance when carcass weight was chosen as the covariate. With a constant age, variance due to total maternal effects for FW or RPP explained 6% more of the variance than with constant fat thickness. The relatively large estimates of variance of total maternal effects for FW and FP relative to those for RPW and RPP at an age endpoint, and the comparatively small estimate for HCW at a constant fat thickness, suggest that maternal effects may have a greater influence on variation in fat accretion rates (FW) and proportions (FP) than on muscle accretion rates (RPW) and proportions (RPP). The relatively small estimate of variance for total maternal effects on HCW when fat thickness was held constant also suggests that maternal effects have somewhat more influence on fatness variation than on muscle accretion rates or proportions.

Phenotypic and Direct Genetic Variances. Estimates of phenotypic and direct genetic variances for carcass traits adjusted to slaughter age, fat thickness, or carcass weight endpoints are shown in Table 3. The effect of endpoint on estimates of phenotypic and genetic variances differed from trait to trait. For example, YG expressed significantly more phenotypic variation when analyzed at constant age or carcass weight endpoints than at constant fat thickness (2.1 and 1.9 times greater, respectively), which was expected because variation in fat thickness was weighted heavily in prediction of YG. The estimate of genetic variance for RPW was larger when either fat thickness or age was included in the model as a covariate than when carcass weight was the covariate (4.3 and 3.4 times greater,

respectively). The relatively high genetic variation in RPW at a fat thickness endpoint compared with an age endpoint, and the relatively low variation in FW at a fat thickness endpoint compared with an age endpoint, indicates that selection for RPW at a constant fat thickness could be effective in changing retail product to fatness accretion rates and ratios. For some traits (e.g., HCW, YG, and RPW), estimates of phenotypic and genetic variances at constant fat thickness were quite different from estimates at constant age or weight. In general, age and weight covariates gave similar estimates of phenotypic and genetic variances for traits related to fat deposition.

Effect of Endpoint on Heritability Estimates

Heritability estimates and standard errors from single-trait analyses for carcass traits adjusted to slaughter age, fat thickness, or carcass weight endpoints are given in Table 3. Estimates indicate that enough genetic variation exists to improve carcass merit through selection. In general, lowly heritable traits were AFT, DP, KPH, and LMA, whereas BP, BNW, FP, FW, HCW, MS, PRP, RPP, RPW, and YG were moderately heritable. Standard errors associated with estimates of h^2 were low and ranged from 0.07 for AFT to 0.09 for RPW across endpoints. In general and within each endpoint, larger standard errors were found for percentages and weights of retail product, fat, and bone, which probably resulted from the relatively few numbers of records for those traits.

Hot Carcass Weight. Heritability estimates for HCW differed greatly with age and fat thickness (0.27 vs. 0.41, respectively) endpoints. Estimates of genetic variance suggest that age adjustment of HCW removed a portion of the genetic variance that was not removed by adjustment for fat thickness (225 vs. 350 kg^2), which

Table 3. Heritability estimates (±SE) and estimates of phenotypic and genetic variances for carcass traits of steers adjusted to constant age, fat thickness, and carcass weight endpoints[a]

Carcass trait	Age constant			Fat thickness constant			Carcass weight constant		
	σ_p^2	σ_g^2	h^2	σ_p^2	σ_g^2	h^2	σ_p^2	σ_g^2	h^2
HCW, kg	825.11	225.05	0.27 ± 0.08	857.76	350.10	0.41 ± 0.09	—	—	—
Dressing percent	3.89	0.75	0.19 ± 0.07	3.82	0.70	0.18 ± 0.07	3.36	0.89	0.26 ± 0.08
Adjusted fat thickness, cm	0.09	0.02	0.20 ± 0.07	—	—	—	0.08	0.02	0.21 ± 0.07
LM area, cm^2	67.46	16.27	0.24 ± 0.07	68.17	16.97	0.25 ± 0.08	56.06	14.26	0.25 ± 0.07
Kidney, pelvic, and heart fat, %	0.37	0.09	0.23 ± 0.08	0.34	0.09	0.26 ± 0.08	0.36	0.08	0.23 ± 0.08
Marbling score[b]	0.34	0.14	0.40 ± 0.09	0.32	0.11	0.35 ± 0.09	0.34	0.14	0.41 ± 0.09
Yield grade	0.33	0.10	0.30 ± 0.08	0.15	0.04	0.24 ± 0.07	0.30	0.09	0.30 ± 0.08
Predicted retail product, %	5.51	1.67	0.30 ± 0.08	2.63	0.62	0.24 ± 0.07	5.06	1.54	0.30 ± 0.08
Retail product weight, kg	340.05	142.11	0.42 ± 0.09	363.99	180.19	0.50 ± 0.09	129.54	41.21	0.32 ± 0.08
Fat weight, kg	203.22	57.32	0.28 ± 0.08	145.71	42.87	0.29 ± 0.09	136.20	48.21	0.35 ± 0.09
Bone weight, kg	19.46	8.28	0.43 ± 0.09	20.49	9.84	0.48 ± 0.09	11.33	3.59	0.32 ± 0.09
Actual retail product, %	9.84	4.16	0.42 ± 0.09	7.12	2.92	0.41 ± 0.09	9.36	4.13	0.44 ± 0.09
Fat, %	13.27	4.16	0.31 ± 0.08	9.25	2.40	0.26 ± 0.08	12.22	4.28	0.35 ± 0.08
Bone, %	1.11	0.31	0.28 ± 0.08	0.94	0.33	0.35 ± 0.09	1.00	0.33	0.33 ± 0.08

[a]σ_p^2 = phenotypic variance; σ_g^2 = genetic variance; h^2 = heritability.
[b]2 = practically devoid, 9 = moderately abundant.

could explain most of the decrease in age-adjusted h^2 because the reduction in phenotypic variance for HCW adjusted for age was comparatively less than that adjusted for fat thickness (825 vs. 857 kg^2). Few previous studies have compared estimates of h^2 for HCW analyzed on an age- or fat thickness-constant basis. In agreement with the present study, Morris et al. (1990) and Devitt and Wilton (2001) obtained similar absolute differences (0.11 and 0.10, respectively) in estimates of h^2 for HCW adjusted to constant age and to constant fat thickness. The difference, however, obtained by Morris et al. (1990) was in the opposite direction. In contrast, Shanks et al. (2001), using information from Simmental and percentage Simmental bulls, steers, and heifers, did not obtain important differences in estimates of h^2 for HCW adjusted to age (0.32), marbling (0.30), or fat thickness (0.33).

Dressing Percent. Heritability estimate for DP at constant carcass weight (0.26) was slightly larger than estimates at constant age (0.19) or constant fat thickness (0.18). The decrease in the estimate of genetic variance for DP caused by adjustment for age or fat thickness relative to adjustment for carcass weight (0.75 and 0.70 vs. 0.89%^{2}, respectively), combined with an increased estimate of phenotypic variance for age- and fat thickness-adjusted DP (3.89 and 3.82 vs. 3.36%^{2}; Table 3), could explain the decrease in age-adjusted and fat thickness-adjusted h^2 estimates. Lee et al. (2000) reported that the h^2 estimate with slaughter weight as a covariate was greater than when either fat thickness or slaughter age was used as the covariate in a model that included direct genetic, total maternal, and sire × region × year-season interaction as random effects. In a review, Koots et al. (1994a) did not find an important difference between weighted averages for h^2 for DP at constant age (0.39) or weight (0.38) endpoints. Similarly, estimates of h^2 for DP by Veseth et al. (1993) with

paternal half-sib analyses were 0.25 and 0.26 on an age-constant basis and a weight-constant basis, respectively. Other reports in the literature (Reynolds et al., 1991; Wheeler et al., 1996; Lee et al., 2000) contained negligible or low estimates of h^2 for DP, which do not correspond to present estimates. On the other hand, the age-constant and fat thickness-constant estimates of h^2 for DP in the present study were half or less than half those documented in other previous reports: Pariacote et al. (1998) for Shorthorn cattle (0.49), Fouilloux et al. (1999) for Limousin cattle (0.50), and Riley et al. (2002) for Brahman cattle (0.77).

Adjusted Fat Thickness. No major difference in h^2 estimates was obtained when AFT was adjusted to constant age (0.20) or weight (0.21). Cundiff et al. (1971), Devitt and Wilton (2001), and Shanks et al. (2001) also found no important differences between estimates of h^2 for AFT at constant age or at constant weight (0.50 vs. 0.53, 0.41 vs. 0.38, and 0.10 vs. 0.14, respectively), but those estimates were greater or less than present estimates. Heritability estimates in the present study correspond to age-constant estimates of h^2 published by Lamb et al. (1990; 0.24) and Pitchford et al. (2002; 0.26). The estimates, however, were substantially less than age-constant estimates (0.68, 0.52, and 0.84) published previously (Koch, 1978; MacNeil et al., 1991; and Wheeler et al., 2001, respectively), and less than weight-constant estimates of 0.57, 0.44, and 0.49 reported by Dinkel and Busch (1973), Benyshek et al. (1988), and Arnold et al. (1991).

Longissimus Muscle Area. With adjustment to constant age, fat thickness, or carcass weight, estimates of h^2 for LMA were similar (0.24, 0.25, and 0.25). Two previous studies (Benyshek, 1981; Koots et al., 1994a) reported h^2 estimates for LMA that were approximately the same when age (0.40 and 0.42, respectively) or weight (0.41 and 0.41, respectively) was included in

the model as a covariate, but in other studies, the h^2 estimate for LMA was decreased when data were adjusted to a constant weight. Comparison of age- (0.26), weight- (0.22), and fat thickness-constant (0.29) h^2 estimates reported by Shanks et al. (2001) show that adjustment to a weight endpoint led to small reduction in the estimate. Devitt and Wilton (2001) obtained a difference of the same magnitude between h^2 estimates for LMA on a weight-constant basis and a fat thickness-constant basis (0.45 and 0.52, respectively). In a more recent study, Kemp et al. (2002) obtained a slightly greater decrease (from 0.45 to 0.36) in the estimate of h^2 for LMA after adding weight as covariate to the model. A similar phenomenon was observed by Cundiff et al. (1971), who argued that the decrease in h^2 estimate was due to the r_g estimate being greater than the estimate of the environmental correlation between HCW and LMA. In two of a set of four analyses with animal models, Lee et al. (2000) obtained slightly smaller estimates of h^2 for LMA with fat depth (0.20, 0.18) or age (0.19, 0.17) as covariates compared with estimates adjusted for slaughter weight (0.25, 0.24).

Percentage of Kidney, Pelvic, and Heart Fat. Kidney, pelvic, and heart fat percent had similar estimates of h^2 at constant age (0.23), fat thickness (0.26), or weight (0.23). Estimates of age-constant and weight-constant h^2 published earlier (Veseth et al., 1993) also were practically the same (0.37 and 0.38) for Hereford bulls, although those estimates are greater than present estimates. Other researchers obtained greater discrepancies. Heritability for KPH was estimated to be 0.72 (quality grade-constant) by Brackelsberg et al. (1971), 0.83 by Koch et al. (1982), and 0.60 by Splan et al. (2002). Wilson et al. (1976) for crossbred cattle, and Elzo et al. (1998) for Angus cattle, reported zero or near-zero estimates of h^2, which are less than the current estimate.

Marbling Score. The estimate of h^2 for MS was slightly less when fat thickness was held constant than when age or carcass weight was held constant (0.35 vs. 0.40 and 0.41). This result could be due to the slight decrease in the estimate of genetic variance for MS adjusted to fat thickness compared with that adjusted to constant age or weight (0.11 vs. 0.14 and 0.14 units^2, respectively), even though the estimate of phenotypic variance for MS adjusted for fat thickness was less than the estimate adjusted to constant age or carcass weight. Devitt and Wilton (2001) reported a decrease of 0.13 in the estimate of h^2 when adjusted for fat thickness relative to when adjusted for weight. The difference between age-constant and fat thickness-constant estimates of h^2 (0.35 vs. 0.30) reported by Devitt and Wilton (2001), however, was of the same magnitude as the difference in the present study. Benyshek (1981) published similar estimates of h^2 for MS adjusted to constant age or constant weight (0.47 and 0.46) for Hereford steers and heifers. Shanks et al. (2001) also obtained similar estimates of h^2 for MS adjusted for age, weight, or fat thickness (0.12, 0.12, and 0.13).

Predicted Percentage of Retail Product. The pattern observed for h^2 estimates for PRP adjusted to different endpoints was the same as for YG. With PRP adjusted to constant fat thickness, a slightly smaller h^2 was estimated than with adjustment to constant age or weight (0.24 vs. 0.30 and 0.30). Age- and weight-constant estimates of h^2 did not differ from each other. In one of three data sets, Shanks et al. (2001), in contrast, reported that estimated percentage of retail cuts was slightly more heritable when data were adjusted to constant fat thickness than to constant age (0.17 vs. 0.09). The age- and weight-adjusted h^2 estimates from the present study are in the range of estimates of 0.28 for constant age to 0.35 for constant weight by Cundiff et al. (1971). Heritability estimates for PRP were smaller than weight-constant estimates of 0.66 and 0.44 by Dinkel and Busch (1973) and Wilson et al. (1976), and fat thickness-constant estimates of 0.55 and 0.71 reported by Gilbert et al. (1993) and Riley et al. (2002), and greater than age-constant estimates of 0.23 and 0.18 reported by Lamb et al. (1990) and Woodward et al. (1992).

Retail Product Weight. All three estimates of h^2 for RPW were moderate, but a reduction in the estimate resulted from adjusting RPW for carcass weight compared with adjustment for age or fat thickness (0.32 vs. 0.42 and 0.50). Cundiff et al. (1969) reported a smaller estimate when carcass weight was included in the model rather than age (0.42 vs. 0.64). The present estimate of age-constant h^2 is consistent with the estimate of 0.38 reported by Koch (1978) but less than age-adjusted estimates of 0.59, 0.58, and 0.66 reported by Dunn et al. (1970), Koch et al. (1982), and Shackelford et al. (1995).

Bone Weight. Adjustment of BNW for weight resulted in considerable reductions in h^2 estimates relative to adjustment for age or fat thickness (0.32 vs. 0.43 and 0.48, respectively). Cundiff et al. (1969) reported little difference in estimates of h^2 for BNW adjusted to constant age and weight (0.38 and 0.39), which is not consistent with the results of the present study. The age-constant estimate was smaller than estimates (0.56, 0.57, 0.62) published by Koch (1978) for Hereford heifers, Koch et al. (1982) for crossbred steers, and Shackelford et al. (1995) for purebred, composite, and F_1 steers, respectively.

Effect of Endpoint on Estimates of Genetic Correlations

Tables 4, 5, and 6 summarize estimates of r_g among carcass traits from two-trait analyses adjusted to constant age, fat thickness, or carcass weight. Larger standard errors were obtained for estimates of r_g relative to those for estimates of h^2. In general, standard errors for estimates of r_g adjusted for fat thickness were larger than those adjusted for age or weight.

The estimate of r_g for HCW and LMA was greater when fat thickness was used as an endpoint than when age was used (0.51 vs. 0.32). From crossbred steers in

Table 4. Estimates (±SE) of genetic (below diagonal) and environmental (above diagonal) correlations among carcass traits of steers adjusted to constant age[a,b]

Trait	HCW	DP	AFT	LMA	KPH	MS	YG	PRP	RPW	FW	BNW	RPP	FP	BP
HCW		0.50 ± 0.05	0.28 ± 0.07	0.49 ± 0.06	0.18 ± 0.07	0.00 ± 0.09	0.29 ± 0.07	-0.25 ± 0.07	0.84 ± 0.03	0.63 ± 0.05	0.63 ± 0.05	-0.27 ± 0.09	0.36 ± 0.08	-0.44 ± 0.07
DP	0.03 ± 0.25		0.15 ± 0.07	0.14 ± 0.06	0.09 ± 0.06	0.01 ± 0.08	0.20 ± 0.07	-0.18 ± 0.07	0.19 ± 0.07	0.19 ± 0.07	0.03 ± 0.08	-0.08 ± 0.08	0.15 ± 0.07	-0.24 ± 0.06
AFT	0.27 ± 0.22	0.09 ± 0.26		0.01 ± 0.07	0.20 ± 0.07	0.19 ± 0.08	0.72 ± 0.03	-0.70 ± 0.03	0.12 ± 0.08	0.60 ± 0.05	-0.12 ± 0.09	-0.54 ± 0.06	0.59 ± 0.05	-0.53 ± 0.06
LMA	0.32 ± 0.18[a]	0.41 ± 0.22	-0.42 ± 0.23		0.03 ± 0.07	-0.06 ± 0.09	-0.57 ± 0.05	0.54 ± 0.05	0.56 ± 0.05	0.05 ± 0.08	0.40 ± 0.08	0.19 ± 0.09	-0.10 ± 0.08	-0.12 ± 0.07
KPH	0.35 ± 0.21	0.26 ± 0.25	0.37 ± 0.24	-0.01 ± 0.23[a]		0.17 ± 0.08	0.43 ± 0.06	-0.55 ± 0.05	0.05 ± 0.08	0.40 ± 0.06	0.00 ± 0.08	-0.41 ± 0.07	0.42 ± 0.06	-0.32 ± 0.06
MS	0.39 ± 0.17[a]	0.29 ± 0.20	0.34 ± 0.19	-0.05 ± 0.19[a]	0.27 ± 0.19		0.22 ± 0.08	-0.24 ± 0.08	-0.13 ± 0.10	0.34 ± 0.08	-0.31 ± 0.11	-0.39 ± 0.09	0.42 ± 0.08	-0.38 ± 0.08
YG	0.42 ± 0.17	-0.14 ± 0.24[a]	0.86 ± 0.07	-0.71 ± 0.12[a]	0.44 ± 0.19[a]	0.32 ± 0.16[a]		-1.00 ± 0.00	-0.01 ± 0.09	0.61 ± 0.05	-0.11 ± 0.09	-0.59 ± 0.06	0.61 ± 0.05	-0.44 ± 0.06
PRP	-0.40 ± 0.18	0.12 ± 0.24[a]	-0.85 ± 0.67	0.68 ± 0.13[a]	-0.53 ± 0.16	-0.34 ± 0.16[a]	-1.00 ± 0.00		0.03 ± 0.08	-0.60 ± 0.05	0.12 ± 0.09	0.62 ± 0.06	-0.62 ± 0.05	0.45 ± 0.06
RPW	0.83 ± 0.06	0.21 ± 0.20[a]	-0.26 ± 0.21[a]	0.62 ± 0.11	-0.02 ± 0.20[a]	-0.06 ± 0.16[a]	-0.23 ± 0.18[a]	0.26 ± 0.17[a]		0.26 ± 0.09	0.77 ± 0.04	0.17 ± 0.10	-0.06 ± 0.09	-0.21 ± 0.08
FW	0.60 ± 0.13	0.15 ± 0.23	0.72 ± 0.10	-0.16 ± 0.21[a]	0.45 ± 0.19	0.64 ± 0.16[a]	0.73 ± 0.08[a]	-0.71 ± 0.09[a]	-0.19 ± 0.20[a]		-0.02 ± 0.10	-0.88 ± 0.02	0.92 ± 0.01	-0.78 ± 0.04
BNW	0.78 ± 0.08	-0.13 ± 0.21[a]	0.04 ± 0.21[a]	0.24 ± 0.17[a]	-0.08 ± 0.20[a]	0.08 ± 0.16[a]	0.16 ± 0.18[a]	-0.12 ± 0.18[a]	0.64 ± 0.08[a]	0.33 ± 0.17[a]		0.26 ± 0.11	-0.32 ± 0.10	0.35 ± 0.08
RPP	-0.25 ± 0.18	0.09 ± 0.21	-0.68 ± 0.10	0.47 ± 0.15[a]	-0.30 ± 0.18[a]	-0.55 ± 0.11	-0.72 ± 0.08[a]	0.72 ± 0.08[a]	0.56 ± 0.12[a]	-0.91 ± 0.03	-0.15 ± 0.16[a]		-0.97 ± 0.00	0.59 ± 0.07
FP	0.25 ± 0.19	0.05 ± 0.23[a]	0.70 ± 0.10	-0.44 ± 0.18[a]	0.40 ± 0.18[a]	0.62 ± 0.12	0.73 ± 0.08[a]	-0.73 ± 0.08[a]	-0.58 ± 0.14[a]	0.94 ± 0.02	0.02 ± 0.18[a]	-0.97 ± 0.01		-0.80 ± 0.04
BP	-0.10 ± 0.21	-0.48 ± 0.21[a]	-0.23 ± 0.20	-0.15 ± 0.21[a]	-0.37 ± 0.20	-0.21 ± 0.17[a]	-0.15 ± 0.19[a]	0.18 ± 0.19[a]	0.00 ± 0.19[a]	-0.29 ± 0.17[a]	0.66 ± 0.12[a]	0.07 ± 0.17[a]	-0.30 ± 0.16[a]	

[a]Estimates of genetic correlation changed in magnitude and/or sign across slaughter endpoints. Change in magnitude was defined as a 0.15 minimum difference, or more, across endpoints.
[b]DP = dressing percent; AFT = adjusted fat thickness; LMA = LM area; MS = marbling score (2 = practically devoid; 9 = moderately abundant); YG = yield grade; PRP = predicted percentage of retail product; RPW = retail product weight; FW = fat weight; BNW = bone weight; RPP = actual retail product percent; FP = fat percent; BP = bone percent.

Table 5. Estimates (±SE) of genetic (below diagonal) and environmental (above diagonal) correlations among carcass traits of steers adjusted to constant fat thickness[a,b]

Trait	HCW	DP	LMA	KPH	MS	YG	PRP	RPW	FW	BNW	RPP	FP	BP
HCW		0.48 ± 0.06	0.48 ± 0.07	0.11 ± 0.08	0.01 ± 0.08	0.08 ± 0.08	-0.07 ± 0.08	0.83 ± 0.03	0.58 ± 0.06	0.68 ± 0.05	-0.17 ± 0.10	0.25 ± 0.09	-0.32 ± 0.09
DP	0.06 ± 0.22		0.15 ± 0.07	0.06 ± 0.07	0.00 ± 0.08	0.13 ± 0.07	-0.11 ± 0.07	0.17 ± 0.08	0.15 ± 0.07	0.01 ± 0.09	-0.02 ± 0.08	0.11 ± 0.07	-0.25 ± 0.07
LMA	0.51 ± 0.14[a]	0.47 ± 0.22		-0.01 ± 0.07	-0.08 ± 0.08	-0.79 ± 0.03	0.76 ± 0.03	0.56 ± 0.06	0.03 ± 0.08	0.39 ± 0.08	0.23 ± 0.09	-0.15 ± 0.08	-0.12 ± 0.08
KPH	0.34 ± 0.19	0.28 ± 0.25	0.25 ± 0.22[a]		0.16 ± 0.08	0.41 ± 0.06	-0.56 ± 0.05	0.01 ± 0.09	0.35 ± 0.07	0.00 ± 0.09	-0.37 ± 0.08	0.39 ± 0.07	-0.27 ± 0.07
MS	0.24 ± 0.17[a]	0.26 ± 0.22	0.10 ± 0.20[a]	0.16 ± 0.20		0.14 ± 0.08	-0.16 ± 0.08	-0.12 ± 0.10	0.40 ± 0.07	-0.24 ± 0.11	-0.40 ± 0.09	0.44 ± 0.08	-0.36 ± 0.09
YG	0.31 ± 0.18	-0.34 ± 0.25[a]	-0.66 ± 0.12[a]	0.29 ± 0.21[a]	0.11 ± 0.20[a]		-1.00 ± 0.01	-0.11 ± 0.09	-0.35 ± 0.07	0.00 ± 0.09	-0.43 ± 0.07	0.40 ± 0.07	-0.12 ± 0.08
PRP	-0.32 ± 0.19	0.29 ± 0.26[a]	0.63 ± 0.13[a]	-0.47 ± 0.19	-0.13 ± 0.20[a]	-1.00 ± 0.10		0.14 ± 0.08	0.20 ± 0.09	0.04 ± 0.09	0.42 ± 0.07	-0.42 ± 0.06	0.14 ± 0.08
RPW	0.93 ± 0.03	0.28 ± 0.20[a]	0.63 ± 0.11	0.15 ± 0.19[a]	0.02 ± 0.16[a]	0.07 ± 0.19[a]	-0.01 ± 0.19[a]			0.78 ± 0.04	0.27 ± 0.10	-0.18 ± 0.09	-0.14 ± 0.09
FW	0.68 ± 0.12	0.03 ± 0.24	0.22 ± 0.21[a]	0.31 ± 0.20	0.43 ± 0.16[a]	0.39 ± 0.18[a]	-0.26 ± 0.18[a]	0.25 ± 0.17[a]		0.08 ± 0.10	-0.84 ± 0.03	0.89 ± 0.01	-0.67 ± 0.06
BNW	0.81 ± 0.06	-0.01 ± 0.21[a]	0.30 ± 0.16[a]	-0.04 ± 0.19[a]	0.17 ± 0.17[a]	0.29 ± 0.18[a]	-0.21 ± 0.19[a]	0.67 ± 0.08[a]	0.54 ± 0.16[a]		0.18 ± 0.12	-0.27 ± 0.10	0.38 ± 0.08
RPP	-0.18 ± 0.16	0.21 ± 0.21	0.27 ± 0.17[a]	-0.12 ± 0.19[a]	-0.46 ± 0.14	-0.44 ± 0.15[a]	0.32 ± 0.15[a]	0.35 ± 0.14[a]	-0.85 ± 0.04	-0.35 ± 0.15[a]		-0.97 ± 0.00	0.48 ± 0.08
FP	0.25 ± 0.18	-0.10 ± 0.24[a]	-0.18 ± 0.19[a]	0.23 ± 0.21[a]	0.53 ± 0.16	0.42 ± 0.17[a]	-0.43 ± 0.17[a]	-0.28 ± 0.17[a]	0.90 ± 0.03	0.25 ± 0.19[a]	-0.94 ± 0.02		-0.71 ± 0.05
BP	-0.22 ± 0.16	-0.31 ± 0.20[a]	-0.32 ± 0.18[a]	-0.32 ± 0.18	-0.06 ± 0.17[a]	0.08 ± 0.19[a]	-0.03 ± 0.20[a]	-0.27 ± 0.16[a]	-0.23 ± 0.17[a]	0.47 ± 0.13[a]	-0.14 ± 0.18[a]	-0.20 ± 0.18[a]	

[a]Estimates of genetic correlation changed in magnitude and/or sign across slaughter endpoints. Change in magnitude was defined as a 0.15 minimum difference, or more, across endpoints.
[b]DP = dressing percent; LMA = LM area; MS = marbling score (2 = practically devoid; 9 = moderately abundant); YG = yield grade; PRP = predicted percentage of retail product; RPW = retail product weight; FW = fat weight; BNW = bone weight; RPP = actual retail product percent; FP = fat percent; BP = bone percent.

Table 6. Estimates (±SE) of genetic (below diagonal) and environmental (above diagonal) correlations among carcass traits of steers adjusted to constant carcass weight[a,b]

Trait	DP	AFT	LMA	KPH	MS	YG	PRP	RPW	FW	BNW	RPP	FP	BP
DP		-0.01 ± 0.07	-0.08 ± 0.07	0.01 ± 0.07	-0.01 ± 0.08	0.06 ± 0.07	-0.06 ± 0.07	-0.38 ± 0.07	-0.19 ± 0.08	-0.40 ± 0.06	0.06 ± 0.09	-0.02 ± 0.08	-0.07 ± 0.07
AFT	0.09 ± 0.24		-0.14 ± 0.07	0.20 ± 0.07	0.18 ± 0.08	0.69 ± 0.04	-0.64 ± 0.04	-0.23 ± 0.08	0.54 ± 0.06	-0.37 ± 0.07	-0.48 ± 0.07	0.53 ± 0.06	-0.46 ± 0.06
LMA	0.50 ± 0.20	-0.55 ± 0.19		-0.07 ± 0.07	-0.13 ± 0.08	-0.81 ± 0.02	0.76 ± 0.03	0.40 ± 0.07	-0.29 ± 0.07	0.20 ± 0.08	0.34 ± 0.08	-0.26 ± 0.08	0.08 ± 0.08
KPH	0.15 ± 0.24	0.42 ± 0.25	-0.10 ± 0.23[a]		0.12 ± 0.08	0.42 ± 0.06	-0.53 ± 0.05	-0.13 ± 0.08	0.35 ± 0.07	-0.12 ± 0.07	-0.35 ± 0.08	0.36 ± 0.07	-0.24 ± 0.07
MS	0.12 ± 0.19	0.35 ± 0.19	-0.14 ± 0.18[a]	0.30 ± 0.18		0.23 ± 0.08	-0.24 ± 0.08	-0.27 ± 0.09	0.40 ± 0.08	-0.34 ± 0.09	-0.40 ± 0.09	0.43 ± 0.08	-0.37 ± 0.08
YG	-0.24 ± 0.21[a]	0.85 ± 0.07	-0.89 ± 0.05[a]	0.43 ± 0.20[a]	0.27 ± 0.16[a]		-1.00 ± 0.00	-0.40 ± 0.09	0.55 ± 0.06	-0.36 ± 0.08	-0.54 ± 0.09	0.55 ± 0.06	-0.36 ± 0.07
PRP	0.21 ± 0.21[a]	-0.82 ± 0.09	0.85 ± 0.07[a]	-0.51 ± 0.18	-0.30 ± 0.08[a]	-1.00 ± 0.01		0.47 ± 0.07	-0.55 ± 0.05	0.35 ± 0.08	0.57 ± 0.06	-0.57 ± 0.08	0.37 ± 0.07
RPW	0.13 ± 0.21[a]	-0.77 ± 0.14[a]	0.51 ± 0.13	-0.48 ± 0.18[a]	-0.48 ± 0.13[a]	-0.72 ± 0.07[a]	0.80 ± 0.08[a]		-0.53 ± 0.06	0.65 ± 0.06	0.64 ± 0.07	-0.63 ± 0.05	0.28 ± 0.08
FW	0.06 ± 0.20	0.71 ± 0.10	-0.51 ± 0.15[a]	0.41 ± 0.19	0.54 ± 0.13[a]	0.72 ± 0.09[a]	-0.70 ± 0.09[a]	-0.99 ± 0.04[a]		-0.54 ± 0.07	-0.93 ± 0.01	0.97 ± 0.00	-0.69 ± 0.06
BNW	-0.39 ± 0.17[a]	-0.15 ± 0.20[a]	-0.19 ± 0.19[a]	-0.55 ± 0.18[a]	-0.14 ± 0.16[a]	0.02 ± 0.19[a]	0.04 ± 0.19[a]	0.08 ± 0.19[a]	-0.09 ± 0.18[a]		0.47 ± 0.09	-0.61 ± 0.07	0.79 ± 0.03
RPP	0.12 ± 0.18	-0.71 ± 0.10	0.57 ± 0.12[a]	-0.31 ± 0.18[a]	-0.50 ± 0.12	-0.73 ± 0.12[a]	0.73 ± 0.08[a]	1.00 ± 0.02[a]	-0.96 ± 0.01	-0.18 ± 0.18[a]		-0.96 ± 0.00	0.51 ± 0.08
FP	-0.01 ± 0.20[a]	0.72 ± 0.10	-0.43 ± 0.16[a]	0.43 ± 0.18[a]	0.56 ± 0.12	0.73 ± 0.08[a]	-0.74 ± 0.05[a]	-0.98 ± 0.04[a]	1.00 ± 0.00	0.51 ± 0.31[a]	-0.97 ± 0.00		-0.72 ± 0.05
BP	-0.45 ± 0.19[a]	-0.25 ± 0.19	-0.12 ± 0.20[a]	-0.44 ± 0.19	-0.20 ± 0.17[a]	-0.15 ± 0.18[a]	0.20 ± 0.18[a]	-0.07 ± 0.20[a]	-0.38 ± 0.14[a]	1.00 ± 0.01[a]	0.11 ± 0.16[a]	-0.38 ± 0.13[a]	

[a]Estimates of genetic correlation changed in magnitude and/or sign across slaughter endpoints. Change in magnitude was defined as a 0.15 minimum difference, or more, across endpoints.
[b]DP = dressing percent; AFT = adjusted fat thickness; LMA = LM area; MS = marbling score (2 = practically devoid; 9 = moderately abundant); YG = yield grade; PRP = predicted percentage of retail product; RPW = retail product weight; FW = fat weight; BNW = bone weight; RPP = actual retail product percent; FP = fat percent; BP = bone percent.

Canada, Devitt and Wilton et al. (2001) also estimated a greater r_g when data were adjusted to constant fat thickness (0.69) than to constant age (0.42). Shanks et al. (2001) reported that the estimate of r_g at constant fat thickness tended to be greater than the estimate at constant age (0.57 vs. 0.49). The age-constant estimate of r_g for HCW with MS (0.39) was greater than the fat thickness-constant estimate (0.24). Shanks et al. (2001) reported the estimate of r_g for HCW with MS was less on a fat thickness-constant basis (0.20) than on an age-constant basis (0.30). Although negative, the estimate of age-constant r_g between HCW and MS (−0.32) was greater in magnitude than the fat thickness-constant estimate (−0.03), both reported by Devitt and Wilton (2001). The age-constant estimate in the present study agrees with age-constant estimates (0.38, 0.44) reported by Veseth et al. (1993) and Wheeler et al. (2001). The fat thickness-constant estimate of r_g in the present study is less than corresponding estimates of 0.55 and 0.39 by Gilbert et al. (1993) and Riley et al. (2002). Hot carcass weight was estimated to be moderately and positively correlated genetically with YG, and moderately and negatively correlated with PRP, but fat thickness-constant estimates (0.31 and −0.32) tended to be less different from zero than age-constant estimates (0.42 and −0.40). The few studies (Pariacote et al., 1998; Wheeler et al., 2001; Riley et al., 2002) found in the literature, however, varied from moderately negative (−0.39), to small (0.23), and to large (0.56) estimates of r_g between HCW and YG. Shanks et al. (2001) reported the estimate of r_g for HCW and PRP to be less different from zero (−0.05) when adjusted to a fat thickness-constant basis than to an age-constant basis (−0.21). The fat thickness-constant estimate of r_g (−0.55) by Riley et al. (2002) is stronger than the estimate obtained in the present study.

In essence, DP and AFT were only slightly genetically linked (0.09) on either an age- or weight-constant basis. All reports in the literature (Dinkel and Busch, 1973; Pariacote et al., 1998; Riley et al., 2002) cited stronger estimates of r_g, which did not all agree in sign (0.25, −0.16, and 0.42, respectively). With any of the three adjustments, age, fat thickness, or weight, estimates of r_g between DP and LMA were moderate and positive (0.41, 0.47, and 0.50). These estimates do not agree with estimates by Lee et al. (2000), who concluded that estimates of r_g differed depending on the covariate used in the model: fat thickness (−0.11), age (0.01), or slaughter weight (0.91). Weight-constant (0.47) and age-constant (0.40) estimates published by Dinkel and Busch (1973) and Morris et al. (1999), respectively, match well with present estimates, but those reported by Veseth et al. (1993), Pariacote et al. (1998), and Riley et al. (2002) do not agree (−0.11, 0.79, and 0.02). Dressing percent had a lowly positive estimate of r_g with MS for all endpoints considered: weight = 0.12; fat thickness = 0.26; and age = 0.29. Lee et al. (2000), for Korean Native (Hanwoo) cattle, found major effects on magnitude of estimates of r_g for DP and MS with much smaller esti-

mates when adjusted for age and fat thickness than when adjusted for weight (–0.88 and –0.99 vs. –0.03). The estimates of r_g from the present study are much greater than the one (0.00) obtained by Veseth et al. (1993) and less than the estimate (0.35) recently reported by Riley et al. (2002). Wulf et al. (1996) reported a fat thickness-constant estimate of 0.68, which is greater than any of the estimates from the present study.

Adjusted fat thickness was favorably and moderately correlated genetically with LMA at both age (–0.42) and weight (–0.55) endpoints. Estimates of r_g of 0.02 and –0.06 at constant age, and of –0.03 and –0.03 at constant weight reported by Devitt and Wilton (2001) and Shanks et al. (2001), respectively, were similar, but do not agree with present estimates. Estimates from the present study correspond with age-adjusted estimates of –0.44 by Koch et al. (1982) and –0.42 by Wheeler et al. (2001), and with weight-adjusted estimates of –0.59 by Dinkel and Busch (1973) and –0.47 by Wilson et al. (1976), although other authors (Koch, 1978; Koots et al., 1994b; Moser et al., 1998) have reported little genetic association between these two traits. With age and weight endpoints, estimates of r_g between AFT and MS were almost the same: 0.34 and 0.35. Shanks et al. (2001) determined that constant age and weight adjustments provided similar estimates of r_g (0.17 and 0.18), but estimates adjusted for age (0.30) and weight (0.41) by Devitt and Wilton (2001) tended to be different. In published studies with only one kind of adjustment, a wide range (–0.83 to 0.73) of estimates has been reported: high and negative (Gilbert et al., 1993), low and negative (Wilson et al., 1993; Hirooka et al., 1996), low and positive (Koch et al., 1982; Arnold et al., 1991; Pariacote et al., 1998), and moderate and positive (Dinkel and Busch, 1973; Wilson et al., 1976; Kemp et al., 2002), which agree closely with present estimates, and moderately high and positive (Brackelsberg et al., 1971; Koch, 1978; Lamb et al., 1990). On either an age- or a weight-constant basis, AFT was estimated to be strongly associated genetically with YG (0.86 and 0.85) and PRP (–0.85 and –0.82). Shanks et al. (2001) reported that fat thickness and estimated percentage of retail cuts also were negatively correlated genetically, but that strength of the correlation varied somewhat with different covariates: strongest on a weight-constant basis (–0.53), weakest on an age-constant basis (–0.29), and intermediate on a marbling-constant basis (–0.40). Generally, estimates of r_g for fat thickness with YG or cutability in the literature (Dinkel and Busch, 1973; Pariacote et al., 1998; Wheeler et al., 2001; Riley et al., 2002) correspond to estimates from the present study. The estimate of r_g between AFT and RPW was much more negative at constant weight than at constant age (–0.77 vs. –0.26). An age-adjusted estimate by Koch et al. (1982) was –0.34. Koch (1978) reported a greater estimate with different sign (0.65). Comparisons between age-constant and weight-constant estimates of r_g for AFT and RPW were not found in the literature.

For LMA and MS, an extremely small, near zero, estimate (–0.05) of r_g was obtained for constant age; a low and positive estimate (0.10) for constant fat thickness; and a low and negative estimate for constant weight (–0.14). The confidence intervals for each estimate would include zero because of the relatively large standard errors (Tables 4, 5, and 6). Other studies also reported considerable differences among estimates at different endpoints. Shanks et al. (2001) concluded that r_g was moderate and positive at age (0.46) and fat thickness (0.48) endpoints but smaller at weight endpoint (0.26). Earlier, Lee et al. (2000) reported that estimates of r_g for LMA and MS were different depending on the covariate used as the endpoint: 0.20 with fat thickness; 0.39 with slaughter weight; and 0.47 with age. Estimates by Devitt and Wilton (2001) were –0.61, –0.37, and –0.35 with age, fat thickness, or weight covariates, respectively. The lack of genetic association between LMA and MS at a constant age found in this study is contrary to the level of genetic association found in other studies with that covariate. Estimates by Lamb et al. (1990), Veseth et al. (1993), and Wheeler et al. (2001) were 0.57, 0.51, and –0.36. In comparative agreement with the present estimate was the age-adjusted estimate of –0.04 by Wilson et al. (1993). Stronger r_g were estimated for LMA and YG and for LMA and PRP when data were adjusted to a constant carcass weight (–0.89 and 0.85) vs. to a constant age (–0.71 and 0.68) or a constant fat thickness (–0.66 and 0.63). Shanks et al. (2001), in contrast, reported estimates of r_g for LMA with percentage of retail cuts to be similar at constant age (0.75), weight (0.75), and fat thickness (0.81) endpoints. Greater estimates of r_g for LMA with YG (–0.26) and smaller estimates for LMA with cutability (0.23) were obtained (Riley et al., 2002) from an analysis with constant fat thickness. On the other hand, the age-constant estimate of –0.72 between LMA and YG reported by Wheeler et al. (2001) is similar to the present estimate.

At a constant fat thickness, MS and YG, and MS and PRP were estimated to be weakly correlated genetically (0.11 and –0.13), but to be moderately correlated at a constant age (0.32 and –0.34) or weight (0.27 and –0.30). Age-adjusted estimates of r_g for MS with YG and cutability of 0.32 and –0.36 were reported by Lamb et al. (1990), which were similar to the present estimates. For crossbred cattle, Wulf et al. (1996) found that MS and YG had little genetic association (0.04) at constant fat thickness. Riley et al. (2002) reported a much larger fat thickness-constant estimate of r_g between MS and YG (0.45) and also a much smaller estimate of the r_g (–0.43) between MS and cutability. Overall, MS and RPP, and MS and FP were as moderately genetically correlated at constant fat thickness as at constant age or weight; estimates by endpoint for the pairs of traits were: –0.46, –0.55, and –0.50; and 0.53, 0.62, and 0.56, respectively. Fat thickness as covariate in the model resulted in a nearly null (–0.06) estimate of r_g between MS and BP, whereas using age or weight as a covariate

resulted in small negative estimates (–0.21 and –0.20). In a study with a constant age (Koch et al., 1982), quite different estimates of r_g for MS with RPP, FP and BP were obtained (–0.37, 0.34, and –0.04). The magnitude of the estimate of the unfavorable r_g (–0.63) between i.m. fat and retail product yield both adjusted to a constant age by Shackelford et al. (1994) is somewhat larger than the magnitude of the present estimate for MS and RPP.

The magnitude and sign of the estimate of the r_g between RPW and FW changed depending on the covariate. The association was highly negative (–0.99) using weight, lowly negative (–0.19) using age, and lowly positive (0.25) using fat thickness as covariates. Cundiff et al. (1969) also observed a remarkable effect of endpoint on estimates of r_g between RPW and fat trim weight adjusted to constant age (0.55) or weight (–0.90), which differed not only in magnitude, but also in sign. Koch (1978) and Morris et al. (1999) reported age-constant estimates of r_g for RPW with trimmed FW of different sign and larger magnitude (0.46 and 0.28).

For each endpoint, differences between estimates of h^2 or r_g reported here and those found in the literature may reflect differences in a series of factors: sex, management, breed, effects included in the model (most reports do not include any kind of maternal effect), measurement errors, number of animals measured, and method of estimation (Ríos-Utrera, 2004). Some breed associations are currently reporting EPD for several carcass traits (e.g., LMA, AFT, and PRP) as a tool for genetic improvement, and most of them adjust such estimates to constant age, but the endpoint to slaughter animals varies among beef cattle producers and age typically is not the endpoint of choice. Because EPD depend on estimates of genetic parameters, the results reported here suggest that ranking of sires based on EPD may be different for some carcass traits depending on endpoint. For percentage of retail cuts of Simmental cattle, Shanks et al. (2001) reported that rank correlations for EBV at constant fat thickness with EBV at constant age or weight were less than 0.74.

Final Remarks. The endpoint used had important effects on estimates of variance and covariance components and, consequently, on h^2 estimates of, and estimates of r_g among, many carcass traits. In general, total maternal effects of the dam accounted for only a small proportion of the total variance for carcass traits. Estimates of fractions of variance due to the dam, however, changed depending on the endpoint and from trait to trait. At a constant age, the estimate of fraction of variance due to dam for AFT was as important as the estimate of h^2 (0.19 and 0.20). For this trait, and perhaps for others (e.g., FW, RPP, FP), removal of dam effects from the model could result in biased estimates of h^2 due to increased (or decreased) estimate of direct genetic variance. The effect of endpoint on estimates of phenotypic and direct genetic variances was important for various carcass traits, but its effect differed among traits. One major effect was observed on estimates of

genetic and phenotypic variances for RPW. Estimates of phenotypic variance for RPW at different endpoints ranked the same as estimates of genetic variance, but differences in phenotypic variance estimates among endpoints were smaller. The largest differences in estimates of h^2 with different endpoints were for HCW, RPW, and BNW. Among all parameters estimated, the greatest effect of endpoint was on estimates of r_g for numerous (54) combinations of traits, which in some cases not only changed in magnitude (0.15 minimum difference, or more), but also in sign depending on the endpoints. Ten of the 13 possible combinations of carcass traits that involved LMA had estimates of r_g that significantly changed in magnitude and/or sign across endpoints. Of particular interest are r_g for MS with AFT, LMA, YG, and PRP. In general, correlations for MS were moderate with AFT, and low with LMA, YG, and PRP. Single trait selection for less AFT would decrease MS at constant age or weight. This implication could be discouraging for beef producers who desire to improve quality grade without increasing fat thickness. Several researchers (Bertrand et al., 1993; Vieselmeyer et al., 1996), however, have demonstrated that marbling can be increased without increasing backfat through selection based on EPD. On the other hand, single trait selection for greater LMA or PRP or improved YG might leave MS unaltered or at least with little change at constant fat thickness. Alternatively, selection for increased LMA at a constant age might improve YG and increase PRP without decreasing marbling score (see Ríos-Utrera, 2004). Lastly, age and weight covariates gave similar estimates of r_g for trait pairs related to fat, age and fat thickness covariates gave similar estimates of r_g for trait pairs related to weight, and weight and fat thickness covariates resulted in different estimates of r_g for most pairs of traits.

Implications

Estimates of heritability indicate that if selection were practiced, response to selection would be possible for the carcass traits evaluated. However, changes in estimates of phenotypic variances, heritabilities, and genetic correlations for different endpoints suggest that direct and correlated responses to single trait selection would be different for some traits depending on endpoint. At the same selection intensity, direct response to single trait selection for retail product weight might be more effective at constant age or constant fat thickness than at constant weight due to greater estimates of phenotypic variance and of heritability at constant age and constant fat thickness.

Literature Cited

Arnold, J. W., J. K. Bertrand, L. L. Benyshek, and C. Ludwig. 1991. Estimates of genetic parameters for live animal ultrasound, actual carcass data, and growth traits in beef cattle. J. Anim. Sci. 69:985–992.

Benyshek, L. L. 1981. Heritabilities for growth and carcass traits estimated from data on Hereford under commercial conditions. J. Anim. Sci. 53:49–56.

Benyshek, L. L., J. W. Comerford, D. E. Little, and C. Ludwig. 1988. Estimates of carcass trait genetic parameters from Hereford field data. J. Anim. Sci. 66(Suppl. 1):10. (Abstr.)

Bertrand, J. K., W. O. Herring, S. E. Williams, and L. L. Benyshek. 1993. Selection for increased marbling and decreased backfat in Angus cattle using expected progeny differences. J. Anim. Sci. 71(Suppl. 1):93. (Abstr.)

BIF. 2002. Guidelines for uniform beef improvement programs. 8th ed. Beef Improv. Fed., Univ. of Georgia, Athens.

Boldman, K. G., L. A. Kriese, L. D. Van Vleck, C. P. Van Tassell, and S. D. Kachman. 1995. A manual for use of MTDFREML: A set of programs to obtain estimates of variances and covariances [Draft]. ARS, USDA, Washington, DC.

Brackelsberg, P. O., E. A. Kline, R. L. Willham, and L. N. Hazel. 1971. Genetic parameters for selected beef-carcass traits. J. Anim. Sci. 33:13–17.

Cundiff, L. V., K. E. Gregory, R. M. Koch, and G. E. Dickerson. 1969. Genetic variation in total and differential growth of carcass components in beef cattle. J. Anim. Sci. 29:233–244.

Cundiff, L. V., K. E. Gregory, R. M. Koch, and G. E. Dickerson. 1971. Genetic relationships among growth and carcass traits of beef cattle. J. Anim. Sci. 33:550–555.

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

Dikeman, M. E., L. V. Cundiff, K. E. Gregory, K. E. Kemp, and R. M. Koch. 1998. Relative contributions of subcutaneous and intermuscular fat to yields and predictability of retail product, fat trim, and bone in beef carcasses. J. Anim. Sci. 76:1604–1612.

Dinkel, C. A., and D. A. Busch. 1973. Genetic parameters among production, carcass composition and carcass quality traits of beef cattle. J. Anim. Sci. 36:832–846.

Dinkel, C. A., L. L. Wilson, H. J. Tuma, and J. A. Minyard. 1965. Ratios and percents as measures of carcass traits. J. Anim. Sci. 24:425–429.

Dodenhoff, J., L. D. Van Vleck, S. D. Kachman, and R. M. Koch. 1998. Parameter estimates for direct, maternal, and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. J. Anim. Sci. 76:2521–2527.

Dunn, R. J., W. T. Magee, K. E. Gregory, L. V. Cundiff, and R. M. Koch. 1970. Genetic parameters in straightbred and crossbred beef cattle. J. Anim. Sci. 31:656–663.

Elzo, M. A., R. L. West, D. D. Johnson, and D. L. Wakeman. 1998. Genetic variation and prediction of additive and nonadditive genetic effects for six carcass traits in an Angus-Brahman multibreed herd. J. Anim. Sci. 76:1810–1823.

Fouilloux, M. N., G. Renand, J. Gaillard, and F. Ménissier. 1999. Genetic parameters of beef traits of Limousin and Charolais progeny-tested AI sires. Genet. Sel. Evol. 31:465–489.

Gilbert, R. P., D. R. C. Bailey, and N. H. Shannon. 1993. Body dimensions and carcass measurements of cattle selected for postweaning gain fed two different diets. J. Anim. Sci. 71:1688–1698.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. J. Anim. Sci. 73:1920–1926.

Hirooka, H., A. F. Groen, and M. Matsumoto. 1996. Genetic parameters for growth and carcass traits in Japanese Brown cattle estimated from field records. J. Anim. Sci. 74:2112–2116.

Johnson, D. L., and R. Thompson. 1995. Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. J. Dairy Sci. 78:449–456.

Kemp, D. J., W. O. Herring, and C. J. Kaiser. 2002. Genetic and environmental parameters for steer ultrasound and carcass traits. J. Anim. Sci. 80:1489–1496.

Koch, R. M. 1978. Selection in beef cattle. III. Correlated response of carcass traits to selection for weaning weight, yearling weight and muscling score in cattle. J. Anim. Sci. 47:142–150.

Koch, R. M., L. V. Cundiff, and K. E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. J. Anim. Sci. 55:1319–1329.

Koch, R. M., K. E. Gregory, and L. V. Cundiff. 1995. Genetic aspects of beef carcass growth and development. Progress report. Pages 9–18 in Proc. 5th Genetic Prediction Workshop, Kansas City, MO. South Dakota State Univ., Brookings.

Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62:309–338.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:825–853.

Lamb, M. A., O. W. Robison, and M. W. Tess. 1990. Genetic parameters for carcass traits in Hereford bulls. J. Anim. Sci. 68:64–69.

Lee, J. W., S. B. Choi, J. S. Kim, J. F. Keown, and L. D. Van Vleck. 2000. Parameter estimates for genetic effects on carcass traits of Korean native cattle. J. Anim. Sci. 78:1181–1190.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS System for Mixed Models. SAS Inst., Inc. Cary, NC.

MacNeil, M. D., D. R. C. Bailey, J. J. Urick, R. P. Gilbert, and W. L. Reynolds. 1991. Heritabilities and genetic correlations for postweaning growth and feed intake of beef bulls and steers. J. Anim. Sci. 69:3183–3189.

Morris, C. A., R. L. Baker, A. H. Carter, and S. M. Hickey. 1990. Evaluation of eleven cattle breeds for crossbred beef production: Carcass data from males slaughtered at two ages. Anim. Prod. 50:79–92.

Morris, C. A., N. G. Cullen, and D. G. McCall. 1999. Genetic and phenotypic relationships among carcass measurements in beef cattle. N. Z. J. of Agric. Res. 42:415–421.

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

Pariacote, F., L. D. Van Vleck, and R. E. Hunsley. 1998. Genetic and phenotypic parameters for carcass traits of American Shorthorn beef cattle. J. Anim. Sci. 76:2584–2588.

Pitchford, W. S., M. P. B. Deland, B. D. Siebert, A. E. O. Malau-Aduli, and C. D. K. Bottema. 2002. Genetic variation in fatness and fatty acid composition of crossbred cattle. J. Anim. Sci. 80:2825–2832.

Reynolds, W. L., J. J. Urick, D. A. Veseth, D. D. Kress, T. C. Nelsen, and R. E. Short. 1991. Genetic parameters by son-sire covariances for growth and carcass traits of Hereford bulls in a nonselected herd. J. Anim. Sci. 69:1000–1007.

Riley, D. G., C. C. Chase, Jr., A. C. Hammond, R. L. West, D. D. Johnson, T. A. Olson, and S. W. Coleman. 2002. Estimated genetic parameters for carcass traits of Brahman cattle. J. Anim. Sci. 80:955–962.

Ríos-Utrera, A. 2004. Genetic evaluation of carcass traits: Looking at the effects of slaughter endpoints. Pages 79–103 in Proc. Beef Improv. Fed. 36th Annu. Res. Symp. and Annu. Mtg., Sioux Falls, SD. Iowa State Univ., Ames.

Shackelford, S. D., L. V. Cundiff, K. E. Gregory, and M. Koohmaraie. 1995. Predicting beef carcass cutability. J. Anim. Sci. 73:406–413.

Shackelford, S. D., M. Koohmaraie, L. V. Cundiff, K. E. Gregory, G. A. Rohrer, and J. W. Savell. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield, and growth rate. J. Anim. Sci. 72:857–863.

Shanks, B. C., M. W. Tess, D. D. Kress, and B. E. Cunningham. 2001. Genetic evaluation of carcass traits in Simmental-sired cattle at different slaughter endpoints. J. Anim. Sci. 79:595–604.

Smith, S. P., and H. U. Graser. 1986. Estimating variance components in a class of mixed models by restricted maximum likelihood. J. Dairy Sci. 69:1156–1165.

Splan, R. K., L. V. Cundiff, M. E. Dikeman, and L. D. Van Vleck. 2002. Estimates of parameters between direct and maternal genetic effects for weaning weight and direct genetic effects for carcass traits in crossbred cattle. J. Anim. Sci. 80:3107–3111.

Veseth, D. A., W. L. Reynolds, J. J. Urick, T. C. Nelsen, R. E. Short, and D. D. Kress. 1993. Paternal half-sib heritabilities and genetic, environmental, and phenotypic correlation estimates from randomly selected Hereford cattle. J. Anim. Sci. 71:1730–1736.

Vieselmeyer, B. A., R. J. Rasby, B. L. Gwartney, C. R. Calkins, R. A. Stock, and J. A. Gosey. 1996. Use of expected progeny differences for marbling in beef. I. Production traits. J. Anim. Sci. 74:1009–1013.

Wheeler, T. L., L. V. Cundiff, R. M. Koch, and J. D. Crouse. 1996. Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. J. Anim. Sci. 74:1023–1035.

Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2001. Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. J. Anim. Sci. 79:1209–1222.

Wilson, L. L., J. R. McCurley, J. H. Ziegler, and J. L. Watkins. 1976. Genetic parameters of live and carcass characters from progeny of Polled Hereford sires and Angus–Holstein cows. J. Anim. Sci. 43:569–576.

Wilson, D. E., R. L. Willham, S. L. Northcutt, and G. H. Rouse. 1993. Genetic parameters for carcass traits estimated from Angus field records. J. Anim. Sci. 71:2365–2370.

Woodward, B. W., E. J. Pollak, and R. L. Quaas. 1992. Parameter estimation for carcass traits including growth information of Simmental beef cattle using restricted maximum likelihood with a multiple-trait model. J. Anim. Sci. 70:1098–1109.

Wulf, D. M., J. D. Tatum, R. D. Green, J. B. Morgan, B. L. Golden, and G. C. Smith. 1996. Genetic influences on beef longissimus palatability in Charolais- and Limousin-sired steers and heifers. J. Anim. Sci. 74:2394–2405.