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Effects of age, weight, and fat slaughter end points on estimates of breed and retained heterosis effects for carcass traits¹

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ABSTRACT: The influence of different levels of adjusted fat thickness (AFT) and HCW slaughter end points (covariates) on estimates of breed and retained heterosis effects was studied for 14 carcass traits from serially slaughtered purebred and composite steers from the US Meat Animal Research Center (MARC). Contrasts among breed solutions were estimated at 0.7, 1.1, and 1.5 cm of AFT, and at 295.1, 340.5, and 385.9 kg of HCW. For constant slaughter age, contrasts were adjusted to the overall mean (432.5 d). Breed effects for Red Poll, Hereford, Limousin, Braunvieh, Pinzgauer, Gelbvieh, Simmental, Charolais, MARC I, MARC II, and MARC III were estimated as deviations from Angus. In addition, purebreds were pooled into 3 groups based on lean-to-fat ratio, and then differences were estimated among groups. Retention of combined individual and maternal heterosis was estimated for each composite. Mean retained heterosis for the 3 composites also was estimated. Breed rankings and expression of heterosis varied within and among end points. For example, Charolais had greater ($P < 0.05$) dressing percentages than Angus at the 2 largest levels of AFT and smaller ($P < 0.01$) percentages at the 2 largest levels of

HCW, whereas the 2 breeds did not differ ($P \geq 0.05$) at a constant age. The MARC III composite produced 9.7 kg more ($P < 0.01$) fat than Angus at AFT of 0.7 cm, but 7.9 kg less ($P < 0.05$) at AFT of 1.5 cm. For MARC III, the estimate of retained heterosis for HCW was significant ($P < 0.05$) at the lowest level of AFT, but at the intermediate and greatest levels estimates were nil. The pattern was the same for MARC I and MARC III for LM area. Adjustment for age resulted in near zero estimates of retained heterosis for AFT, and similarly, adjustment for HCW resulted in nil estimates of retained heterosis for LM area. For actual retail product as a percentage of HCW, the estimate of retained heterosis for MARC III was negative (-1.27% ; $P < 0.05$) at 0.7 cm but was significantly positive (2.55% ; $P < 0.05$) at 1.5 cm of AFT. Furthermore, for MARC III, estimates of heterosis for some traits (fat as a percentage of HCW as another example) also doubled in magnitude depending on different levels of AFT end point. Rational exploitation of breeds requires special attention to use of different end points and levels of those end points, mainly for fat thickness.

Key words: beef cattle, breed effect, carcass trait, heterosis, slaughter end point

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INTRODUCTION

Numerous attempts have been made in the US to characterize many breeds and breed crosses for carcass traits (Fuller, 1927; Koch et al., 1976; Wertz et al., 2002). Two studies (Koch et al., 1979; Wheeler et al.,

1996) concluded that ranking of breed groups varies for several carcass traits depending on different slaughter end points (age, carcass weight, fat thickness, fat trim percentage, and marbling score). Furthermore, if growth and/or fattening rates differ among breed groups evaluated, comparison of breeds at different levels of a physiological end point could result in reranking of breeds or changes in magnitude of differences. For carcass length, maturity score, fat thickness, and carcass weight, Baker et al. (1984) reported that estimates of regression coefficients on proportion of estimated mature size at slaughter differed among breed types in a 5-diallel system. Baker et al. did not, however, estimate heterosis effects at different values of that covariate; instead, they speculated, “the heterogeneity of slopes

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would indicate that the magnitude and sign of heterosis may change for other values of proportion of estimated mature size." From information from the germplasm utilization (GPU) project at the US Meat Animal Research Center (MARC), Koch et al. (1995) suggested that the intercepts and regressions within breeds for lean percentage on HCW or on fat thickness seemed to differ enough that a common regression equation would not be appropriate. Gregory et al. (1994) reported estimates of breed and retained heterosis effects for age-adjusted carcass traits of steers from the GPU project. The purpose of the current study was to examine steer carcass traits of several breeds and composites at different levels of fat thickness and HCW slaughter end points.

MATERIALS AND METHODS

Populations

Carcass data from purebred and composite steers included in this study were from the GPU project at the MARC and were the unselected progeny of 21 Red Poll (R), 22 Hereford (H), 23 Angus (A), 24 Limousin (L), 26 Braunvieh (B), 27 Pinzgauer (P), 27 Gelbvieh (G), 19 Simmental (S), 25 Charolais (C), 39 MARC I ($\frac{1}{4}$ L, $\frac{1}{4}$ B, $\frac{1}{4}$ C, $\frac{1}{8}$ H, $\frac{1}{8}$ A), 30 MARC II ($\frac{1}{4}$ H, $\frac{1}{4}$ A, $\frac{1}{4}$ G, $\frac{1}{4}$ S), and 24 MARC III ($\frac{1}{4}$ P, $\frac{1}{4}$ R, $\frac{1}{4}$ H, $\frac{1}{4}$ A) sires mated to cows of the same breed. These steers were born from 1988 to 1991 from dams that were 2 yr old or older. The numbers of steer progeny per breed of sire were 114, 146, 119, 142, 139, 119, 150, 127, 126, 178, 148, and 156, respectively.

Feeding and Management

From 1989 to 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 15.40% CP (DM basis). Later, steers were kept on a backgrounding diet (2.69 Mcal of ME/kg and 12.88% CP on a 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, assigned to 1 of 2 finishing diets (treatments) on a random basis, and stratified by weight. Dietary energy density was the basis for the 2 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). Feeding and management after weaning were described in detail by Gregory et al. (1994).

Slaughter and Processing Procedures

Animals were serially harvested at 4 dates each year with 20, 21, or 22 d between slaughter dates and 63 d between first and fourth slaughter dates. Initial slaugh-

ter dates were between May 21 and 26. Days from initial weight (203 d) to final weight averaged 204, 224, 245, and 267 d for the 4 slaughter groups; mean days fed was thus 235 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 harvest schedule. The final weight was a single full weight taken starting at 0700; steers had overnight access to feed and water. All steers were weighed at each slaughter date. Average weights of steers harvested at each of the first 3 slaughter dates were approximately the same as average weights of steers remaining in pens.

Steers were slaughtered in a commercial facility. Following a chill period of 24 h, data on fat thickness at the 12th rib, perirenal fat percentage, and LMA (LMA), using a grid, were obtained. The right side of each carcass was returned to 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 from a total of 1,664 animals born in those 3 yr. Carcasses were processed into wholesale cuts of round, loin, rib, chuck, plate, flank, and brisket plus shank in accordance with National Association of Meat Processors Guidelines (NAMP, 1997). Each wholesale cut was processed further by cutting into boneless steaks, roasts, lean trim, and fat trim to 8 mm, 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 i.m. 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, 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 i.m. fat plus that from the lean trim based on chemical analysis. Carcass bone included all bone from the carcass.

Carcass Traits

Fourteen carcass characteristics were included in this analysis: HCW (kg), dressing percent [DP; (HCW/final live weight) \times 100]; fat thickness measured at the 12th rib and adjusted to reflect unusual distribution of fat on other parts of the carcass (AFT, cm); LMA at

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
Kidney-pelvic-heart fat, %	1,664	2.78	0.69	24.95	0.50	5.00
Marbling score ¹	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

¹2 = practically devoid; 9 = moderately abundant.

the 12th rib (cm²); kidney, pelvic, and heart fat as a percentage of carcass weight (**KPH**); 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 HCW. Marbling was evaluated at the 12th rib interface and scored on a 10-point scale within each of 8 categories, which were converted to numeric scores (BIF, 2002). Estimation of YG (BIF, 2002) was: $YG = 2.5 + (0.98 \times \text{AFT, cm}) + (0.2 \times \text{KPH, \%}) + (0.0084 \times \text{HCW, kg}) - (0.05 \times \text{LMA, cm}^2)$. Percentage of total retail product trimmed to zero surface fat was predicted (Dikeman et al., 1998) as $PRP = 65.69 - (3.91 \times \text{AFT, cm}) - (1.29 \times \text{KPH, \%}) - (0.029 \times \text{HCW, kg}) + (0.19 \times \text{LMA, cm}^2)$.

End Points

Carcass traits adjusted to different end points, such as those (age, weight, and fat thickness) used in the current study, are biologically different. Thus, they should be regarded as distinct although possibly correlated traits. At a common age end point, variation in 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 HCW focuses on variation in carcass composition. At a constant HCW, RPP, FP, and BP are perfectly correlated with RPW, FW, and BNW, respectively, and reflect variation in carcass composition independent of HCW. Dinkel et al. (1965) advanced the argument that use of carcass weight as a covariate was more appropriate than use of percentages or ratios (e.g., RPW/HCW) because ratios were forced to be negatively correlated with their denominator. Adjustment to a common AFT end point is appropriate if the objective is to select for a trait independent of AFT. For example, selection for marbling adjusted for AFT would be expected to improve marbling with little or no change in AFT. Simi-

larly, response to selection for weight (or percentage) of retail product adjusted for AFT would be expected to result from changes in proportion of muscle and fat deposits at sites other than those associated with AFT.

Statistical Analyses

Preliminary Analyses. Simple descriptive statistics are in Table 1. Number of records for the carcass traits ranged from 1,599 to 1,664. Preliminary statistical analyses for each trait by end point were performed to determine fixed effects that were important sources of variation using the Mixed procedure of SAS (SAS Inst., Inc., Cary, NC). Fixed effects in the model were breed group, birth year, dam age, energy level of treatment, all 2-way interactions, linear effect of number of days on feed, and linear effect of end point (slaughter age, AFT, or HCW) nested within breed group. Random effects in the model, other than the error term, were unrelated sires nested within breed. Sequential analyses were run by removing from the full model interactions and covariates that were not significant. An interaction effect remained in the model if significant ($P < 0.05$) for at least one carcass trait within end point. The effects of linear slaughter age nested within breed were not different in preliminary analyses; therefore, only the overall 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 partially have caused failure to detect differences in slaughter age within breeds. The final model included all main effects, significant interactions, a covariate for number of days on feed, and a second covariate, either AFT or HCW (both nested within breed), or slaughter age. Days on feed and slaughter age were included simultaneously in the age-constant analysis to be able to compare with field data analyses available in the literature and 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 \times energy level, breed group \times birth year, energy level \times birth year, and dam age \times birth year. With HCW nested within breed group, the model included the same interactions as for carcass traits adjusted to a common age, except for dam age \times birth year. The model for carcass traits adjusted to a common AFT nested within breed group included the same interactions as for carcass traits adjusted to common age and also breed group \times dam age.

Estimation of Breed Effects and Retained Heterosis. Linear contrasts among breed solutions for each carcass trait within end point were estimated using single-trait animal models and estimates of (co)variances obtained by derivative-free REML (Boldman et al., 1995). The animal model (with additive relationships among all animals of a breed at MARC) used to estimate (co)variances for each carcass trait included all of the fixed effects mentioned earlier as well as additive genetic effects of the animals and total maternal effects of dams of the animals as random effects. The effect of the dam was used to account jointly for total genetic and permanent environmental effects of the dam as an uncorrelated random effect because not enough data were available to separate components of variance due to genetic and permanent environmental maternal effects. To estimate breed effects and retained heterosis, all interactions involving the breed group effect were excluded from the mixed model and (co)variances previously estimated were used. More information on estimation of (co)variances can be found in Ríos-Utrera et al. (2005). When AFT was held constant, breed comparisons were at 0.7, 1.1, and 1.5 cm, and when HCW was held constant, comparisons were at 295.1, 340.5, and 385.9 kg. For running any constant AFT or constant HCW analysis in MTDFREML, every record ($n = 1,663$; Table 1) associated with the AFT or HCW covariate was deviated from each of the 3 values chosen as the end point. For example, if the value for the AFT covariate was 2.0 cm and the comparison was at 0.7 cm end point, the new value for that covariate was 1.3 cm, or if the value for the HCW covariate was 350 kg and the comparison was at 340.5 kg end point, the new value for the HCW covariate was 9.5 kg. The same procedure was applied for levels for each end point. In addition, the MTDFREML program was modified to prevent the program from deviating each observation from the mean value of the respective covariate. Use of different levels of an end point would allow detection of changes in sign and/or size of estimates of breed and retained heterosis effects for carcass traits due to differences in type of association (positive or negative) between dependent variables and the covariate, and/or differences in rates of growth and fattening in the breeds studied. Age-constant differences were adjusted to the overall mean (432.5 d). In all cases, breed effects were estimated as a deviation from the A breed effect because that breed has been a conventional standard for carcass traits in the United States.

Eight different types of linear contrasts of breed solutions were tested ($P < 0.01$ and $P < 0.05$) for each carcass trait within end point: 1) each of 11 breed group solutions minus solution for breed A; 2) mean solution for B, S, G, and P minus mean solution for R, H, and A; 3) mean solution for L and C minus mean solution for R, H, and A; 4) mean solution for L and C minus mean solution for B, S, G, and P; 5) solution for MARC I minus mean solution for its contributing purebreds; 6) solution for MARC II minus mean solution for its contributing purebreds; 7) solution for MARC III minus mean solution for its contributing purebreds; and 8) mean solution for MARC I, MARC II, and MARC III minus mean solution for their 9 contributing purebreds. The rationale for linear contrasts 2, 3, and 4 was based on relative differences in lean-to-fat ratio (Martin et al., 1992). Contrasts 5, 6, and 7 were computed to estimate retained heterosis (combined individual and maternal heterosis) for F_3 generation progeny of MARC I, MARC II, and MARC III composite populations, respectively. Mean heterosis effects for the 3 composite breeds were estimated with contrast 8. Retained heterosis was estimated from the composite breed solution minus the contributing purebred solutions weighted by the contributions (1/4 or 1/8) of each purebred to the composite (Gregory et al., 1994). Contrasts for breed solutions are described in Tables 2 through 15. In addition, for each carcass trait, 12 contrasts were evaluated corresponding to either the AFT or HCW covariate to estimate the regression coefficient for each breed group, and one contrast was evaluated corresponding to the age covariate to estimate the overall linear regression coefficient (Table 16).

RESULTS AND DISCUSSION

Hot Carcass Weight

Breed Effects. Absolute differences from breed A and other specific contrasts in HCW were generally greater at every constant AFT end point than at 432.5-d constant age end point (Table 2). When steers reached 0.7 cm of AFT, most breeds had heavier ($P < 0.01$ or $P < 0.05$) carcasses than A. The 2 exceptions were R and H, which had HCW similar to those of A. However, when steers reached 1.1 and 1.5 cm of AFT or 432.5 d of age, only B, S, C, G, MARC I, and MARC II had heavier ($P < 0.01$) carcasses than A. Red Poll, H, L, P, and MARC III resembled A in HCW. Previous constant age research also showed that S and C carcasses (Peacock et al., 1982; Cross et al., 1984; DeRouen et al., 1992) were heavier than A carcasses. Vanderwert et al. (1985) reported L males had heavier carcasses than A males slaughtered when they reached 0.76 cm of fat thickness, in agreement with the present comparison. As the AFT end point increased, significant ($P < 0.01$ or $P < 0.05$) differences for MARC II tended to decrease across end points, but for B, S, C, G, and MARC I, differences tended to increase, mainly for C (from 62

Table 2. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for HCW (kg) adjusted to different fat thickness and slaughter age end points¹

Contrast ²	Fat thickness constant, cm			Age constant, d
	0.7	1.1	1.5	432.5
Breed effect³				
R	9.04 \pm 9.50	5.12 \pm 9.26	1.20 \pm 10.31	-1.54 \pm 7.64
B	39.24 \pm 9.14**	45.04 \pm 10.31**	50.85 \pm 13.00**	20.71 \pm 7.12**
H	-12.32 \pm 9.56	-14.32 \pm 8.88	-16.31 \pm 9.22	-10.18 \pm 7.51
A	0.00	0.00	0.00	0.00
S	57.66 \pm 9.15**	67.76 \pm 10.58**	77.85 \pm 13.43**	33.63 \pm 7.00**
L	22.58 \pm 9.03*	18.86 \pm 9.66	15.13 \pm 11.51	12.93 \pm 7.08
C	62.43 \pm 9.77**	77.11 \pm 12.02**	91.79 \pm 15.81**	32.72 \pm 7.27**
G	51.43 \pm 9.36**	62.08 \pm 11.38**	72.73 \pm 14.79**	22.58 \pm 6.86**
P	28.56 \pm 9.55**	22.39 \pm 11.46	16.23 \pm 15.06	14.46 \pm 7.39
MARC I	40.84 \pm 8.01**	44.08 \pm 8.31**	47.32 \pm 10.11**	27.96 \pm 6.35**
MARC II	36.01 \pm 8.18**	33.40 \pm 7.91**	30.78 \pm 9.10**	29.25 \pm 6.55**
MARC III	24.65 \pm 8.40**	13.84 \pm 7.89	3.03 \pm 8.10	12.63 \pm 6.72
(B,S,G,P) - (A,H,R) ⁴	45.32 \pm 5.17**	52.39 \pm 6.03**	59.45 \pm 7.65**	26.75 \pm 4.03**
(L,C) - (A,H,R) ⁵	43.59 \pm 6.19**	51.05 \pm 7.54**	58.50 \pm 9.71**	26.73 \pm 4.80**
(L,C) - (B,S,G,P) ⁶	-1.72 \pm 5.74	-1.34 \pm 7.92	-0.95 \pm 10.80	-0.02 \pm 4.40
Heterosis for				
MARC I ⁷	11.31 \pm 5.49	10.62 \pm 7.05	9.92 \pm 9.59	12.64 \pm 4.53*
MARC II ⁸	11.82 \pm 5.92	4.51 \pm 6.60	-2.78 \pm 8.40	17.74 \pm 4.90**
MARC III ⁹	18.33 \pm 6.25**	10.54 \pm 6.44	2.76 \pm 7.02	11.94 \pm 5.23*
Mean heterosis ¹⁰	13.82 \pm 3.75**	8.56 \pm 4.14	3.30 \pm 5.09	14.11 \pm 3.09**

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, US Meat Animal Research Center (MARC) I = ($\frac{1}{4}$ A + $\frac{1}{8}$ H + $\frac{1}{4}$ B + $\frac{1}{4}$ L + $\frac{1}{4}$ C), MARC II = $\frac{1}{4}$ (A + H + S + G), and MARC III = $\frac{1}{4}$ (A + H + R + P).

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}$ (B + S + G + P) - $\frac{1}{3}$ (A + H + R).

⁵Contrast = $\frac{1}{2}$ (L + C) - $\frac{1}{3}$ (A + H + R).

⁶Contrast = $\frac{1}{2}$ (L + C) - $\frac{1}{4}$ (B + S + G + P).

⁷Contrast = MARC I - ($\frac{1}{8}$ A + $\frac{1}{8}$ H + $\frac{1}{4}$ B + $\frac{1}{4}$ L + $\frac{1}{4}$ C).

⁸Contrast = MARC II - $\frac{1}{4}$ (A + H + S + G).

⁹Contrast = MARC III - $\frac{1}{4}$ (A + H + R + P).

¹⁰Contrast = $\frac{1}{3}$ (MARC I + MARC II + MARC III) - ($\frac{5}{24}$ A + $\frac{5}{24}$ H + $\frac{1}{12}$ R + $\frac{1}{12}$ B + $\frac{1}{12}$ S + $\frac{1}{12}$ G + $\frac{1}{12}$ P + $\frac{1}{12}$ L + $\frac{1}{12}$ C).

to 92 kg). The estimate of the regression coefficient for C was greater than the estimate for each of the other breeds, indicating a faster growth rate for C per cm of fat (Table 16). Medium- (B, S, G, and P) and high-lean-to-fat-ratio breeds (L and C) had heavier ($P < 0.01$) carcasses than low-lean-to-fat-ratio breeds (A, H, and R) when steers attained each constant-AFT end point or a constant-age end point of 432.5 d. Similarly, Morris et al. (1990), from constant-fat and constant-age analyses, found C- and L-sired males had heavier carcasses than A- and H-sired males in New Zealand. At equal AFT or equal age end points, medium- and high-lean-to-fat-ratio breeds were comparable to each other. For Canadian data, Fiss and Wilton (1993) reported C- and S-sired calves had similar HCW when slaughtered at common fat thickness of 0.7 cm.

Retained Heterosis. For MARC III and for the mean of the 3 composite populations, positive estimates of heterosis were significant ($P < 0.01$) at the lowest level of fatness (0.7 cm), but not for 1.1 or 1.5 cm. Hence, an increase in AFT end point resulted in a reduction in estimates of retained heterosis for HCW. Age-constant heterotic effects were significant (heavier carcass) for MARC I ($P < 0.05$), MARC II ($P < 0.01$), and MARC III

($P < 0.05$), and for their mean ($P < 0.01$). Thus, expression of heterosis varied with level of fatness and choice of end point. Estimates of age-adjusted heterosis were generally greater than estimates of fat-adjusted heterosis.

Dressing Percent

Breed Effects. In most cases, absolute differences relative to A in DP tended to be greater at HCW end points than at AFT or age (Table 3) end points. Charolais had greater ($P < 0.05$) DP than A at the 2 largest AFT levels, smaller ($P < 0.01$) DP at the 2 largest HCW levels, and similar DP at 0.7 cm of AFT, at 295.1 kg of HCW, and at 432.5 d of age. The estimate of the linear regression coefficient on AFT also was greater for C than for A ($2.93 \pm 0.81\%$ vs. $1.25 \pm 0.41\%$ per cm), but the estimate on HCW was smaller ($0.023 \pm 0.004\%$ vs. $0.033 \pm 0.005\%$ per kg; Table 16). At the constant AFT end points, L had significantly greater DP than A, which, on the whole, had significantly greater DP than R, B, and H. Angus also had greater DP than MARC II ($P < 0.05$) and MARC III ($P < 0.01$) at 1.5 cm of AFT. The superiority of L over A agrees with Vanderwert et

Table 3. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for dressing percent adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	1.1	295.1	340.5	385.9	432.5	
Breed effect³									
R	-0.80 \pm 0.49	-1.34 \pm 0.47*	-1.89 \pm 0.57**	-0.97 \pm 0.50	-1.68 \pm 0.50**	-2.39 \pm 0.66**	-1.40 \pm 0.46**		
B	-1.30 \pm 0.49*	-1.93 \pm 0.59**	-2.56 \pm 0.80**	-2.14 \pm 0.50**	-2.43 \pm 0.45**	-2.71 \pm 0.57**	-1.80 \pm 0.43**		
H	-1.03 \pm 0.50	-1.10 \pm 0.44*	-1.16 \pm 0.47*	-0.61 \pm 0.48	-0.75 \pm 0.51	-0.89 \pm 0.67	-1.11 \pm 0.45*		
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
S	-0.78 \pm 0.50	-0.95 \pm 0.62	-1.12 \pm 0.84	-2.30 \pm 0.50**	-2.54 \pm 0.45**	-2.79 \pm 0.55**	-1.57 \pm 0.42**		
L	2.68 \pm 0.49**	2.18 \pm 0.54**	1.68 \pm 0.69*	2.15 \pm 0.48**	1.87 \pm 0.45**	1.58 \pm 0.59*	2.17 \pm 0.43**		
C	0.90 \pm 0.54	1.57 \pm 0.72*	2.24 \pm 1.01*	-1.01 \pm 0.52	-1.47 \pm 0.47**	-1.94 \pm 0.56**	-0.59 \pm 0.44		
G	-0.53 \pm 0.52	-0.53 \pm 0.68	-0.54 \pm 0.94	-1.61 \pm 0.48**	-2.28 \pm 0.44**	-2.96 \pm 0.55**	-1.54 \pm 0.42**		
P	-0.98 \pm 0.52	-0.97 \pm 0.68	-0.97 \pm 0.95	-1.66 \pm 0.51**	-2.42 \pm 0.47**	-3.19 \pm 0.60**	-1.87 \pm 0.45**		
MARC I	0.52 \pm 0.43	0.40 \pm 0.45	0.28 \pm 0.60	-0.31 \pm 0.45	-0.94 \pm 0.41*	-1.58 \pm 0.52**	-0.15 \pm 0.39		
MARC II	-0.31 \pm 0.44	-0.69 \pm 0.41	-1.08 \pm 0.51*	-1.54 \pm 0.46**	-1.71 \pm 0.42**	-1.88 \pm 0.53**	-0.84 \pm 0.40*		
MARC III	-0.23 \pm 0.45	-0.73 \pm 0.40	-1.22 \pm 0.42**	-0.89 \pm 0.45	-1.30 \pm 0.43**	-1.70 \pm 0.56**	-0.82 \pm 0.41		
(B,S,G,P) - (A,H,R) ⁴	-0.29 \pm 0.27	-0.28 \pm 0.35	-0.28 \pm 0.47	-1.40 \pm 0.27**	-1.61 \pm 0.26**	-1.82 \pm 0.33**	-0.86 \pm 0.24**		
(L,C) - (A,H,R) ⁵	2.40 \pm 0.33**	2.69 \pm 0.44**	2.98 \pm 0.61**	1.10 \pm 0.33**	1.01 \pm 0.31**	0.91 \pm 0.38*	1.62 \pm 0.29**		
(L,C) - (B,S,G,P) ⁶	2.68 \pm 0.31**	2.97 \pm 0.49**	3.25 \pm 0.70**	2.50 \pm 0.32**	2.62 \pm 0.28**	2.73 \pm 0.32**	2.48 \pm 0.27**		
Heterosis for									
MARC I ⁷	0.08 \pm 0.29	0.09 \pm 0.42	0.09 \pm 0.60	0.02 \pm 0.35	-0.34 \pm 0.29	-0.70 \pm 0.33*	0.05 \pm 0.28		
MARC II ⁸	0.27 \pm 0.31	-0.05 \pm 0.37	-0.37 \pm 0.51	-0.41 \pm 0.37	-0.32 \pm 0.31	-0.22 \pm 0.37	0.22 \pm 0.30		
MARC III ⁹	0.47 \pm 0.32	0.12 \pm 0.34	-0.22 \pm 0.39	-0.09 \pm 0.36	-0.09 \pm 0.33	-0.08 \pm 0.42	0.27 \pm 0.32		
Mean heterosis ¹⁰	0.27 \pm 0.19	0.05 \pm 0.23	-0.17 \pm 0.30	-0.16 \pm 0.22	-0.25 \pm 0.20	-0.33 \pm 0.24	0.18 \pm 0.19		

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{2}(B + S + G + P) - \frac{1}{4}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 4. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for adjusted fat thickness (cm) adjusted to different carcass weight and slaughter age end points¹

Contrast ²	Carcass weight constant, kg			Age constant, d
	295.1	340.5	385.9	432.5
Breed effect ³				
R	-0.36 \pm 0.07**	-0.46 \pm 0.07**	-0.56 \pm 0.10**	-0.42 \pm 0.07**
B	-0.71 \pm 0.07**	-0.88 \pm 0.07**	-1.06 \pm 0.08**	-0.75 \pm 0.07**
H	0.03 \pm 0.07	0.09 \pm 0.07	0.16 \pm 0.10	-0.04 \pm 0.07
A	0.00	0.00	0.00	0.00
S	-0.78 \pm 0.07**	-0.96 \pm 0.07**	-1.13 \pm 0.08**	-0.79 \pm 0.07**
L	-0.73 \pm 0.07**	-0.91 \pm 0.07**	-1.08 \pm 0.09**	-0.79 \pm 0.07**
C	-0.75 \pm 0.08**	-0.96 \pm 0.07**	-1.18 \pm 0.08**	-0.81 \pm 0.07**
G	-0.78 \pm 0.07**	-0.98 \pm 0.06**	-1.18 \pm 0.08**	-0.84 \pm 0.06**
P	-0.61 \pm 0.07**	-0.88 \pm 0.07**	-1.14 \pm 0.09**	-0.75 \pm 0.07**
MARC I	-0.58 \pm 0.07**	-0.76 \pm 0.06**	-0.93 \pm 0.08**	-0.60 \pm 0.06**
MARC II	-0.36 \pm 0.07**	-0.54 \pm 0.06**	-0.72 \pm 0.08**	-0.38 \pm 0.06**
MARC III	-0.27 \pm 0.07**	-0.37 \pm 0.06**	-0.48 \pm 0.08**	-0.27 \pm 0.06**
(B,S,G,P) - (A,H,R) ⁴	-0.61 \pm 0.04**	-0.80 \pm 0.04**	-0.99 \pm 0.05**	-0.63 \pm 0.04**
(L,C) - (A,H,R) ⁵	-0.63 \pm 0.05**	-0.81 \pm 0.04**	-0.99 \pm 0.06**	-0.65 \pm 0.04**
(L,C) - (B,S,G,P) ⁶	-0.02 \pm 0.05	-0.01 \pm 0.04	-0.00 \pm 0.05	-0.02 \pm 0.04
Heterosis for				
MARC I ⁷	-0.04 \pm 0.05	-0.08 \pm 0.04	-0.12 \pm 0.05*	-0.01 \pm 0.04
MARC II ⁸	0.02 \pm 0.05	-0.08 \pm 0.05	-0.18 \pm 0.05**	0.03 \pm 0.05
MARC III ⁹	-0.03 \pm 0.05	-0.06 \pm 0.05	-0.10 \pm 0.06	0.03 \pm 0.05
Mean heterosis ¹⁰	-0.02 \pm 0.03	-0.07 \pm 0.03*	-0.13 \pm 0.04**	0.02 \pm 0.03

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = ($\frac{1}{8}$ A + $\frac{1}{8}$ H + $\frac{1}{4}$ B + $\frac{1}{4}$ L + $\frac{1}{4}$ C), MARC II = $\frac{1}{4}$ (A + H + S + G), and MARC III = $\frac{1}{4}$ (A + H + R + P).

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}$ (B + S + G + P) - $\frac{1}{8}$ (A + H + R).

⁵Contrast = $\frac{1}{2}$ (L + C) - $\frac{1}{8}$ (A + H + R).

⁶Contrast = $\frac{1}{2}$ (L + C) - $\frac{1}{4}$ (B + S + G + P).

⁷Contrast = MARC I - ($\frac{1}{8}$ A + $\frac{1}{8}$ H + $\frac{1}{4}$ B + $\frac{1}{4}$ L + $\frac{1}{4}$ C).

⁸Contrast = MARC II - $\frac{1}{4}$ (A + H + S + G).

⁹Contrast = MARC III - $\frac{1}{4}$ (A + H + R + P).

¹⁰Contrast = $\frac{1}{8}$ (MARC I + MARC II + MARC III) - ($\frac{5}{24}$ A + $\frac{5}{24}$ H + $\frac{1}{12}$ R + $\frac{1}{12}$ B + $\frac{1}{12}$ S + $\frac{1}{12}$ G + $\frac{1}{12}$ L + $\frac{1}{12}$ C).

al. (1985) based on a fat thickness end point. Angus DP adjusted to different constants for HCW was generally greater ($P < 0.01$ or $P < 0.05$) than DP of all other breeds, except L, which had significantly greater DP, and H, which had similar measures of DP. On an age-constant basis, A had significantly greater DP than any of the other breeds, except for L, which was superior ($P < 0.01$), and MARC I and MARC III composites, which were similar to A. Absolute differences from A for L tended to decrease, but for R, B, H, and C tended to increase, with larger levels for AFT and HCW end points. Breeds with medium-lean-to-fat ratios had smaller ($P < 0.01$) DP than breeds with low-lean-to-fat ratios at each constant HCW end point and at the constant age end point, whereas the 2 groups were similar at all AFT end points. High-lean-to-fat-ratio breeds had significantly greater DP than low- and medium-lean-to-fat-ratio breeds at all end points. Results from a New Zealand experiment (Morris et al., 1990) showed C- and L-sired offspring had greater age-constant DP than A- and H-sired offspring. With a terminal cross system, Rahnefeld et al. (1983) found that C and L progeny had greater DP than S progeny, which also agrees with present results. At constant age, Comerford

et al. (1988) observed that progeny of L sires had greater DP than progeny of S and H sires.

Retained Heterosis. Estimates of effects of retained heterosis were basically not significant for DP. The MARC I composite was the only breed to display heterosis ($P < 0.05$), and that occurred only at the largest HCW end point.

Adjusted Fat Thickness

Breed Effects. Significant differences from A for AFT tended to increase with increased HCW (Table 4). At the age end point and at every HCW end point, A steers had more ($P < 0.01$) cm of s.c. fat at the 12th rib than steers from the other breeds, except Hereford, which was similar to A. In addition, estimated regression coefficients on HCW for A and H steers (Table 16) suggest that they fattened more rapidly than steers of the other breeds. More backfat in purebred or crossbred progeny of A sires than in purebred or crossbred progeny of sires of some of the other breeds evaluated here has also been reported from constant fat (Adams et al., 1973; Vanderwert et al., 1985), constant weight (Urlick et al., 1974), and constant age studies (Peacock et al., 1982;

Table 5. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for LM area (cm^2) adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d	
	0.7	1.1	1.5	1.5	295.1	340.5	385.9	432.5		
Breed effect ³										
R	0.36 \pm 2.30	0.13 \pm 2.22	-0.10 \pm 2.57	-0.10 \pm 2.57	-0.50 \pm 2.05	1.64 \pm 2.03	3.77 \pm 2.67	3.77 \pm 2.67	0.30 \pm 2.09	
B	15.80 \pm 2.26**	15.84 \pm 2.63**	15.88 \pm 3.46**	15.88 \pm 3.46**	13.50 \pm 2.02**	14.34 \pm 1.85**	15.18 \pm 2.32**	15.18 \pm 2.32**	15.93 \pm 1.95**	
H	-1.08 \pm 2.33	-1.17 \pm 2.09	-1.26 \pm 2.21	-1.26 \pm 2.21	-0.01 \pm 1.97	0.65 \pm 2.07	1.30 \pm 2.75	1.30 \pm 2.75	-0.79 \pm 2.05	
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
S	13.23 \pm 2.29**	13.77 \pm 2.75**	14.30 \pm 3.63**	14.30 \pm 3.63**	9.04 \pm 2.03**	9.97 \pm 1.83**	10.89 \pm 2.25**	10.89 \pm 2.25**	12.96 \pm 1.92**	
L	16.70 \pm 2.24**	14.35 \pm 2.43**	12.00 \pm 3.01**	12.00 \pm 3.01**	15.89 \pm 1.95**	18.79 \pm 1.85**	21.70 \pm 2.39**	21.70 \pm 2.39**	18.89 \pm 1.94**	
C	11.00 \pm 2.45**	9.25 \pm 3.17**	7.51 \pm 4.32	7.51 \pm 4.32	9.18 \pm 2.12**	9.52 \pm 1.90**	9.86 \pm 2.30**	9.86 \pm 2.30**	12.32 \pm 1.99**	
G	14.81 \pm 2.36**	14.92 \pm 2.99**	15.03 \pm 4.03**	15.03 \pm 4.03**	11.03 \pm 1.94**	12.74 \pm 1.79**	14.45 \pm 2.25**	14.45 \pm 2.25**	14.68 \pm 1.88**	
P	10.45 \pm 2.39**	10.73 \pm 3.01**	11.02 \pm 4.11**	11.02 \pm 4.11**	9.07 \pm 2.03**	9.47 \pm 1.92**	9.86 \pm 2.41**	9.86 \pm 2.41**	10.19 \pm 2.03**	
MARC I	13.99 \pm 1.98**	11.81 \pm 2.07**	9.64 \pm 2.64**	9.64 \pm 2.64**	11.48 \pm 1.84**	12.21 \pm 1.67**	12.93 \pm 2.12**	12.93 \pm 2.12**	14.68 \pm 1.74**	
MARC II	8.92 \pm 2.02**	8.39 \pm 1.92**	7.86 \pm 2.30**	7.86 \pm 2.30**	6.26 \pm 1.90**	6.55 \pm 1.72**	6.84 \pm 2.18**	6.84 \pm 2.18**	9.00 \pm 1.80**	
MARC III	5.75 \pm 2.06*	5.58 \pm 1.88**	5.42 \pm 1.95*	5.42 \pm 1.95*	3.84 \pm 1.85*	4.67 \pm 1.76*	5.50 \pm 2.26*	5.50 \pm 2.26*	5.53 \pm 1.85**	
(B,S,G,P) - (A,H,R) ⁴	13.81 \pm 1.27**	14.16 \pm 1.55**	14.51 \pm 2.05**	14.51 \pm 2.05**	10.83 \pm 1.11**	10.87 \pm 1.07**	10.91 \pm 1.36**	10.91 \pm 1.36**	13.60 \pm 1.10**	
(L,C) - (A,H,R) ⁵	14.09 \pm 1.52**	12.15 \pm 1.96**	10.20 \pm 2.63**	10.20 \pm 2.63**	12.70 \pm 1.36**	13.40 \pm 1.26**	14.09 \pm 1.57**	14.09 \pm 1.57**	15.77 \pm 1.31**	
(L,C) - (B,S,G,P) ⁶	0.28 \pm 1.43	-2.01 \pm 2.12	-4.30 \pm 2.98	-4.30 \pm 2.98	1.87 \pm 1.30	2.53 \pm 1.12*	3.18 \pm 1.30*	3.18 \pm 1.30*	2.16 \pm 1.20	
Heterosis for										
MARC I ⁷	3.24 \pm 1.33*	2.09 \pm 1.83	0.95 \pm 2.61	0.95 \pm 2.61	1.84 \pm 1.42	1.46 \pm 1.17	1.08 \pm 1.35	1.08 \pm 1.35	2.99 \pm 1.24*	
MARC II ⁸	2.18 \pm 1.44	1.51 \pm 1.66	0.84 \pm 2.22	0.84 \pm 2.22	1.25 \pm 1.50	0.71 \pm 1.27	0.18 \pm 1.50	0.18 \pm 1.50	2.29 \pm 1.34	
MARC III ⁹	3.32 \pm 1.50*	3.16 \pm 1.56	3.00 \pm 1.75	3.00 \pm 1.75	1.70 \pm 1.45	1.73 \pm 1.36	1.77 \pm 1.69	1.77 \pm 1.69	3.11 \pm 1.43*	
Mean heterosis ¹⁰	2.91 \pm 0.91**	2.25 \pm 1.03*	1.60 \pm 1.33	1.60 \pm 1.33	1.60 \pm 0.90	1.30 \pm 0.81	1.01 \pm 0.99	1.01 \pm 0.99	2.79 \pm 0.85**	

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{4}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{3}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 6. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for kidney, pelvic, and heart fat percentage adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm			Carcass weight constant, kg			Age constant, d
	0.7	1.1	1.5	295.1	340.5	385.9	
Breed effect ³							
R	0.74 \pm 0.16**	0.67 \pm 0.16**	0.59 \pm 0.18**	0.60 \pm 0.16**	0.64 \pm 0.16**	0.69 \pm 0.21**	0.62 \pm 0.15**
B	0.31 \pm 0.16	0.36 \pm 0.19	0.41 \pm 0.24	0.02 \pm 0.16	-0.03 \pm 0.14	-0.08 \pm 0.18	0.09 \pm 0.14
H	-0.24 \pm 0.16	-0.27 \pm 0.15	-0.29 \pm 0.16	-0.22 \pm 0.15	-0.20 \pm 0.16	-0.18 \pm 0.22	-0.25 \pm 0.15
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S	0.10 \pm 0.16	0.20 \pm 0.19	0.29 \pm 0.25	-0.43 \pm 0.16*	-0.36 \pm 0.14*	-0.28 \pm 0.18	-0.16 \pm 0.14
L	-0.03 \pm 0.16	0.03 \pm 0.17	0.09 \pm 0.21	-0.30 \pm 0.15	-0.34 \pm 0.14*	-0.37 \pm 0.19	-0.25 \pm 0.14
C	0.53 \pm 0.17**	0.75 \pm 0.22**	0.97 \pm 0.30**	0.15 \pm 0.16	0.01 \pm 0.15	-0.12 \pm 0.18	0.14 \pm 0.14
G	0.39 \pm 0.17*	0.54 \pm 0.21*	0.70 \pm 0.28*	-0.10 \pm 0.15	-0.10 \pm 0.14	-0.09 \pm 0.18	0.02 \pm 0.14
P	0.40 \pm 0.17*	0.56 \pm 0.21*	0.72 \pm 0.29*	0.12 \pm 0.16	0.02 \pm 0.15	-0.08 \pm 0.19	0.10 \pm 0.15
MARC I	0.45 \pm 0.14**	0.62 \pm 0.15**	0.78 \pm 0.19**	0.16 \pm 0.14	0.10 \pm 0.13	0.04 \pm 0.17	0.25 \pm 0.13
MARC II	0.28 \pm 0.14	0.42 \pm 0.14**	0.56 \pm 0.16**	0.15 \pm 0.15	0.07 \pm 0.13	0.00 \pm 0.17	0.22 \pm 0.13
MARC III	0.53 \pm 0.15**	0.42 \pm 0.13**	0.30 \pm 0.14*	0.31 \pm 0.14*	0.35 \pm 0.14*	0.39 \pm 0.18*	0.40 \pm 0.13**
(B,S,G,P) - (A,H,R) ⁴	0.13 \pm 0.09	0.28 \pm 0.11*	0.43 \pm 0.14**	-0.22 \pm 0.09*	-0.26 \pm 0.08**	-0.30 \pm 0.11*	-0.11 \pm 0.08
(L,C) - (A,H,R) ⁵	0.09 \pm 0.11	0.26 \pm 0.14	0.43 \pm 0.18*	-0.20 \pm 0.10	-0.31 \pm 0.10**	-0.42 \pm 0.12**	-0.18 \pm 0.10
(L,C) - (B,S,G,P) ⁶	-0.05 \pm 0.10	-0.02 \pm 0.15	0.00 \pm 0.21	0.02 \pm 0.10	-0.05 \pm 0.09	-0.12 \pm 0.10	-0.07 \pm 0.09
Heterosis for							
MARC I ⁷	0.27 \pm 0.09**	0.36 \pm 0.13*	0.45 \pm 0.18*	0.22 \pm 0.11	0.21 \pm 0.09*	0.21 \pm 0.10	0.29 \pm 0.09**
MARC II ⁸	0.22 \pm 0.10*	0.30 \pm 0.12*	0.38 \pm 0.16*	0.34 \pm 0.12**	0.24 \pm 0.10*	0.14 \pm 0.12	0.32 \pm 0.10**
MARC III ⁹	0.31 \pm 0.11**	0.18 \pm 0.11	0.04 \pm 0.12	0.18 \pm 0.11	0.23 \pm 0.10*	0.28 \pm 0.13*	0.28 \pm 0.10*
Mean heterosis ¹⁰	0.27 \pm 0.06**	0.28 \pm 0.07**	0.29 \pm 0.09**	0.25 \pm 0.07**	0.23 \pm 0.06**	0.21 \pm 0.08*	0.30 \pm 0.06**

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.³Contrast = respective breed solution vs. A solution.⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{4}(A + H + R)$.⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 7. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for marbling score¹ adjusted to different fat thickness, carcass weight and slaughter age end points²

Contrast ³	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d	
	0.7	1.1	1.5	295.1	340.5	385.9	432.5			
Breed effect ⁴										
R	-0.01 \pm 0.17	-0.03 \pm 0.17	-0.04 \pm 0.19	-0.10 \pm 0.19	-0.16 \pm 0.18	-0.21 \pm 0.22	-0.13 \pm 0.18			
B	-0.29 \pm 0.17	-0.16 \pm 0.19	-0.03 \pm 0.25	-0.68 \pm 0.18**	-0.65 \pm 0.17**	-0.63 \pm 0.20**	-0.57 \pm 0.16**			
H	-0.15 \pm 0.18	-0.19 \pm 0.16	-0.23 \pm 0.17	-0.14 \pm 0.18	-0.20 \pm 0.18	-0.25 \pm 0.23	-0.18 \pm 0.17			
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
S	-0.23 \pm 0.17	-0.00 \pm 0.20	0.23 \pm 0.26	-0.92 \pm 0.18**	-0.77 \pm 0.16**	-0.62 \pm 0.19**	-0.61 \pm 0.16**			
L	-0.79 \pm 0.17**	-0.76 \pm 0.18**	-0.73 \pm 0.22**	-1.01 \pm 0.17**	-1.09 \pm 0.17**	-1.18 \pm 0.20**	-1.01 \pm 0.16**			
C	-0.24 \pm 0.18	0.06 \pm 0.23	0.36 \pm 0.30	-0.70 \pm 0.19**	-0.78 \pm 0.17**	-0.87 \pm 0.20**	-0.70 \pm 0.17**			
G	-0.57 \pm 0.17**	-0.52 \pm 0.21*	-0.47 \pm 0.28	-0.91 \pm 0.17**	-0.92 \pm 0.16**	-0.93 \pm 0.19**	-0.85 \pm 0.16**			
P	0.14 \pm 0.18	0.47 \pm 0.22*	0.80 \pm 0.29*	-0.29 \pm 0.18	-0.32 \pm 0.17	-0.34 \pm 0.20	-0.26 \pm 0.17			
MARC I	-0.45 \pm 0.15**	-0.38 \pm 0.15*	-0.31 \pm 0.19	-0.76 \pm 0.16**	-0.74 \pm 0.15**	-0.72 \pm 0.18**	-0.64 \pm 0.15**			
MARC II	-0.17 \pm 0.15	-0.11 \pm 0.14	-0.05 \pm 0.17	-0.20 \pm 0.16	-0.34 \pm 0.15*	-0.49 \pm 0.18*	-0.25 \pm 0.15			
MARC III	0.07 \pm 0.15	-0.04 \pm 0.14	-0.16 \pm 0.15	-0.11 \pm 0.16	-0.11 \pm 0.16	-0.12 \pm 0.19	-0.07 \pm 0.15			
(B,S,G,P) - (A,H,R) ⁵	-0.18 \pm 0.09	0.02 \pm 0.11	0.22 \pm 0.14	-0.62 \pm 0.10**	-0.55 \pm 0.10**	-0.47 \pm 0.11**	-0.47 \pm 0.09**			
(L,C) - (A,H,R) ⁶	-0.46 \pm 0.11**	-0.28 \pm 0.14	-0.09 \pm 0.18	-0.78 \pm 0.12**	-0.82 \pm 0.11**	-0.86 \pm 0.13**	-0.75 \pm 0.11**			
(L,C) - (B,S,G,P) ⁷	-0.28 \pm 0.11*	-0.30 \pm 0.15	-0.32 \pm 0.21	-0.16 \pm 0.11	-0.27 \pm 0.10*	-0.39 \pm 0.11**	-0.28 \pm 0.10**			
Heterosis for										
MARC I ⁸	-0.10 \pm 0.10	-0.14 \pm 0.13	-0.18 \pm 0.18	-0.15 \pm 0.12	-0.08 \pm 0.10	-0.02 \pm 0.12	-0.04 \pm 0.10			
MARC II ⁹	0.07 \pm 0.11	0.07 \pm 0.12	0.07 \pm 0.16	0.29 \pm 0.13*	0.13 \pm 0.11	-0.03 \pm 0.13	0.16 \pm 0.11			
MARC III ¹⁰	0.08 \pm 0.11	-0.11 \pm 0.12	-0.29 \pm 0.13*	0.03 \pm 0.13	0.05 \pm 0.12	0.08 \pm 0.14	0.07 \pm 0.12			
Mean heterosis ¹¹	0.01 \pm 0.07	-0.06 \pm 0.08	-0.13 \pm 0.10	0.06 \pm 0.08	0.03 \pm 0.07	0.01 \pm 0.08	0.06 \pm 0.07			

¹₂ = practically devoid; 9 = moderately abundant.

²Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

³A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{6}A + \frac{1}{6}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

⁴Contrast = respective breed solution vs. A solution.

⁵Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{8}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{6}(A + H + R)$.

⁷Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁸Contrast = MARC I - $(\frac{1}{6}A + \frac{1}{6}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁹Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

¹⁰Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹¹Contrast = $\frac{1}{3}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (\frac{5}{24}A + \frac{5}{24}H + \frac{1}{12}R + \frac{1}{12}B + \frac{1}{12}S + \frac{1}{12}G + \frac{1}{12}P + \frac{1}{12}L + \frac{1}{12}C)$.

Table 8. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for yield grade adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	1.9	295.1	340.5	385.9	432.5	
Breed effect ³									
R	0.20 \pm 0.11	0.17 \pm 0.10	0.14 \pm 0.12	0.14 \pm 0.12	-0.22 \pm 0.16	-0.41 \pm 0.16*	-0.60 \pm 0.20**	-0.33 \pm 0.16	
B	-0.38 \pm 0.11**	-0.32 \pm 0.12*	-0.26 \pm 0.16	-0.26 \pm 0.16	-1.38 \pm 0.15**	-1.59 \pm 0.14**	-1.81 \pm 0.17**	-1.35 \pm 0.15**	
H	-0.10 \pm 0.11	-0.11 \pm 0.10	-0.13 \pm 0.10	-0.13 \pm 0.10	-0.03 \pm 0.15	0.01 \pm 0.16	0.05 \pm 0.21	-0.15 \pm 0.16	
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
S	-0.14 \pm 0.11	-0.06 \pm 0.13	0.02 \pm 0.17	0.02 \pm 0.17	-1.31 \pm 0.15**	-1.51 \pm 0.14**	-1.71 \pm 0.17**	-1.19 \pm 0.14**	
L	-0.64 \pm 0.10**	-0.54 \pm 0.11**	-0.45 \pm 0.14**	-0.45 \pm 0.14**	-1.59 \pm 0.15**	-1.91 \pm 0.14**	-2.23 \pm 0.18**	-1.69 \pm 0.15**	
C	0.10 \pm 0.11	0.36 \pm 0.15*	0.62 \pm 0.20**	0.62 \pm 0.20**	-1.17 \pm 0.16**	-1.42 \pm 0.15**	-1.67 \pm 0.17**	-1.12 \pm 0.15**	
G	-0.21 \pm 0.11	-0.10 \pm 0.14	0.02 \pm 0.19	0.02 \pm 0.19	-1.34 \pm 0.15**	-1.62 \pm 0.14**	-1.89 \pm 0.17**	-1.38 \pm 0.14**	
P	-0.20 \pm 0.11	-0.23 \pm 0.14	-0.26 \pm 0.19	-0.26 \pm 0.19	-1.00 \pm 0.16**	-1.33 \pm 0.15**	-1.66 \pm 0.18**	-1.12 \pm 0.15**	
MARC I	-0.25 \pm 0.09*	-0.08 \pm 0.10	0.09 \pm 0.12	0.09 \pm 0.12	-1.12 \pm 0.14**	-1.34 \pm 0.13**	-1.55 \pm 0.16**	-1.06 \pm 0.13**	
MARC II	-0.08 \pm 0.09	-0.05 \pm 0.09	-0.01 \pm 0.11	-0.01 \pm 0.11	-0.65 \pm 0.14**	-0.85 \pm 0.13**	-1.05 \pm 0.16**	-0.55 \pm 0.14**	
MARC III	-0.06 \pm 0.10	0.00 \pm 0.09	0.06 \pm 0.10	0.06 \pm 0.10	-0.41 \pm 0.14**	-0.54 \pm 0.14**	-0.67 \pm 0.17**	-0.38 \pm 0.14**	
(B,S,G,P) - (A,H,R) ⁴	-0.27 \pm 0.06**	-0.20 \pm 0.07*	-0.12 \pm 0.10	-0.12 \pm 0.10	-1.18 \pm 0.09**	-1.38 \pm 0.08**	-1.59 \pm 0.10**	-1.10 \pm 0.08**	
(L,C) - (A,H,R) ⁵	-0.30 \pm 0.07**	-0.11 \pm 0.09	0.08 \pm 0.12	0.08 \pm 0.12	-1.30 \pm 0.10**	-1.53 \pm 0.10**	-1.77 \pm 0.12**	-1.25 \pm 0.10**	
(L,C) - (B,S,G,P) ⁶	-0.03 \pm 0.07	0.08 \pm 0.10	0.21 \pm 0.14	0.21 \pm 0.14	-0.12 \pm 0.10	-0.15 \pm 0.09	-0.18 \pm 0.10	-0.15 \pm 0.09	
Heterosis for									
MARC I ⁷	-0.01 \pm 0.06	0.06 \pm 0.09	0.13 \pm 0.12	0.13 \pm 0.12	-0.08 \pm 0.11	-0.10 \pm 0.09	-0.12 \pm 0.10	0.00 \pm 0.09	
MARC II ⁸	0.03 \pm 0.07	0.02 \pm 0.08	0.01 \pm 0.10	0.01 \pm 0.10	0.02 \pm 0.11	-0.07 \pm 0.10	-0.16 \pm 0.11	0.13 \pm 0.10	
MARC III ⁹	-0.03 \pm 0.07	0.05 \pm 0.07	0.13 \pm 0.09	0.13 \pm 0.09	-0.10 \pm 0.11	-0.11 \pm 0.10	-0.12 \pm 0.13	0.02 \pm 0.11	
Mean heterosis ¹⁰	-0.00 \pm 0.04	0.04 \pm 0.05	0.09 \pm 0.06	0.09 \pm 0.06	-0.05 \pm 0.07	-0.09 \pm 0.06	-0.13 \pm 0.07	0.05 \pm 0.06	

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{4}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 9. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for predicted percentage of retail product adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	1.1	295.1	340.5	385.9	432.5	
Breed effect³									
R	-1.14 \pm 0.44*	-0.99 \pm 0.43*	-0.83 \pm 0.50	0.00	0.58 \pm 0.65	1.31 \pm 0.65	2.04 \pm 0.83*	1.00 \pm 0.65	
B	1.44 \pm 0.44**	1.20 \pm 0.51*	0.95 \pm 0.68	0.00	5.39 \pm 0.64**	6.27 \pm 0.59**	7.14 \pm 0.72**	5.35 \pm 0.60**	
H	0.47 \pm 0.45	0.54 \pm 0.40	0.60 \pm 0.43	0.00	0.23 \pm 0.63	0.06 \pm 0.65	-0.12 \pm 0.85	0.69 \pm 0.64	
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
S	0.71 \pm 0.44	0.37 \pm 0.54	0.03 \pm 0.71	0.00	5.39 \pm 0.64**	6.13 \pm 0.58**	6.88 \pm 0.70**	4.90 \pm 0.59**	
L	2.55 \pm 0.43**	2.12 \pm 0.47**	1.70 \pm 0.59**	0.00	6.40 \pm 0.62**	7.66 \pm 0.59**	8.92 \pm 0.74**	6.80 \pm 0.60**	
C	-0.44 \pm 0.48	-1.50 \pm 0.62	-2.57 \pm 0.85**	0.00	4.52 \pm 0.67**	5.59 \pm 0.61**	6.66 \pm 0.72**	4.48 \pm 0.62**	
G	0.81 \pm 0.46	0.31 \pm 0.58	-0.20 \pm 0.79	0.00	5.34 \pm 0.61**	6.40 \pm 0.57**	7.47 \pm 0.70**	5.49 \pm 0.58**	
P	0.65 \pm 0.46	0.67 \pm 0.59	0.69 \pm 0.81	0.00	3.89 \pm 0.65**	5.22 \pm 0.61**	6.54 \pm 0.76**	4.41 \pm 0.63**	
MARC I	0.88 \pm 0.38*	0.15 \pm 0.40	-0.59 \pm 0.51	0.00	4.33 \pm 0.58**	5.19 \pm 0.53**	6.05 \pm 0.66**	4.13 \pm 0.54**	
MARC II	0.30 \pm 0.39	0.08 \pm 0.37	-0.13 \pm 0.45	0.00	2.46 \pm 0.60**	3.29 \pm 0.55**	4.13 \pm 0.68**	2.17 \pm 0.56**	
MARC III	0.05 \pm 0.40	-0.20 \pm 0.37	-0.45 \pm 0.42	0.00	1.45 \pm 0.58*	1.95 \pm 0.56**	2.45 \pm 0.70**	1.35 \pm 0.57*	
(B,S,G,P) - (A,H,R) ⁴	1.13 \pm 0.24**	0.79 \pm 0.30*	0.45 \pm 0.40	0.00	4.73 \pm 0.35**	5.55 \pm 0.34**	6.37 \pm 0.42**	4.47 \pm 0.34**	
(L,C) - (A,H,R) ⁵	1.28 \pm 0.29**	0.46 \pm 0.38	-0.35 \pm 0.51	0.00	5.19 \pm 0.43**	6.17 \pm 0.40**	7.14 \pm 0.49**	5.08 \pm 0.41**	
(L,C) - (B,S,G,P) ⁶	0.15 \pm 0.28	-0.33 \pm 0.41	-0.80 \pm 0.58	0.00	0.46 \pm 0.41	0.62 \pm 0.36	0.78 \pm 0.41	0.60 \pm 0.37	
Heterosis for									
MARC I ⁷	-0.06 \pm 0.26	-0.37 \pm 0.36	-0.69 \pm 0.51	0.00	0.22 \pm 0.44	0.30 \pm 0.37	0.39 \pm 0.42	-0.11 \pm 0.38	
MARC II ⁸	-0.20 \pm 0.28	-0.22 \pm 0.32	-0.24 \pm 0.43	0.00	-0.28 \pm 0.47	0.14 \pm 0.40	0.57 \pm 0.47	-0.59 \pm 0.41	
MARC III ⁹	0.06 \pm 0.30	-0.25 \pm 0.31	-0.56 \pm 0.38	0.00	0.28 \pm 0.46	0.31 \pm 0.43	0.34 \pm 0.53	-0.17 \pm 0.44	
Mean heterosis ¹⁰	-0.07 \pm 0.18	-0.28 \pm 0.20	-0.50 \pm 0.27	0.00	0.07 \pm 0.28	0.25 \pm 0.26	0.43 \pm 0.31	-0.29 \pm 0.26	

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 10. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for retail product weight (kg) adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm			Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	295.1	340.5	385.9	432.5	
Breed effect ³								
R	4.18 \pm 6.62	1.34 \pm 6.47	-1.51 \pm 7.10	1.74 \pm 3.36	5.06 \pm 3.32	8.39 \pm 4.23	2.95 \pm 5.74	
B	33.89 \pm 6.32**	36.70 \pm 7.05**	39.50 \pm 8.73**	20.54 \pm 3.27**	23.23 \pm 3.04**	25.92 \pm 3.70**	32.36 \pm 5.31**	
H	-10.10 \pm 6.67	-11.31 \pm 6.25	-12.51 \pm 6.46	-4.83 \pm 3.25	-6.80 \pm 3.39	-8.78 \pm 4.39	-8.60 \pm 5.66	
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
S	46.33 \pm 6.30**	52.09 \pm 7.17**	57.85 \pm 8.94**	23.02 \pm 3.28**	26.00 \pm 3.00**	28.99 \pm 3.58**	42.00 \pm 5.20**	
L	38.94 \pm 6.25**	33.56 \pm 6.67**	28.18 \pm 7.84**	32.31 \pm 3.17**	39.59 \pm 3.03**	46.88 \pm 3.79**	45.09 \pm 5.27**	
C	43.94 \pm 6.72**	45.06 \pm 8.09**	46.17 \pm 9.98**	24.34 \pm 3.43**	27.37 \pm 3.12**	30.40 \pm 3.67**	42.02 \pm 5.44**	
G	45.20 \pm 6.42**	48.13 \pm 7.70**	51.06 \pm 9.86**	26.17 \pm 3.16**	31.11 \pm 2.94**	36.04 \pm 3.58**	41.22 \pm 5.11**	
P	23.84 \pm 6.56**	17.62 \pm 7.72*	11.39 \pm 9.96	21.72 \pm 3.29**	20.92 \pm 3.15**	20.12 \pm 3.83**	26.05 \pm 5.49**	
MARC I	35.43 \pm 5.59**	31.55 \pm 5.93**	27.68 \pm 7.25**	19.93 \pm 3.00**	24.00 \pm 2.75**	28.07 \pm 3.41**	36.54 \pm 4.74**	
MARC II	24.10 \pm 5.66**	19.91 \pm 5.50**	15.71 \pm 6.23**	10.50 \pm 3.08**	10.64 \pm 2.82**	10.77 \pm 3.45**	23.76 \pm 4.86**	
MARC III	11.20 \pm 5.85	9.70 \pm 5.55	8.19 \pm 5.68	2.39 \pm 3.04	3.91 \pm 2.91	5.43 \pm 3.61	10.02 \pm 5.04	
(B,S,G,P) - (A,H,R) ⁴	39.29 \pm 3.59**	41.96 \pm 4.11**	44.62 \pm 5.12**	23.89 \pm 1.82**	25.89 \pm 1.76**	27.90 \pm 2.17**	37.29 \pm 3.02**	
(L,C) - (A,H,R) ⁵	43.41 \pm 4.30**	42.63 \pm 5.12**	41.85 \pm 6.48**	29.36 \pm 2.21**	34.06 \pm 2.08**	38.77 \pm 2.51**	45.44 \pm 3.61**	
(L,C) - (B,S,G,P) ⁶	4.12 \pm 3.97	0.68 \pm 5.31	-2.77 \pm 7.13	5.46 \pm 2.11*	8.17 \pm 1.85**	10.87 \pm 2.10**	8.15 \pm 3.28*	
Heterosis for								
MARC I ⁷	7.50 \pm 3.89	4.14 \pm 5.02	0.78 \pm 6.81	1.24 \pm 2.32	2.31 \pm 1.94	3.37 \pm 2.25	7.75 \pm 3.41*	
MARC II ⁸	3.74 \pm 4.12	-2.32 \pm 4.53	-8.39 \pm 5.65	-0.59 \pm 2.44	-1.94 \pm 2.09	-3.29 \pm 2.42	5.10 \pm 3.64	
MARC III ⁹	6.72 \pm 4.41	7.79 \pm 4.52	8.85 \pm 4.86	-2.27 \pm 2.40	-0.89 \pm 2.26	0.50 \pm 2.72	4.92 \pm 3.95	
Mean heterosis ¹⁰	5.99 \pm 2.64*	3.20 \pm 2.91	0.41 \pm 3.54	-0.54 \pm 1.48	-0.17 \pm 1.34	0.19 \pm 1.61	5.92 \pm 2.32*	

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.³Contrast = respective breed solution vs. A solution.⁴Contrast = $\frac{1}{2}(B + S + G + P) - \frac{1}{4}(A + H + R)$.⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.¹⁰Contrast = $\frac{1}{5}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 11. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for fat weight (kg) adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	1.1	295.1	340.5	385.9	432.5	
Breed effect ³									
R	1.67 \pm 3.53	2.44 \pm 3.42	3.20 \pm 3.91	-5.43 \pm 3.57	-7.47 \pm 3.53*	-9.51 \pm 4.42*	-6.86 \pm 3.85		
B	-4.23 \pm 3.44	1.13 \pm 3.97	6.49 \pm 5.16	-27.44 \pm 3.46**	-30.88 \pm 3.23**	-34.31 \pm 3.88**	-22.51 \pm 3.59**		
H	-0.49 \pm 3.61	-0.41 \pm 3.27	-0.33 \pm 3.43	3.14 \pm 3.46	6.30 \pm 3.60	9.45 \pm 4.59	0.31 \pm 3.81		
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
S	-1.65 \pm 3.48	4.21 \pm 4.13	10.07 \pm 5.38	-30.69 \pm 3.47**	-34.12 \pm 3.19**	-37.55 \pm 3.75**	-21.84 \pm 3.53**		
L	-18.04 \pm 3.42**	-16.91 \pm 3.72**	-15.78 \pm 4.56**	-34.41 \pm 3.36**	-40.90 \pm 3.22**	-47.39 \pm 3.97**	-33.47 \pm 3.58**		
C	1.73 \pm 3.72	12.60 \pm 4.73*	23.46 \pm 6.37**	-29.98 \pm 3.62**	-34.97 \pm 3.32**	-39.96 \pm 3.86**	-23.67 \pm 3.67**		
G	-5.40 \pm 3.58	0.12 \pm 4.49	5.64 \pm 5.99	-31.13 \pm 3.34**	-36.37 \pm 3.12**	-41.61 \pm 3.75**	-27.92 \pm 3.47**		
P	-1.95 \pm 3.63	2.13 \pm 4.51	6.22 \pm 6.09	-16.90 \pm 3.49**	-26.67 \pm 3.35**	-36.43 \pm 4.01**	-20.42 \pm 3.73**		
MARC I	-1.81 \pm 3.05	3.77 \pm 3.30	9.35 \pm 4.24*	-22.18 \pm 3.17**	-26.48 \pm 2.92**	-30.79 \pm 3.57**	-16.32 \pm 3.23**		
MARC II	5.55 \pm 3.09	9.34 \pm 2.95**	13.12 \pm 3.48**	-6.88 \pm 3.25*	-11.71 \pm 2.99**	-16.54 \pm 3.62**	-0.84 \pm 3.31		
MARC III	9.68 \pm 3.17**	0.87 \pm 2.94	-7.93 \pm 3.03*	-4.53 \pm 3.21	-6.41 \pm 3.09	-8.29 \pm 3.78*	-0.77 \pm 3.42		
(B,S,G,P) - (A,H,R) ⁴	-3.70 \pm 1.95	1.22 \pm 2.34	6.14 \pm 3.06	-25.77 \pm 1.93**	-31.62 \pm 1.87**	-37.46 \pm 2.27**	-20.99 \pm 2.04**		
(L,C) - (A,H,R) ⁵	-8.55 \pm 2.34**	-2.83 \pm 2.95	2.88 \pm 3.90	-31.43 \pm 2.34**	-37.55 \pm 2.21**	-43.66 \pm 2.64**	-26.39 \pm 2.43**		
(L,C) - (B,S,G,P) ⁶	-4.85 \pm 2.18*	-4.06 \pm 3.16	-3.27 \pm 4.40	-5.66 \pm 2.22*	-5.93 \pm 1.98**	-6.20 \pm 2.21*	-5.40 \pm 2.22*		
Heterosis for									
MARC I ⁷	3.38 \pm 2.11	4.62 \pm 2.92	5.85 \pm 4.15	0.39 \pm 2.44	-0.58 \pm 2.06	-1.55 \pm 2.37	3.55 \pm 2.33		
MARC II ⁸	7.44 \pm 2.22**	8.36 \pm 2.52**	9.28 \pm 3.32*	7.78 \pm 2.56**	4.33 \pm 2.22	0.88 \pm 2.54	11.52 \pm 2.48**		
MARC III ⁹	9.87 \pm 2.35**	-0.17 \pm 2.44	-10.21 \pm 2.70**	0.27 \pm 2.54	0.55 \pm 2.40	0.84 \pm 2.86	5.96 \pm 2.68*		
Mean heterosis ¹⁰	6.90 \pm 1.42**	4.27 \pm 1.61*	1.64 \pm 2.07	2.81 \pm 1.56	1.43 \pm 1.42	0.06 \pm 1.69	7.01 \pm 1.57**		

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{2}(B + S + G + P) - \frac{1}{2}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 12. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for bone weight (kg) adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	1.5	295.1	340.5	385.9	432.5	
Breed effect ³									
R	2.68 \pm 1.55	2.09 \pm 1.52	1.50 \pm 1.67	1.50 \pm 1.67	2.41 \pm 0.99*	2.77 \pm 0.98*	3.14 \pm 1.25*	2.56 \pm 1.38	
B	10.57 \pm 1.49**	10.67 \pm 1.66**	10.77 \pm 2.06**	10.77 \pm 2.06**	8.60 \pm 0.97**	9.14 \pm 0.89**	9.69 \pm 1.09**	10.79 \pm 1.28**	
H	-0.26 \pm 1.57	-0.47 \pm 1.47	-0.67 \pm 1.52	-0.67 \pm 1.52	0.55 \pm 0.96	0.56 \pm 1.00	0.56 \pm 1.30	0.02 \pm 1.37	
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
S	11.31 \pm 1.48**	11.59 \pm 1.69**	11.86 \pm 2.11**	11.86 \pm 2.11**	7.36 \pm 0.97**	8.20 \pm 0.88**	9.04 \pm 1.06**	11.30 \pm 1.26**	
L	2.24 \pm 1.47	2.39 \pm 1.57	2.53 \pm 1.85	2.53 \pm 1.85	1.24 \pm 0.94	1.61 \pm 0.89	1.98 \pm 1.12	2.88 \pm 1.27*	
C	10.83 \pm 1.58**	10.17 \pm 1.91**	9.52 \pm 2.47**	9.52 \pm 2.47**	7.51 \pm 1.01**	8.50 \pm 0.92**	9.49 \pm 1.08**	11.37 \pm 1.31**	
G	9.24 \pm 1.51**	9.33 \pm 1.82**	9.41 \pm 2.33**	9.41 \pm 2.33**	6.52 \pm 0.93**	7.22 \pm 0.86**	7.93 \pm 1.06**	9.15 \pm 1.23**	
P	6.97 \pm 1.55**	4.56 \pm 1.83*	2.16 \pm 2.36	2.16 \pm 2.36	7.16 \pm 0.97**	7.50 \pm 0.93**	7.84 \pm 1.13**	8.37 \pm 1.33**	
MARC I	6.36 \pm 1.32**	5.94 \pm 1.40**	5.52 \pm 1.71**	5.52 \pm 1.71**	2.76 \pm 0.88**	4.34 \pm 0.81**	5.92 \pm 1.01**	6.69 \pm 1.15**	
MARC II	6.02 \pm 1.33**	4.93 \pm 1.29**	3.84 \pm 1.47*	3.84 \pm 1.47*	2.86 \pm 0.91**	3.51 \pm 0.83**	4.15 \pm 1.02**	6.01 \pm 1.17**	
MARC III	4.03 \pm 1.38**	3.87 \pm 1.31**	3.72 \pm 1.33*	3.72 \pm 1.33*	1.92 \pm 0.89*	3.06 \pm 0.86**	4.19 \pm 1.07**	3.98 \pm 1.22**	
(B,S,G,P) - (A,H,R) ⁴	8.72 \pm 0.84**	8.50 \pm 0.97**	8.27 \pm 1.21**	8.27 \pm 1.21**	6.42 \pm 0.54**	6.91 \pm 0.52**	7.39 \pm 0.64**	9.04 \pm 0.73**	
(L,C) - (A,H,R) ⁵	5.73 \pm 1.01**	5.74 \pm 1.21**	5.75 \pm 1.53**	5.75 \pm 1.53**	3.39 \pm 0.65**	3.94 \pm 0.61**	4.50 \pm 0.74**	6.26 \pm 0.87**	
(L,C) - (B,S,G,P) ⁶	-2.99 \pm 0.93**	-2.76 \pm 1.25*	-2.52 \pm 1.69	-2.52 \pm 1.69	-3.03 \pm 0.62**	-2.96 \pm 0.55**	-2.89 \pm 0.62**	-2.78 \pm 0.79**	
Heterosis for									
MARC I ⁷	0.49 \pm 0.92	0.19 \pm 1.18	-0.10 \pm 1.61	-0.10 \pm 1.61	-1.64 \pm 0.68*	-0.54 \pm 0.57	0.56 \pm 0.66	0.42 \pm 0.82	
MARC II ⁸	0.94 \pm 0.97	-0.18 \pm 1.07	-1.31 \pm 1.33	-1.31 \pm 1.33	-0.74 \pm 0.72	-0.49 \pm 0.61	-0.23 \pm 0.71	0.89 \pm 0.88	
MARC III ⁹	1.68 \pm 1.04	2.33 \pm 1.06*	2.97 \pm 1.14*	2.97 \pm 1.14*	-0.61 \pm 0.71	0.35 \pm 0.66	1.31 \pm 0.80	1.24 \pm 0.95	
Mean heterosis ¹⁰	1.04 \pm 0.62	0.78 \pm 0.68	0.52 \pm 0.83	0.52 \pm 0.83	-1.00 \pm 0.44*	-0.23 \pm 0.39	0.55 \pm 0.47	0.85 \pm 0.56	

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{8}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $(\frac{1}{4}(A + H + S + G))$.

⁹Contrast = MARC III - $(\frac{1}{4}(A + H + R + P))$.

¹⁰Contrast = $\frac{1}{6}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (\frac{5}{24}A + \frac{5}{24}H + \frac{1}{12}R + \frac{1}{12}B + \frac{1}{12}S + \frac{1}{12}G + \frac{1}{12}P + \frac{1}{12}L + \frac{1}{12}C)$.

Table 13. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for actual percentage of retail product adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm					Carcass weight constant, kg					Age constant, d	
	0.7	1.1	1.5	295.1	340.5	385.9	432.5					
Breed effect ³												
R	-0.21 \pm 0.87	-0.59 \pm 0.85	-0.98 \pm 0.94	0.84 \pm 1.01	1.46 \pm 1.00	2.09 \pm 1.21	1.19 \pm 0.98					
B	2.87 \pm 0.84**	1.88 \pm 0.94	0.89 \pm 1.18	6.74 \pm 0.97**	6.96 \pm 0.91**	7.19 \pm 1.07**	6.11 \pm 0.91**					
H	-1.11 \pm 0.88	-1.24 \pm 0.82	-1.38 \pm 0.85	-1.42 \pm 0.98	-2.31 \pm 1.01*	-3.20 \pm 1.25*	-1.29 \pm 0.97					
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
S	3.57 \pm 0.84**	2.85 \pm 0.97**	2.13 \pm 1.23	7.82 \pm 0.97**	8.10 \pm 0.90**	8.38 \pm 1.04**	6.83 \pm 0.89**					
L	7.71 \pm 0.83**	6.28 \pm 0.89**	4.86 \pm 1.06**	11.64 \pm 0.94**	12.22 \pm 0.91*	12.79 \pm 1.09**	11.42 \pm 0.91**					
C	2.83 \pm 0.89**	0.96 \pm 1.10	-0.90 \pm 1.44	7.75 \pm 1.01**	8.28 \pm 0.94**	8.81 \pm 1.07**	7.14 \pm 0.93**					
G	4.30 \pm 0.86**	3.09 \pm 1.04**	1.89 \pm 1.36	8.65 \pm 0.93**	9.19 \pm 0.88**	9.73 \pm 1.03**	8.37 \pm 0.88**					
P	1.87 \pm 0.88*	0.62 \pm 1.05	-0.63 \pm 1.38	4.70 \pm 0.98**	6.00 \pm 0.95**	7.30 \pm 1.10**	5.31 \pm 0.94**					
MARC I	3.33 \pm 0.74**	1.70 \pm 0.79*	0.07 \pm 0.98	6.62 \pm 0.88**	7.07 \pm 0.82**	7.52 \pm 0.98**	6.08 \pm 0.81**					
MARC II	0.74 \pm 0.75	-0.21 \pm 0.72	-1.16 \pm 0.83	2.09 \pm 0.90*	2.86 \pm 0.84**	3.64 \pm 1.00**	1.82 \pm 0.84*					
MARC III	-1.13 \pm 0.77	0.34 \pm 0.73	1.80 \pm 0.75*	0.89 \pm 0.90	1.20 \pm 0.87	1.52 \pm 1.04	0.64 \pm 0.87					
(B,S,G,P) - (A,H,R) ⁴	3.59 \pm 0.47**	2.72 \pm 0.55**	1.85 \pm 0.70*	7.17 \pm 0.54**	7.85 \pm 0.53**	8.52 \pm 0.62**	6.69 \pm 0.52**					
(L,C) - (A,H,R) ⁵	5.71 \pm 0.57**	4.24 \pm 0.69**	2.77 \pm 0.89**	9.89 \pm 0.66**	10.53 \pm 0.63**	11.17 \pm 0.73**	9.32 \pm 0.62**					
(L,C) - (B,S,G,P) ⁶	2.11 \pm 0.53**	1.51 \pm 0.72*	0.91 \pm 0.99	2.72 \pm 0.62	2.68 \pm 0.56**	2.65 \pm 0.62**	2.63 \pm 0.56**					
Heterosis for												
MARC I ⁷	0.11 \pm 0.51	-0.42 \pm 0.68	-0.96 \pm 0.94	0.27 \pm 0.67	0.50 \pm 0.58	0.73 \pm 0.66	0.07 \pm 0.58					
MARC II ⁸	-0.95 \pm 0.54	-1.39 \pm 0.60*	-1.82 \pm 0.77*	-1.67 \pm 0.71*	-0.88 \pm 0.63	-0.09 \pm 0.70	-1.66 \pm 0.62*					
MARC III ⁹	-1.27 \pm 0.58*	0.64 \pm 0.60	2.55 \pm 0.65**	-0.14 \pm 0.71	-0.08 \pm 0.68	-0.03 \pm 0.79	-0.66 \pm 0.68					
Mean heterosis ¹⁰	-0.70 \pm 0.35	-0.39 \pm 0.39	-0.08 \pm 0.48	-0.51 \pm 0.43	-0.15 \pm 0.40	0.20 \pm 0.47	-0.75 \pm 0.40					

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{4}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 14. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for fat percentage adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	295.1	340.5	385.9	432.5		
Breed effect ³									
R	-0.31 ± 0.86	0.17 ± 0.83	0.64 ± 0.96	-1.80 ± 1.07	-2.35 ± 1.05*	-2.89 ± 1.32*	-2.10 ± 1.02		
B	-4.34 ± 0.84**	-2.86 ± 0.98**	-1.38 ± 1.28	-9.65 ± 1.03**	-9.78 ± 0.96**	-9.91 ± 1.16**	-8.55 ± 0.95**		
H	0.62 ± 0.88	0.79 ± 0.79	0.96 ± 0.83	1.11 ± 1.03	2.15 ± 1.07	3.19 ± 1.37*	0.89 ± 1.01		
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
S	-4.50 ± 0.85**	-3.22 ± 1.02**	-1.94 ± 1.34	-10.39 ± 1.04**	-10.72 ± 0.95**	-11.06 ± 1.12**	-8.91 ± 0.94**		
L	-7.34 ± 0.83**	-6.11 ± 0.91**	-4.87 ± 1.13**	-12.03 ± 1.00**	-12.68 ± 0.96**	-13.32 ± 1.19**	-11.59 ± 0.95**		
C	-3.58 ± 0.91**	-0.93 ± 1.17	1.71 ± 1.59	-10.26 ± 1.08**	-10.94 ± 0.99**	-11.62 ± 1.15**	-9.32 ± 0.97**		
G	-4.98 ± 0.88**	-3.33 ± 1.11**	-1.67 ± 1.49	-10.88 ± 1.00**	-11.43 ± 0.93**	-11.99 ± 1.12**	-10.24 ± 0.92**		
P	-2.74 ± 0.89**	-0.83 ± 1.12	1.07 ± 1.52	-6.59 ± 1.04**	-8.29 ± 1.00**	-9.99 ± 1.20**	-7.32 ± 0.99**		
MARC I	-3.51 ± 0.75**	-1.75 ± 0.81*	0.01 ± 1.05	-7.48 ± 0.95**	-8.31 ± 0.87**	-9.15 ± 1.07**	-6.89 ± 0.85**		
MARC II	-1.02 ± 0.75	0.19 ± 0.72	1.40 ± 0.85	-2.74 ± 0.97*	-3.85 ± 0.89**	-4.97 ± 1.08**	-2.36 ± 0.88*		
MARC III	0.98 ± 0.77	-0.89 ± 0.71	-2.77 ± 0.74**	-1.54 ± 0.96	-2.15 ± 0.92*	-2.76 ± 1.13*	-1.29 ± 0.91		
(B,S,G,P) - (A,H,R) ⁴	-4.25 ± 0.47**	-2.88 ± 0.58**	-1.51 ± 0.76	-9.15 ± 0.58**	-9.99 ± 0.56**	-10.83 ± 0.68**	-8.35 ± 0.54**		
(L,C) - (A,H,R) ⁵	-5.57 ± 0.57**	-3.84 ± 0.73**	-2.11 ± 0.97*	-10.92 ± 0.70**	-11.74 ± 0.66**	-12.57 ± 0.79**	-10.05 ± 0.64**		
(L,C) - (B,S,G,P) ⁶	-1.32 ± 0.53*	-0.96 ± 0.78	-0.60 ± 1.10	-1.77 ± 0.66*	-1.75 ± 0.59**	-1.73 ± 0.66*	-1.70 ± 0.59**		
Heterosis for									
MARC I ⁷	0.23 ± 0.51	0.63 ± 0.72	1.03 ± 1.03	0.37 ± 0.73	-0.23 ± 0.61	-0.83 ± 0.71	0.36 ± 0.61		
MARC II ⁸	1.20 ± 0.54*	1.63 ± 0.62*	2.07 ± 0.82*	2.30 ± 0.77**	1.15 ± 0.66	-0.01 ± 0.76	2.20 ± 0.66**		
MARC III ⁹	1.59 ± 0.57*	-0.93 ± 0.59	-3.44 ± 0.66**	0.28 ± 0.76	-0.03 ± 0.72	-0.33 ± 0.85	0.84 ± 0.71		
Mean heterosis ¹⁰	1.00 ± 0.34**	0.44 ± 0.40	-0.11 ± 0.51	0.98 ± 0.47*	0.30 ± 0.42	-0.39 ± 0.50	1.13 ± 0.42*		

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{4}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{2}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 15. Estimates of breed (\pm SE) and retained heterosis (\pm SE) effects for bone percentage adjusted to different fat thickness, carcass weight, and slaughter age end points¹

Contrast ²	Fat thickness constant, cm				Carcass weight constant, kg				Age constant, d
	0.7	1.1	1.5	295.1	340.5	385.9	432.5		
Breed effect ³									
R	0.51 \pm 0.30	0.43 \pm 0.29	0.36 \pm 0.33	0.93 \pm 0.30**	0.87 \pm 0.29**	0.80 \pm 0.37*	0.89 \pm 0.28**		
B	1.45 \pm 0.29**	0.96 \pm 0.33**	0.48 \pm 0.42	2.89 \pm 0.29**	2.81 \pm 0.27**	2.73 \pm 0.33**	2.44 \pm 0.26**		
H	0.43 \pm 0.30	0.40 \pm 0.28	0.37 \pm 0.29	0.27 \pm 0.29	0.14 \pm 0.30	0.01 \pm 0.39	0.35 \pm 0.28		
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
S	0.93 \pm 0.29**	0.42 \pm 0.34	-0.09 \pm 0.44	2.51 \pm 0.29**	2.58 \pm 0.26**	2.66 \pm 0.32**	2.03 \pm 0.26**		
L	-0.28 \pm 0.29	-0.03 \pm 0.31	0.22 \pm 0.38	0.46 \pm 0.28	0.50 \pm 0.27	0.55 \pm 0.33	0.23 \pm 0.26		
C	0.78 \pm 0.31*	0.05 \pm 0.39	-0.67 \pm 0.52	2.44 \pm 0.30**	2.62 \pm 0.28**	2.80 \pm 0.32**	2.14 \pm 0.27**		
G	0.60 \pm 0.30	0.18 \pm 0.37	-0.25 \pm 0.49	2.16 \pm 0.28**	2.19 \pm 0.26**	2.21 \pm 0.32**	1.80 \pm 0.25**		
P	0.82 \pm 0.30*	0.18 \pm 0.37	-0.45 \pm 0.49	1.83 \pm 0.29**	2.23 \pm 0.28**	2.63 \pm 0.34**	1.95 \pm 0.27**		
MARC I	0.20 \pm 0.26	0.04 \pm 0.27	-0.12 \pm 0.35	0.87 \pm 0.26**	1.26 \pm 0.24**	1.65 \pm 0.30**	0.85 \pm 0.24**		
MARC II	0.28 \pm 0.26	0.03 \pm 0.25	-0.21 \pm 0.29	0.65 \pm 0.27*	1.00 \pm 0.25**	1.35 \pm 0.30**	0.56 \pm 0.24*		
MARC III	0.18 \pm 0.27	0.60 \pm 0.25*	1.01 \pm 0.26**	0.69 \pm 0.27*	0.96 \pm 0.26**	1.23 \pm 0.32**	0.67 \pm 0.25*		
(B,S,G,P) - (A,H,R) ⁴	0.64 \pm 0.16**	0.16 \pm 0.19	-0.32 \pm 0.25	1.95 \pm 0.16**	2.12 \pm 0.16**	2.29 \pm 0.19**	1.64 \pm 0.15**		
(L,C) - (A,H,R) ⁵	-0.06 \pm 0.20	-0.27 \pm 0.24	-0.47 \pm 0.32	1.05 \pm 0.20**	1.23 \pm 0.18**	1.41 \pm 0.22**	0.77 \pm 0.18**		
(L,C) - (B,S,G,P) ⁶	-0.70 \pm 0.18**	-0.42 \pm 0.26	-0.15 \pm 0.36	-0.90 \pm 0.19**	-0.89 \pm 0.16**	-0.88 \pm 0.19**	-0.87 \pm 0.16**		
Heterosis for									
MARC I ⁷	-0.34 \pm 0.18	-0.26 \pm 0.24	-0.18 \pm 0.34	-0.61 \pm 0.20**	-0.24 \pm 0.17	0.12 \pm 0.20	-0.40 \pm 0.17*		
MARC II ⁸	-0.21 \pm 0.19	-0.21 \pm 0.21	-0.22 \pm 0.27	-0.58 \pm 0.21*	-0.23 \pm 0.18	0.13 \pm 0.21	-0.48 \pm 0.18*		
MARC III ⁹	-0.26 \pm 0.20	0.34 \pm 0.20	0.94 \pm 0.22**	-0.07 \pm 0.21	0.15 \pm 0.20	0.37 \pm 0.24	-0.12 \pm 0.20		
Mean heterosis ¹⁰	-0.27 \pm 0.12*	-0.04 \pm 0.13	0.18 \pm 0.17	-0.42 \pm 0.13**	-0.11 \pm 0.12	0.21 \pm 0.14	-0.33 \pm 0.11**		

¹Significant effects are indicated by **($P < 0.01$) and *($P < 0.05$).

²A = Angus, H = Hereford, R = Red Poll, B = Braunvieh, S = Simmental, G = Gelbvieh, P = Pinzgauer, L = Limousin, C = Charolais, MARC I = $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}L + \frac{1}{4}C)$, MARC II = $\frac{1}{4}(A + H + S + G)$, and MARC III = $\frac{1}{4}(A + H + R + P)$.

³Contrast = respective breed solution vs. A solution.

⁴Contrast = $\frac{1}{4}(B + S + G + P) - \frac{1}{8}(A + H + R)$.

⁵Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(A + H + R)$.

⁶Contrast = $\frac{1}{2}(L + C) - \frac{1}{4}(B + S + G + P)$.

⁷Contrast = MARC I - $(\frac{1}{8}A + \frac{1}{8}H + \frac{1}{4}B + \frac{1}{4}L + \frac{1}{4}C)$.

⁸Contrast = MARC II - $\frac{1}{4}(A + H + S + G)$.

⁹Contrast = MARC III - $\frac{1}{4}(A + H + R + P)$.

¹⁰Contrast = $\frac{1}{6}(\text{MARC I} + \text{MARC II} + \text{MARC III}) - (5/24A + 5/24H + 1/12R + 1/12B + 1/12S + 1/12G + 1/12P + 1/12L + 1/12C)$.

Table 16. Estimates of overall linear regression coefficients for carcass traits of steers on age (d) and estimates of individual breed group linear regression coefficients for carcass traits of steers on fat thickness (cm) or HCW (kg)¹

Trait ⁴	Covariate ²		Breed group ³												
	A		R	B	H	A	S	L	C	G	P	M I	M II	M III	
HCW	0.702**	F	17.433*	41.746**	22.247**	27.239**	52.479**	17.938*	63.942**	53.866**	11.822	35.343**	20.705**	0.213	
		W	—	—	—	—	—	—	—	—	—	—	—	—	
DP	0.009*	F	-0.116	-0.326	1.086**	1.248**	0.823	0.002	2.925**	1.239	1.261	0.949	0.288	0.011	
		W	0.018**	0.027**	0.030**	0.033**	0.028**	0.027**	0.023**	0.018**	0.016**	0.019**	0.030**	0.024**	
AFT	0.002**	F	—	—	—	—	—	—	—	—	—	—	—	—	
		W	0.004**	0.002**	0.008**	0.006**	0.002**	0.002**	0.001*	0.002**	0.000	0.002**	0.002**	0.004**	
LMA	0.050**	F	-0.214	0.465	0.133	0.356	1.694	-5.525*	-4.016	0.623	1.068	-5.081*	-0.967	-0.054	
		W	0.137**	0.108**	0.104**	0.090**	0.110**	0.154**	0.097**	0.127**	0.098**	0.106**	0.096**	0.108**	
KPH	0.004**	F	0.111	0.423*	0.237*	0.295*	0.532*	0.447**	0.849**	0.687**	0.690**	0.718**	0.644**	0.002	
		W	0.006**	0.004**	0.005**	0.005**	0.007**	0.004**	0.002	0.005**	0.003*	0.004**	0.003*	0.006**	
MS	0.004**	F	0.257	0.621**	0.194	0.295*	0.882**	0.375*	1.053**	0.419	1.117**	0.477**	0.453**	-0.003	
		W	0.002	0.004**	0.002	0.003*	0.007**	0.001	0.001	0.003*	0.003*	0.004**	0.000	0.003*	
YG	0.007**	F	1.178**	1.417**	1.221**	1.264**	1.474**	1.503**	1.912**	1.559**	1.180**	1.692**	1.351**	1.415**	
		W	0.007**	0.006**	0.012**	0.011**	0.006**	0.004**	0.005**	0.005**	0.004*	0.006**	0.006**	0.008**	
PRP	-0.026**	F	-4.656**	-5.648**	-4.871**	-5.036**	-5.886**	-6.087**	-7.699**	-6.301**	-4.989**	-6.881**	-5.581**	-5.661**	
		W	-0.026**	-0.023**	-0.046**	-0.042**	-0.026**	-0.014*	-0.018**	-0.018**	-0.013*	-0.023**	-0.024**	-0.031**	
RPW	0.370**	F	-3.195	10.926	0.906	3.920	18.318**	-9.529	6.715	11.255	-11.650	-5.770	-6.564	0.158	
		W	0.510**	0.496**	0.393**	0.437**	0.503**	0.597**	0.504**	0.546**	0.419**	0.527**	0.440**	0.470**	
FW	0.266**	F	23.970**	35.455**	22.268**	22.059**	36.704**	24.886**	49.212**	35.859**	32.279**	36.019**	31.524**	0.043	
		W	0.335**	0.304**	0.449**	0.380**	0.304**	0.237**	0.270**	0.264**	0.165**	0.285**	0.274**	0.339**	
BNW	0.072**	F	-1.059	0.659	-0.103	0.416	1.098	0.774	-1.215	0.622	-5.605**	-0.635	-2.308*	0.026	
		W	0.088**	0.092**	0.080**	0.080**	0.098**	0.088**	0.101**	0.095**	0.087**	0.114**	0.094**	0.105**	
RPP	-0.034**	F	-4.632**	-6.149**	-3.999**	-3.664**	-5.460**	-7.231**	-8.321**	-6.681**	-6.802**	-7.730**	-6.042**	0.004	
		W	-0.024**	-0.033**	-0.057**	-0.037**	-0.031**	-0.025**	-0.026**	-0.025**	-0.009	-0.027**	-0.020**	-0.030**	
FP	0.046*	F	5.876**	8.393**	5.109**	4.691**	7.891**	7.778**	11.306**	8.832**	9.459**	9.096**	7.720**	0.000	
		W	0.041**	0.050**	0.076**	0.053**	0.046**	0.039**	0.038**	0.041**	0.015*	0.035**	0.028**	0.040**	
BP	-0.012**	F	-1.227**	-2.249**	-1.115**	-1.041**	-2.309**	-0.416	-2.863**	-2.115**	-2.634**	-1.445**	-1.651**	-0.003	
		W	-0.017**	-0.017**	-0.018**	-0.016**	-0.014**	-0.014**	-0.012**	-0.015**	-0.007**	-0.007**	-0.008**	-0.010**	

¹Estimates of regression coefficients are different from zero: *($P < 0.05$) and **($P < 0.01$).²A = age; F = fat thickness; W = HCW.³R = Red Poll; B = Braunvieh; H = Hereford; A = Angus; S = Simmental; L = Limousin; C = Charolais; G = Gelbvieh; P = Pinzgauer; M I = MARC I; M II = MARC II; M III = MARC III.⁴DP = dressing percentage; AFT = adjusted fat thickness, cm; LMA = LM area, cm²; KPH = kidney, pelvic, and heart fat percentage; MS = marbling score (2 = practically devoid; 9 = moderately abundant); YG = yield grade; PRP = predicted percentage of retail product; RPW = predicted percentage of retail product; BP = bone percentage; FP = fat percentage; BP = bone percentage.

Cross et al., 1984; Anderson et al., 1999). Crouse et al. (1985), on the contrary, reported S and A males did not differ significantly in fat thickness adjusted to a constant percentage (33.5%) of rib fat. Low-lean-to-fat-ratio breeds had more ($P < 0.01$) backfat than did medium- and high-lean-to-fat-ratio breeds at all HCW end points and at the 432.5-d age end point. Constant weight and constant age comparisons by Morris et al. (1990) indicated A- and H-sired males had thicker fat cover than C- and L-sired males at both end points. High- and medium-lean-to-fat-ratio breeds were similar for all end points. A constant age study under subtropical conditions by Crockett et al. (1979) revealed similar fat thickness for L- and S-sired steers.

Retained Heterosis. When adjusted to the greatest HCW level, backfat cover was 0.12 ($P < 0.05$) and 0.18 cm ($P < 0.01$) less in MARC I and MARC II carcasses than in carcasses of their contributing purebreds. Estimates of heterosis for the mean of the 3 composites were significant (less AFT) only when data were adjusted to 340.5 ($P < 0.05$) or 385.9 kg ($P < 0.01$) of HCW and tended to be greater with heavier carcasses. Adjustment for age resulted in near zero estimates of heterosis for all comparisons. In agreement, Alenda et al. (1980) observed significant, negative individual heterosis when fat cover was adjusted for carcass weight (-0.18 cm), but nonsignificant, small heterosis effects were observed when adjusted for age (-0.03 cm) in A \times C crosses.

Longissimus Muscle Area

Breed Effects. Most breeds had significant estimates of an advantage in area of the LM over A at constant AFT, HCW, and age end points (Table 5). Red Poll and H did not significantly differ from A. The superiority of B, S, G, and P tended to increase (positive regression coefficient estimates) with increased AFT, whereas the superiority of L, C, MARC I, MARC II, and MARC III tended to decrease (negative regression coefficient estimates). Differences tended to increase (positive regression coefficient estimates) from the 295.1 to the 385.9 kg adjustments for constant HCW for all breeds, especially for L (from 15.9 to 21.7 cm²), which had the largest estimate of the regression coefficient (Table 16). Consistent with these results, breed A has been reported to have less LMA than Brown Swiss (Bertrand et al., 1983), L (Vanderwert et al., 1985), and S (Laborde et al., 2001) at a grade of Choice or at a constant fat thickness. After adjustment for age, Anderson et al. (1999) found that C-sired steers were superior to A-sired steers. With constant fat at slaughter and market-weight adjustments, G- and P-sired calves had greater LMA than A-sired calves in Canada (Fiss and Wilton, 1993). When compared at constant AFT, HCW or age, carcasses from steers with medium- and high-lean-to-fat-ratios had more ($P < 0.01$) LMA than carcasses from low-lean-to-fat-ratio steers. For steers and bulls, with constant weight and age adjustments, Morris et al.

(1990) found that progeny of C and L sires had greater LMA than progeny of A and H sires. Longissimus muscle area of high-lean-to-fat-ratio breeds was larger ($P < 0.05$) than that of medium-lean-to-fat-ratio breeds only with adjustment to HCW of 340.5 and 385.9 kg.

Retained Heterosis. Steers from MARC I and MARC III composite populations exhibited positive retained heterosis ($P < 0.05$) for LMA only with a constant AFT of 0.7 cm or with a constant age of 432.5 d. Positive estimates of retained heterosis for the mean of the 3 composites were significant only with constant AFT (0.7 and 1.1 cm) and age analyses. Estimates of retained heterotic effects were not significant when adjusted to the greatest degree of fatness or adjusted for HCW. Investigations of combined individual and maternal heterosis retained on carcass traits with comparable composite breeds and end points apparently have not been done previously. From a study with A, C, and H with constant weight at slaughter, Urick et al. (1974) reported that heterosis for LMA was not evident. Estimates of weight-adjusted heterosis by Koch et al. (1976) also were not important for A and H cattle. Alenda et al. (1980) previously suggested, "adjustment of rib eye area to constant weight masks any heterosis in muscle growth." Other researchers (Long and Gregory, 1975; Alenda et al., 1980; Comerford et al., 1988) also have observed that estimates of individual heterosis are reduced after adjustment for carcass weight.

Kidney, Pelvic, and Heart Fat Percentage

Breed Effects. More breeds were significantly different from A for KPH at constant AFT end points than at HCW end points, indicating ranking of breeds was changed by end point classification (Table 6). Adjustment of data for all AFT end points generally resulted in greater ($P < 0.01$ or $P < 0.05$) estimates of KPH for R, C, G, P, MARC I, MARC II, and MARC III than for A. However, differences for R and MARC III tended to decrease with increased AFT end point, whereas differences from A for the other 5 breeds tended to increase. No significant differences were observed between A and B, H, S, and L. Unlike the current study, Crouse et al. (1985), with adjustment to a constant rib-fat percentage, and Vanderwert et al. (1985), with slaughter at a constant fat thickness, reported S had significantly greater and L had significantly smaller KPH than A, respectively. Weight constant KPH was smaller for A than for R ($P < 0.01$) and MARC III ($P < 0.05$), but was larger ($P < 0.05$) for A than for S (except at 385.9 kg) and L (only at 340.5 kg). On an age constant basis, only R and MARC III were different from A, both having greater ($P < 0.01$) estimates of KPH. In disagreement, Cross et al. (1984) reported that at constant age A had greater KPH than S, C, and H. At constant AFT end points (except at 0.7 cm), medium-lean-to-fat-ratio breeds had significantly larger KPH than low-lean-to-fat-ratio breeds, whereas at each constant HCW end point, medium-lean-to-fat-ratio breeds had signifi-

cantly smaller KPH than low-lean-to-fat-ratio breeds. High-lean-to-fat-ratio breeds had greater ($P < 0.05$) KPH than low-lean-to-fat-ratio breeds at 1.5 cm of AFT, but smaller ($P < 0.01$) KPH at 340.5 and 385.9 kg HCW end points.

Retained Heterosis. Estimates of heterotic effects for MARC I and MARC II were positive ($P < 0.01$ or $P < 0.05$) when KPH was adjusted for age and for each level of AFT. At constant HCW, the positive estimates of heterosis were significant for MARC I at 340.5 kg ($P < 0.05$) and for MARC II at 295.1 ($P < 0.01$) and 340.5 kg ($P < 0.05$). Estimates for MARC III were significant with the lowest fat thickness end point, with the 2 largest HCW end points, and with the age end point. Estimates of retained heterosis for the mean of the 3 composites were positive ($P < 0.01$ or $P < 0.05$) at all AFT, HCW, and age end points.

Marbling Score

Breed Effects. At common AFT end points, A had a significantly larger MS when compared with L, G (except at 1.5 cm), and MARC I (except at 1.5 cm), but smaller ($P < 0.05$) MS when compared with P, except at 0.7 cm (Table 7). Red Poll, B, H, S, MARC II, and MARC III resembled A. In agreement with this finding, Vanderwert et al. (1985) reported that A had greater MS than L for measurements at a constant degree of fatness. Two other constant fat studies (Crouse et al., 1985; Laborde et al., 2001) reported MS did not significantly differ between A and S, also in agreement with present comparisons. In contrast to comparisons of MS at constant AFT, significant differences at constant HCW included more end points and a larger number of breeds with A significantly exceeding B, S, L, C, G, MARC I, and MARC II (except at 295.1 kg). Although not significant, P had less marbling than A at constant HCW, in contrast to differences at constant AFT. At the constant age end point, MS of A was greater ($P < 0.01$) compared with the same breeds that A surpassed at constant HCW end points, except that A was similar to MARC II at the constant age end point. Marbling score has been reported to be greater for A than for S and C (Cross et al., 1984; DeRouen et al., 1992) at constant age, in agreement with present findings. Medium- and high-lean-to-fat-ratio breeds displayed less ($P < 0.01$) marbling than low-lean-to-fat-ratio breeds on HCW and age constant bases. For every AFT end point, however, medium- and high-lean-to-fat-ratio breeds generally had the same ability to marble as did low-lean-to-fat-ratio breeds. With adjustment to 0.7 cm of AFT ($P < 0.05$), or 340.5 ($P < 0.05$) and 385.9 kg of HCW ($P < 0.01$), or 432.5 d of age ($P < 0.01$), high-lean-to-fat-ratio breeds had smaller scores for marbling than medium-lean-to-fat-ratio breeds. These results agree with age, weight, and fat constant comparisons by Wheeler et al. (1996), who reported that C-sired steers had smaller MS than the average of G- and P-sired steers.

Retained Heterosis. In general, estimates of effects of heterosis were not significant for MS, except for positive heterosis ($P < 0.05$) at 295.1 kg of HCW and negative heterosis ($P < 0.05$) at 1.5 cm of AFT for MARC II and MARC III, respectively.

Yield Grade

Breed Effects. With the 2 largest end points for AFT, contrasts for YG significantly favored A over C, but with any HCW end point and with the age end point, contrasts favored ($P < 0.01$) C over A (Table 8). Unlike with the constant AFT end points, almost all breeds had estimates of more desirable ($P < 0.01$ or $P < 0.05$) YG than A for the different end points for HCW (except H was similar to A) and the end point for age (for which R and H were similar to A). Significant negative differences were not consistent across AFT end points and a smaller number of breeds, B, L, and MARC I, had significantly smaller YG than A. Estimates of absolute differences for L from A tended to decrease with increased AFT end points but to increase with increased HCW end points. A previous constant age analysis (Cross et al., 1984) favored C and S over A, and a previous constant fat analysis (Vanderwert et al., 1985) favored L over A, as in the current study. Low-lean-to-fat-ratio breeds had significantly greater YG than medium-lean-to-fat-ratio breeds at the 2 smallest end points for AFT, at every end point for HCW, and at the age end point. Low-lean-to-fat-ratio breeds had greater ($P < 0.01$) YG than high-lean-to-fat-ratio breeds at 0.7 cm constant AFT, at all HCW end points, and at the constant age end point. High- and medium-lean-to-fat-ratio breeds were similar for all end points.

Retained Heterosis. No significant estimates of retained heterotic effects were detected for YG with any end point. Estimates of individual heterosis effects were negligible for S, L, Polled H, and Brahman cattle in a diallel mating design (Comerford et al., 1988), in agreement with present findings.

Predicted Percentage of Retail Product

Breed Effects. Red Poll had smaller ($P < 0.05$) PRP than A at end points of 0.7 and 1.1 cm for AFT, larger ($P < 0.05$) PRP at the 385.9 kg end point for HCW, and similar PRP at the end point of 432.5 d of age (Table 9). Charolais had smaller ($P < 0.01$) PRP than A when adjustment was to 1.5 cm of AFT, but larger ($P < 0.01$) PRP when adjustment was for any HCW end point or for the age end point. In addition, linear regression coefficients were estimated to be $-7.70 \pm 0.67\%$ and $-5.04 \pm 0.34\%$ per cm of fat, and $-0.018 \pm 0.0050\%$ and $-0.042 \pm 0.0057\%$ per kg of carcass for C and A, respectively (Table 16). Increasing the end point for HCW was associated with a tendency to increase the number of significant differences from A and differences based on lean-to-fat ratio. For all HCW end points, A had generally less ($P < 0.01$) PRP compared with the

other breeds, except for H, which was similar to A. Charolais steers fed to a constant live weight (Urlick et al., 1974) and Brown Swiss steers fed to a Choice grade (Bertrand et al., 1983) have been reported to have greater estimated percentage of cutability than A steers. At a constant age, most breeds were significantly superior to A, except for R and H, which did not significantly differ from A. Low-lean-to-fat-ratio breeds had smaller ($P < 0.01$) PRP than medium-lean-to-fat-ratio breeds at the different AFT end points (except at 1.5 cm), the different HCW end points, and the age-constant end point. Low-lean-to-fat-ratio breeds had significantly smaller PRP than the high-lean-to-fat-ratio breeds for the 0.7 cm AFT end point, for all HCW end points, and for the age end point. High- and medium-lean-to-fat-ratio breeds were similar regardless of end point classification and level.

Retained Heterosis. As with YG, estimates of retained heterosis for PRP were negligible in all cases.

Retail Product Weight

Breed Effects. With AFT, HCW, and age end points, estimates of RPW were generally greater ($P < 0.01$) for B, S, L, C, G, P, MARC I, and MARC II than for A (Table 10). In all cases, R, H, and MARC III were similar to A. In agreement, the review by Marshall (1994) indicated that P, B, G, and L were superior to A as sire breeds for RPW at constant age or constant time in feedlot, and that A as a sire breed was similar to R and H. With AFT, HCW, and age end points, larger ($P < 0.01$) estimates of RPW were obtained for high- and medium-lean-to-fat-ratio steers than for low-lean-to-fat-ratio steers. With weight and age end points, estimates of RPW were significantly larger for high-lean-to-fat-ratio steers than for medium-lean-to-fat-ratio steers. However, when adjustment was to different AFT end points, the high- and medium-lean-to-fat-ratio breeds were not significantly different.

Retained Heterosis. With AFT and HCW end points, estimates of retained heterosis were generally negligible for RPW. With the age end point, estimates of retained heterosis were significant ($P < 0.05$) only for MARC I and for the mean of the 3 composites. Mean heterosis also was significant with the lowest fat thickness end point.

Fat Weight

Breed Effects. Relative to A, C and MARC II had significantly more FW when adjustment was to 1.1 and 1.5 cm of AFT, but significantly less when end points were age (MARC II did not differ significantly) or HCW (Table 11). Estimates of the linear regression coefficients on AFT were larger for C and MARC II than for A (49.21 ± 4.96 kg and 31.52 ± 2.69 kg vs. 22.06 ± 2.50 kg per cm), but with regression on HCW the reverse occurred (0.27 ± 0.025 kg and 0.27 ± 0.025 kg vs. 0.38 ± 0.029 kg per kg). Limousin ranked lower ($P < 0.01$)

than A at all levels of AFT end points. The estimate for the MARC III composite vs. the estimate for A, in contrast, was 9.7 kg greater ($P < 0.01$) fat for the 0.7 cm AFT end point, essentially the same for the 1.1 cm end point, and 7.9 kg less ($P < 0.05$) for the 1.5 cm end point, suggesting that the intercepts for the 2 breeds were different. The estimates of linear regression coefficients for FW on AFT also were quite different for A and MARC III (22.059 ± 2.503 kg vs. 0.043 ± 0.122 kg per cm). Estimates of absolute breed differences from A tended to increase with increases in level of the HCW end point. With HCW end points, H was similar to A, but estimates for R (except at end point of 295.1 kg), B, S, L, G, P, MARC I, and MARC III (only at end point of 385.9 kg) were significantly less than estimates for A. On a constant age basis, A had more fat ($P < 0.01$) than B, S, L, G, P, and MARC I. At the lowest level of the AFT end point, low- and medium-lean-to-fat-ratio breeds were estimated to have more ($P < 0.05$) fat than high-lean-to-fat-ratio breeds, but at the 1.1 or 1.5 cm AFT end points, low- and medium-lean-to-fat-ratio breeds were similar to high-lean-to-fat-ratio breeds. At common HCW and age end points, low-lean-to-fat-ratio steers were estimated to have more ($P < 0.01$) fat than medium- and high-lean-to-fat-ratio steers, and similarly, medium-lean-to-fat-ratio steers had fatter ($P < 0.01$ or $P < 0.05$) carcasses than high-lean-to-fat-ratio steers.

Retained Heterosis. The estimates of heterosis for FW for MARC II were significantly positive ($P < 0.01$ or $P < 0.05$) for all AFT end points. In contrast, estimates of heterosis for MARC III were positive (9.9 kg; $P < 0.01$) for 0.7 cm of AFT, negligible at 1.1 cm, and negative (-10.2 kg; $P < 0.01$) at 1.5 cm. With the age end point, estimates of heterosis (more FW) were significant for MARC II and MARC III and for the mean of the 3 composite breeds. Absolute estimates of effects of heterosis at HCW end points were not as great as at the AFT or age end points.

Bone Weight

Breed Effects. Contrasts in Table 12 indicate A was estimated generally to have less ($P < 0.01$ or $P < 0.05$) BNW when compared with each of the other breeds at constant AFT (except that R, H, and L were comparable to A), constant HCW (H and L again comparable to A) and constant age (R and H again comparable to A). On a constant age and a constant weight basis, similar rankings were reported by Gregory et al. (1978) for R, Brown Swiss, and H when contrasted with A. On AFT, HCW, and age-constant bases, medium- and high-lean-to-fat-ratio breeds were estimated to have more ($P < 0.01$) BNW than low-lean-to-fat-ratio breeds, and generally, medium-lean-to-fat-ratio breeds significantly exceeded high-lean-to-fat-ratio breeds.

Retained Heterosis. Estimates of heterotic effects were significant ($P < 0.05$) for MARC III (more BNW) only at 1.1 and 1.5 cm of AFT, and for MARC I (less

BNW) and for the mean of the composite breeds (less BNW) only at 295.1 kg of HCW.

Actual Percentage of Retail Product

Breed Effects. Generally, estimated differences from A for RPP at AFT or age end points were not as large as at HCW end points (Table 13), in agreement with the conclusion of Koch et al. (1979), who stated, "differences in composition were greatest at a common weight because that contrast emphasized differences in maturity." When adjustments were for different levels of AFT, estimate of RPP was smaller for A than for most breeds: B ($P < 0.01$), C ($P < 0.01$), and P ($P < 0.05$) at end point of 0.7 cm; S ($P < 0.01$), G ($P < 0.01$), and MARC I ($P < 0.01$ or $P < 0.05$) at 0.7 and 1.1 cm; MARC III ($P < 0.05$) at 1.5 cm; and L ($P < 0.01$) at 0.7, 1.1, and 1.5 cm. For males fed to a targeted fat thickness end point, Vanderwert et al. (1985) found that L had a greater percentage of major cuts than A. End points of HCW and age significantly favored most breeds relative to A at all levels of those end points, except for R and MARC III, which were comparable to A. Comparisons at HCW end points also indicated that A exceeded ($P < 0.05$) H at 340.5 and 385.9 kg. Medium- and high-lean-to-fat-ratio breeds were significantly superior to low-lean-to-fat-ratio breeds in RPP at each level of each end point. High-lean-to-fat-ratio breeds had significantly greater RPP than medium-lean-to-fat-ratio breeds at the 2 lowest AFT end points, at the 2 heaviest HCW end points, and at the age end point of 432.5 d.

Retained Heterosis. For MARC III, estimates of heterotic effects for RPP for AFT end points were unfavorable ($P < 0.05$) at 0.7 cm, neutral at 1.1 cm, and favorable ($P < 0.01$) at 1.5 cm end points with the favorable estimate 2 times greater in absolute value than the unfavorable estimate (2.55 vs. -1.27%). Estimates of effects of heterosis for MARC II were negative ($P < 0.05$) at 1.1 and 1.5 cm of AFT, at 295.1 kg of HCW, and at 432.5 d of age.

Fat Percentage

Breed Effects. Angus steers had significantly greater estimates of FP than B, S, G, and MARC I at end points of 0.7 and 1.1 cm of AFT, C and P at 0.7 cm, MARC III at 1.5 cm, and L at 0.7, 1.1, and 1.5 cm (Table 14). With HCW-constant end points, estimates of FP were significantly greater for A than for B, S, L, C, G, P, MARC I, and MARC II at all levels of the HCW end points, and R and MARC III at 340.5- and 385.9-kg end points. On an age-constant basis, estimates of FP were significantly greater for A than for all breeds, except R, H, and MARC III. In an experiment with short- and long-fed heifers, greater percentages of fat trim also were obtained for A than for C (Hedrick et al., 1970). Generally, low-lean-to-fat-ratio breeds had significantly greater FP than medium- and high-lean-to-fat-ratio breeds with all AFT, HCW, and age end points.

Medium-lean-to-fat-ratio breeds had significantly greater estimates of FP than high-lean-to-fat-ratio breeds at the 0.7-cm AFT end point, at all HCW end points, and at the 432.5-d-of-age end point.

Retained Heterosis. For MARC III, the estimate of fat-adjusted heterosis effect for FP was positive ($P < 0.05$) at 0.7 cm of AFT, was negligible at 1.1 cm, and was negative ($P < 0.01$) at 1.5 cm. The positive estimate was about 2 times smaller in absolute value than the negative estimate (1.59 vs. -3.44%). The MARC II composite had significantly positive estimates of heterotic effects at all AFT end points ($P < 0.05$), at end point of 295.1 kg of HCW ($P < 0.01$), and at end point of 432.5 d of age ($P < 0.01$). Mean estimates of positive retained heterosis effects for the 3 composites were significant at the smallest AFT ($P < 0.01$), at the smallest HCW ($P < 0.05$), and at the age ($P < 0.05$) end points.

Bone Percentage

Breed Effects. Estimates of differences from A for BP were generally larger at constant HCW than at AFT or age end points (Table 15). Angus steers had significantly less BP than B at 0.7 and 1.1 cm, S, C, and P at 0.7 cm, and MARC III at 1.1 and 1.5 cm AFT end points. Estimates of BP adjusted for HCW or for age were significantly smaller for A than for nearly all other breeds, except that H and L did not differ significantly from A. Hedrick et al. (1970) reported greater BP for C than for A heifers. With adjustment to 0.7 cm of AFT, medium-lean-to-fat-ratio breeds had larger ($P < 0.01$) estimates of BP than low- and high-lean-to-fat-ratio breeds, but at the other 2 AFT end points, differences for these comparisons were not significant. At HCW and age constant end points, low-lean-to-fat-ratio breeds had smaller ($P < 0.01$) estimates of BP than medium- and high-lean-to-fat-ratio breeds, which also were significantly different ($P < 0.01$) from each other.

Retained Heterosis. Significant negative estimates of heterosis effects were obtained for MARC I and MARC II at the end point of 295.1 kg of HCW and at 432.5 d of age, and for the mean of the 3 composite populations at end points of 0.7 cm of AFT, 295.1 kg of HCW, and 432.5 d of age. In contrast, a positive estimate of heterosis ($P < 0.01$) was found for MARC III at the largest fatness end point.

Final Remarks

Differences by breed in estimates of regression coefficients for carcass measurements on covariates of HCW and AFT indicate variation in growth and maturity patterns among breeds. Estimates of breed differences revealed ranking of breeds for carcass characters may change for different physiological (fat, weight, or age) end points and by level within a type of end point. For example, the estimate of FW for MARC III was greater at 0.7 cm of AFT, but was less at 1.5 cm when compared

with A. Significant estimates of differences in YG and PRP favored A over C at constant AFT end points, whereas estimates favored C over A at constant HCW end points. At any given end point, A was estimated to have thicker external fat than all other breeds (except for H), but less LMA (except for R and H) and RPW (except for R, H, and MARC III). Differences from A across AFT end points were not as consistent as across HCW endpoints for most traits and breeds. There is some evidence that L and C performed differently for some carcass traits (e.g., RPP, BP), indicating that those 2 breeds should not be combined to form the high-lean-to-fat-ratio group. Regardless of slaughter end point, high- and medium-lean-to-fat-ratio breeds were estimated to have more desirable YG, LMA, PRP, RPW, and RPP, but smaller AFT and FP than low-lean-to-fat-ratio breeds. In general, high-lean-to-fat-ratio breeds had greater DP and RPW than medium-lean-to-fat-ratio breeds but smaller MS and less fat (weight and percentage) and bone (weight and percentage). For HCW, AFT, KPH, YG, and PRP, high- and medium-lean-to-fat-ratio breeds were comparable. Significance and estimates of expression of retained heterotic effects also depended on the type of slaughter end point and levels of the end points. Adjustment for age resulted in little evidence for effects of heterosis retained for AFT, whereas adjustment for HCW resulted in no evidence for effects of heterosis for LMA. For some traits (e.g., RPP and FP), estimates of effect of retained heterosis for MARC III at an intermediate degree (1.1 cm) of fatness were not important, but at extreme end points (0.7 and 1.5 cm), effects for heterosis were not only significant, but also the signs of the estimates changed. Estimates of retained heterosis were generally not important for DP, MS, YG, and PRP with any end point. For all of the carcass traits, except KPH, little evidence of retained heterosis was found for MARC I on an AFT constant basis, and no evidence of retained heterosis was found for MARC III on an HCW-constant basis.

IMPLICATIONS

Important differences in carcass characteristics existed among the purebred and composite steers evaluated. Rational exploitation of breed groups for beef production, however, requires special attention to use of different slaughter end points and levels of those end points, particularly for fat thickness. As an example, with respect to the US Meat Animal Research Center III composite, to take advantage of retained heterosis effects (or to avoid negative effects of heterosis) for actual percentage of retail product or fat percentage, beef producers should wait until steers get to intermediate levels of finish (1.2 or 1.3 cm of fat thickness) before harvest. Extrapolation of such results for US Meat Animal Research Center III heifers, bulls or hormonally implanted steers may not be appropriate because of potential differences in composition relative to nonimplanted steers, such as those in the current study.

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