Breed Effects, Retained Heterosis, and Estimates of Genetic and Phenotypic Parameters for Carcass and Meat Traits of Beef Cattle[1,2]

K. E. Gregory, L. V. Cundiff, R. M. Koch[3], M. E. Dikeman[4], and M. Koohmaraie

Roman L. Hruska U.S. Meat Animal Research Center, ARS, USDA, Clay Center, NE 68933

ABSTRACT: Retained heterosis for meat traits was estimated in F_3 generation castrate males in three composite populations of beef cattle finished on two levels of dietary energy density (2.82 Mcal of ME and 3.07 Mcal of ME and 11.50% CP) and serially slaughtered at four end points at intervals of 20 to 22 d. Breed effects were evaluated in nine parental breeds (Red Poll [R], Hereford [H], Angus [A], Limousin [L], Braunvieh [B], Pinzgauer [P], Gelbvieh [G], Simmental [S], and Charolais [C]) that contributed to the three composite populations (MARC I = 1/4 B, 1/4 C, 1/4 L, 1/8 H, 1/8 A; MARC II = 1/4 G, 1/4 S, 1/4 H, 1/4 A; and MARC III = 1/4 R, 1/4 P, 1/4 H, and 1/4 A). Breed effects were important ($P < .01$) for all carcass and meat traits evaluated. Dietary energy density and slaughter group affected ($P < .05$) most traits evaluated. The effects of retained heterosis were not consistent among composites. For the mean of the three composites, retained heterosis was significant only for percentage of 9-10-11th rib fat and for percentage of retail product. Phenotypic correlations indicated that marbling score was a poor predictor of palatability attributes of individual carcasses. Estimates of heritability were intermediate to high for measures of fatness but were generally low for palatability attributes. The high negative genetic correlation (−.56) between percentage of retail product and marbling score and the relatively low genetic correlations between percentage of retail product and palatability attributes suggests the need for simultaneous attention to percentage of retail product and palatability attributes rather than to marbling score. Correlations among breed group means were generally high for measures of fatness with palatability attributes and were high and negative for percentage of retail product with marbling score and with other measures of fatness. Limited opportunity exists for selecting among breeds to achieve high levels of marbling in the longissimus muscle simultaneously with a high percentage of retail product. These results suggest that the most logical approach to resolution of the genetic antagonism between favorable carcass composition and less favorable palatability attributes is to form composite breeds with breed contributions organized to achieve an optimum balance between favorable carcass composition and desirable palatability attributes at optimum slaughter weights.

Key Words: Cattle, Heterosis, Breeds, Genetic Parameters, Energy Intake, Meat Characteristics

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Introduction

Heterosis achieved through continuous crossbreeding can be used to increase weight of calf weaned per cow exposed to breeding by 20% (Gregory and Cundiff, 1980). Comprehensive programs of breed characterization have revealed large differences among breeds for most bioeconomic traits (Gregory et al., 1982; Cundiff et al., 1986). Fluctuation in breed composition between generations in rotational crossbreeding systems can result in considerable variation among both cows and calves in level of performance for major bioeconomic traits unless breeds used in the rotation are similar in performance characteristics. Use of breeds with similar performance characteristics restricts the use that can be made of breed differences in average genetic merit to meet requirements for

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[3]Anim. Sci. Dept., Univ. of Nebraska, Lincoln 68583-0908.

[4]Dept. of Anim. Sci. and Ind., Kansas State Univ., Manhattan 66506-0201.

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specific production and marketing situations (Gregory and Cundiff, 1980). Retention of initial (F_1) heterozygosity after crossing and subsequent random (*inter se*) mating within the crosses is proportional to $(n - 1)/n$, where n breeds contribute equally to the foundation (Wright, 1922; Dickerson, 1969, 1973). When breeds used in the foundation of a composite breed do not contribute equally, percentage of mean (F_1) heterozygosity retained is proportional to $1 - \sum_i^n P_i^2$, where P_i is the fraction of each of n breeds contributing to the foundation of a composite breed (Dickerson, 1973). This loss of heterozygosity occurs between the F_1 and F_2 generations, and if inbreeding is avoided, further loss of heterozygosity in *inter se*-mated populations does not occur (Wright, 1922; Dickerson, 1969, 1973).

The objectives of this study were 1) to evaluate differences among parental breeds in carcass and meat traits of castrate males finished on two levels of dietary energy density, 2) to estimate retention of combined individual and maternal heterosis in the F_3 generation for carcass and meat traits in *inter se*-mated composite populations of beef cattle, and 3) to estimate phenotypic and genetic (co)variation for carcass and meat traits of beef cattle.

Materials and Methods

Populations. Matings to establish three composite populations are shown in Table 1. In this experiment the F_1 is defined as the first generation that reflects the final breed composition of a composite population. As indicated by Table 1, F_1, F_2, and F_3 generations were mated *inter se* to produce, respectively, F_2, F_3, and F_4 generation progeny. Composite populations were formed from the same sires and dams that were represented in the nine contributing parental breeds listed in Table 2. Contributing purebred contemporaries have been maintained for Pinzgauer since 1982 and for all other breeds since 1978 when the first calves were born in the experiment. The first 3/4 Pinzgauer were produced in 1980, 7/8 Pinzgauer (purebred for females in breed registry) were born in 1982, and 15/16 Pinzgauer (purebred for registry of males) have been produced since 1984. Pinzgauer females (7/8) producing (15/16) Pinzgauer progeny were included in this data set.

The Braunvieh population averaged between 3/4 and 7/8 Braunvieh and was established by using semen from nine Braunvieh sires originating in Switzerland and the Federal Republic of Germany (Bavaria) on a foundation of purebred (registered and unregistered) Brown Swiss females obtained from dairy herds in Wisconsin and Minnesota as calves in 1967 and 1968. The breed substitution from Brown Swiss to Braunvieh started in 1969. The Simmental, Limousin, Gelbvieh, and Pinzgauer populations were established by mating 20 or more sires of each breed to purebred females from the same Hereford and Angus populations used in the experiment (except as noted) and subsequently repeatedly backcrossed to the four breeds of sires. Grade-up programs to these breeds started at the U.S. Meat Animal Research Center (MARC) in 1969 for Simmental, in 1970 for

Table 1. Matings to establish composites, retention of heterozygosity, and expected retention of heterosis

			Composite populations			
			MARC I	MARC II	MARC III	Mean
Parents of F_1 generation[a]			(C × LH) × (B × LA) or (C × LA) × (B × LH) Reciprocals	(GH) × (SA) or (GA) × (SH)	(PA) × (RH) or (PA) × (HR) Reciprocals	—
Breed composition of F_1 and subsequent generations			.25B, .25C, .25L .125H, .125A	.25G, .25S .25H, .25A	.25P, .25R .25H, .25A	— —
F_1 Heterozygosity[b]			.94[d]	1	1	.98
F_2 Heterozygosity			.78	.75	.75	.76
F_3 Heterozygosity			.78	.75	.75	.76
	Dam	Progeny				
Heterosis[c]	F_1	F_2	.78 H^i + .94 H^m	.75 H^i + 1 H^m	.75 H^i + 1 H^m	.76 H^i + .98 H^m
Heterosis	F_2	F_3	.78 H^i + .78 H^m	.75 H^i + .75 H^m	.75 H^i + .75 H^m	.76 H^i + .76 H^m
Heterosis	F_3	F_4	.78 H^i + .78 H^m	.75 H^i + .75 H^m	.75 H^i + .75 H^m	.76 H^i + .76 H^m

[a]Composite populations were established from the same animals used in the purebred foundation, where C = Charolais, L = Limousin, H = Hereford, B = Braunvieh, A = Angus, G = Gelbvieh, S = Simmental, P = Pinzgauer, and R = Red Poll.

[b]Retention of initial (F_1) heterozygosity following crossing and subsequent random mating within the crosses (*inter se*) is proportional to $1 - \sum_i^n P_i^2$, where P_i is the fraction of each of n breeds contributing to the foundation of a composite population. Loss of heterozygosity occurs between the F_1 and F_2 generations. If inbreeding is avoided, further loss of heterozygosity is not expected.

[c]H^i denotes individual heterosis expressed by progeny of a given generation and H^m denotes maternal heterosis expressed by their dams assuming that retention of heterosis is proportional to retention of heterozygosity.

[d].94 instead of 1 because both sires and dams of F_1 generation were one-fourth Limousin.

Table 2. Summary of *F*-statistics, residual mean squares, and least squares breed group means for mean traits

Item	df or n	Adj. fat, cm[a]	Marbling score[b]	Longissimus muscle fat, %	Fat 9-10-11th rib cut, %	Shear force, kg[c]	Sensory panel			Retail product, % 0 mm of fat trim
							Tenderness[d]	Juiciness[e]	Flavor[f]	
Analysis of variance										
Breed group (B)	11	100.97**	27.21**	31.84**	109.90**	14.97**	16.03**	5.02**	4.29**	130.0**
Sires/B[g]	294	.12	.50	1.70	32.30	1.38	.50	.24	.12	14.9
Feed level (F)	1	147.21**	84.58**	42.09**	177.11**	11.50**	1.65	.06	65.18**	135.4**
Slaughter group (S)	3	58.10**	26.64**	16.49**	45.15**	1.30	3.26*	1.12	3.10*	49.8**
Year	3	3.79**	21.80**	25.43**	3.82**	47.69**	13.58**	1.20	106.07**	17.8**
B × F	11	5.58**	.76	.60	1.36	1.30	1.43	1.53	1.01	1.8
B × S	33	1.78**	1.22	1.34	1.33	.90	.74	.78	1.13	1.1
F × S	3	1.49	.87	2.34	.68	2.73*	.16	.79	.37	1.7
F × Y	3	3.60**	12.80**	8.25**	6.64**	5.05**	1.94	1.39	2.62*	8.0**
Regression										
Initial age, d	1	6.18**	18.95**	33.67**	27.87**	5.78*	3.2	5.29*	.00	30.3**
Remainder[g]	1,235	.08	.29	1.03	23.56	1.19	.40	.18	.11	8.8
Least squares means										
μ	1,599	.65	4.97	3.96	33.01	5.09	5.07	5.17	4.87	65.8
Breed group means										
Red Poll	114	.76	5.30	4.65	38.34	4.72	5.15	5.25	4.96	62.6
Hereford	133	1.16	5.24	4.53	40.09	5.06	5.10	5.25	4.80	60.1
Angus	117	1.18	5.40	4.80	40.01	4.50	5.55	5.38	4.92	61.5
Limousin	138	.42	4.46	2.82	26.51	5.62	4.88	5.01	4.82	72.3
Braunvieh	138	.46	4.85	3.67	29.83	5.09	5.06	5.12	4.90	67.3
Pinzgauer	119	.43	5.16	4.22	30.82	4.47	5.43	5.20	4.96	66.8
Gelbvieh	148	.36	4.53	3.22	27.60	5.78	4.63	5.04	4.75	70.0
Simmental	126	.39	4.80	3.72	28.67	5.48	4.80	5.14	4.83	68.4
Charolais	125	.37	4.71	3.38	28.02	5.16	4.95	5.12	4.88	68.7
D.05[h]		.13	.27	.50	2.20	.45	.27	.19	.13	1.5
MARC I F_3	157	.57	4.80	3.56	31.15	5.01	5.22	5.14	4.87	67.2
MARC II F_3	146	.80	5.15	4.36	36.37	5.05	5.04	5.18	4.90	63.1
MARC III F_3	138	.92	5.30	4.59	38.69	5.12	5.06	5.20	4.88	61.9
D.05[i]		.14	.28	.52	2.28	.47	.28	.20	.14	1.5

[a]Subcutaneous fat at 12th rib.
[b]4.00 to 4.90 = slight; 5.00 to 5.90 = small.
[c]Shear force required to cut a 1.27-cm core.
[d]4 = slightly tough; 5 = slightly tender; 8 = extremely tender.
[e]4 = slightly dry; 5 = slightly juicy; 8 = extremely juicy.
[f]4 = slightly bland; 5 = slightly intense; 8 = extremely intense.
[g]Sires within breed group and residual mean squares.
[h]D.05 is the approximate difference between means of parental breeds required for significance.
[i]D.05 is the approximate difference between means of all breed groups required for significance.
*$P < .05$.
**$P < .01$.

Limousin, in 1975 for Gelbvieh, and in 1977 for Pinzgauer. A sample of 3/4 Gelbvieh females bred to produce 7/8 Gelbvieh progeny was purchased in 1977 to augment the Gelbvieh population that was graded-up from a female population of Charolais × Angus with the same sample of Gelbvieh sires used in the Gelbvieh grade-up program at the MARC. The Charolais population was established primarily with the purchase of registered purebred Charolais females in 1977 and was augmented by Charolais graded-up from Angus × Hereford females at the MARC starting in 1967. Charolais sires were sampled from a broad genetic base. The Red Poll population was established from registered females purchased from several sources in 1966, 1967, and 1968, with sires sampled from a broad genetic base. The Hereford and Angus breeds have been maintained as closed populations (except as noted) since about 1960. A sample of Hereford males and females was added in 1966, but this sample did not produce any male progeny that were used to maintain the population. A sample of Angus sires was introduced in 1967 and 1968, but no male progeny were produced from these matings that were used to maintain the population. Sires used to maintain the purebred populations were descendents from males and females used in the foundation of the composite population to which a pure breed contributed. The purebreds have been maintained as registered populations recorded in the appropriate Herd Book of a breed record society.

The castrate males included in this study were the unselected male progeny of 21 Red Poll, 22 Hereford, 23 Angus, 24 Limousin, 26 Braunvieh, 27 Pinzgauer, 27 Gelbvieh, 19 Simmental, 25 Charolais, 39 MARC I, 30 MARC II, and 24 MARC III sires. Animals included in this study were born in 1988, 1989, 1990, and 1991 from dams that were 2, 3, 4, and ≥ 5 yr old.

Feeding and Management. Mean birth date of animals included in this experiment was April 13. In the last 3 yr animals were weaned at an average age of approximately 150 d on September 7 or 11. Because of drought in 1988, animals were weaned on August 18 at an average age of 127 d. Animals were started on a diet of 2.65 Mcal of ME/kg of dry matter and 15.4% crude protein composed of ground alfalfa hay, corn, corn silage, and protein-mineral supplement. Corn silage replaced ground alfalfa hay and corn on a gradual basis to a backgrounding diet that was 2.69 Mcal of ME/kg of dry matter and 12.88% crude protein composed of corn silage (66%), corn (22%), and protein-mineral supplement (12%). At an average age of 203 d between October 30 and November 15 over the 4 yr, animals of each breed group were weighed and were assigned to treatment on a random basis stratified by weight. Prior to assigning animals to treatment, seven to nine males in each breed group were identified as candidate replacement sires. Candidate replacement sires were identified to represent a broad pedigree base and were near the mean weight of their respective breed group.

Treatment was dietary energy density with two finishing diets for each year-breed group subclass. Feed level 1 (finishing diet) was 2.82 Mcal of ME/kg of dry matter and 11.50% crude protein. Feed level 2 (finishing diet) was 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein. Composition of diet (dry matter basis) for feed level 1 was corn silage (59.77%), rolled corn (32.77%), and protein-mineral supplement (7.46%). Composition of diet (dry matter basis) for feed level 2 was corn silage (18.00%), corn (75.24%), and protein-mineral supplement (6.76%).

Animals were kept on the backgrounding diet (2.69 Mcal of ME/kg of dry matter and 12.88% CP) for different periods in different years before they were changed to the finishing diet. Dietary change dates by birth year were as follows: 1988, February 27; 1989, January 31; 1990, January 2; and 1991, November 11. Feed consumption data were recorded on a pen basis starting on November 9 in 1988 and on December 4 in 1989, 1990, and 1991. Animals had ad libitum access to feed two times each day.

Immediately after assignment to treatment, animals were castrated. Animals born in 1988 and 1989 were castrated by standard surgical procedures, whereas animals born in 1990 and 1991 were castrated by a banding procedure that prevented circulation of blood to the testes.

Slaughter and Processing Procedures. Animals were serially slaughtered at four end points with 20, 21, or 22 d between slaughter dates and 63 d between first and fourth slaughter. The initial slaughter date was between May 21 and 26 for the 4 yr. Days between initial weight (203 d) to final weight averaged 204, 224, 245, and 267 d for the four slaughter groups. Thus, mean days fed from initial to final weight was 235 and mean slaughter age was 438 d. Steers were assigned to slaughter group on a random basis stratified by weight based on the last weight taken before the start of the serial slaughter schedule. Final weight was a single weight taken starting at 0700 after overnight access to feed and water 7 or 8 d before slaughter. All steers were weighed before each slaughter date. Weights of animals slaughtered at the first three slaughter dates averaged approximately the same as those of animals remaining in a pen.

Animals were slaughtered in a commercial facility. Following a chill period of 24 h, fat thickness at the 12th rib, fat thickness at 12th rib adjusted for differences in distribution of subcutaneous fat over the entire carcass, estimated perirenal fat percentage, and longissimus muscle area were obtained and the right side of each carcass was returned to the MARC to obtain carcass cut-out, chemical composition, and meat sensory data. For animals born in 1988, 1989, and 1990, limitations on carcass processing capability forced random sampling of sides for detailed cut-out and meat sensory data. This included a total of 65 carcasses on which cut-out data were not obtained in the 3 yr.

Carcasses were processed into wholesale cuts of round, loin, rib, chuck, plate, flank, and brisket plus shank. Each wholesale cut was fabricated into boneless steaks, roasts, lean trim, and fat trim to 8 mm of fat trim, except that the dorsal and lateral vertebral processes in the short loin and dorsal vertebral processes and ribs were left in standing rib roasts. Lean trim was targeted to contain 20% fat. Further processing removed all subcutaneous and accessible intermuscular fat (0 mm of fat trim) from any surface, and the remaining bone was removed from the short loin and from the standing rib roasts. The 9-10-11th rib cut was removed and processed by the procedures described for wholesale cuts and kept separate from the remainder of the rib. Soft tissue (lean and fat) from the 9-10-11th rib cut was ground and sampled to determine water and fat.

Retail product included trimmed (8 mm or 0 mm of 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.

Three longissimus muscle steaks, cut 2.5 cm thick from the 5-6th and 12th ribs, were frozen on d 9 after slaughter and were used for chemical determination of water and fat in the longissimus muscle, for Warner-Bratzler shear force, and for trained sensory panel evaluation of the longissimus muscle. Water was determined by oven drying and fat was determined by ether extraction. Procedures for thawing, cooking, coring, and serving samples to the trained sensory panel and for shearing cores followed AMSA (1978) guidelines, except that steaks for shear force determination were chilled overnight.

Analyses of Data. Data were analyzed by least squares mixed-model procedures (Harvey, 1985). The model included breed group, sires within breed group (random effect), feed level, slaughter group, year of birth, the interactions of breed group with feed level and with slaughter group, and the interactions of feed level with year of birth and with slaughter group. Age at initial weight was included in the model as a covariate to adjust to a common initial age. Age of dam was not significant for the traits evaluated. Interactions that were significant for any trait were included in the final analysis. Three-way interactions were assumed to be unimportant.

Studentized Range [$D = Q_{.05}(S\bar{X})$] as described by Snedecor and Cochran (1980) was computed to obtain approximations of differences among breed groups required for significance. Linear functions of means for parental breeds and for F_3 generation progeny of each composite population and for the mean of the three composite populations were computed to estimate retained heterosis. Heterosis was not estimated in the F_1 and F_2 generations for the traits reported in this paper. Retained heterosis in the F_3 generation was estimated from the mean of a composite population minus the mean of the contributing purebreds weighted by their contribution (1/4 or 1/8) to the composite population. Genetic expectations for individual and maternal heterosis ($H^i + H^m$) are presented in Table 1 for each generation. Sires within breed group mean square was used as the error term to test significance of differences among breed groups (F-test), to determine the approxmiate difference between specific breed groups required for significance, and as the error term for linear contrasts to estimate retained heterosis.

Results and Discussion

Analysis of Variance

Analyses of variance for the traits analyzed are presented in Table 2. Differences among breed groups were important ($P < .01$) for all traits analyzed. Differences between dietary energy densities were important ($P < .01$) for all traits except sensory panel tenderness and juiciness scores for the longissimus muscle. The effects of slaughter group were significant for all traits except shear force of longissimus muscle steaks and sensory panel juiciness score. Year effects were important ($P < .01$) for all traits except sensory panel juiciness score. The interactions of breed group × feed level and breed group × slaughter group were significant only for 12th rib adjusted fat thickness. The interaction of feed level × slaughter group was significant only for Warner-Bratzler shear force. The interaction of feed level × year was significant for all traits except sensory panel tenderness and juiciness scores.

Differences Among Breed Groups

Differences among parental breeds reported here include the sum of the additive direct and additive maternal genetic effects ($G^i + G^m$) (Table 2). Differences between each composite and mean of contributing parental breeds weighted by their contribution (1/4 or 1/8) include either .75 or .78 (Table 1) of the F_1 level of heterosis (Gregory et al., 1991a,b,c,d; 1992a,b,c; 1994).

Large differences were observed among breed groups in 12th rib adjusted fat thickness. The three composite populations were intermediate in 12th rib adjusted fat thickness.

Marbling score ranged from 4.46 in Limousin to 5.40 in Angus, with a mean of 4.97. Pinzgauer had the highest score (5.16) for marbling among the European Continental breeds. The composites tended to be intermediate.

Mean longissimus muscle fat was 3.96%, ranging from 2.82% in Limousin to 4.80% in Angus. The composites ranged from 3.56% longissimus muscle fat in MARC I to 4.59% in MARC III. The magnitude of differences among breed groups was greater for percentage of longissimus muscle fat than for marbling score. This suggests a reluctance by USDA beef graders to score marbling below the degree of slight, or lower than the degree required for the quality grade of USDA Select.

The regression of percentage of longissimus fat on marbling score was 1.18 for one degree of marbling (i.e., 4.00 to 4.90 = slight degree of marbling) with an intercept of −1.90.

Mean percentage of fat in the 9-10-11th rib cut was 33.01%, ranging from 26.51% in Limousin to 40.09% in Hereford. Although Pinzgauer had a mean marbling score similar to that of Hereford, they had 9.27% less 9-10-11th rib fat and .73 cm less 12th rib adjusted fat thickness. Composites ranged from 31.15% in MARC I to 38.69% in MARC III.

Mean shear force was 5.09 kg, ranging from 4.47 kg in Pinzgauer to 5.78 kg in Gelbvieh. Pinzgauer, Angus, and Red Poll required the least shear force (kilograms) and did not differ ($P > .05$) from each other. Gelbvieh, Limousin, and Simmental required the most shear force and did not differ ($P > .05$) from each other. Charolais, Braunvieh, and Hereford were intermediate in shear force and were not different ($P > .05$) from each other. Composites were intermediate and were similar in shear force value.

Mean sensory panel evaluation for tenderness, juiciness, and flavor scores were, respectively, 5.07, 5.17, and 4.87. It should be noted that these mean sensory panel scores are relatively low for young cattle from *Bos taurus* breeds fed for a long period on diets with relatively high energy densities. These relatively low sensory panel scores suggest that the sensory panelists may have used a scale that is lower than that generally used. The magnitude of differences among breeds for tenderness evaluated by sensory panel was less than that for shear force. For sensory panel tenderness score, Gelbvieh, Limousin, and Simmental were lowest and were not different ($P > .05$) from each other; Angus and Pinzgauer were highest and were not different ($P > .05$) from each other. Charolais, Braunvieh, Red Poll, and Hereford had intermediate tenderness scores and were not different ($P > .05$) from each other.

Although differences among breed groups in sensory panel juiciness and flavor scores were significant, they were of smaller magnitude than breed group differences in sensory panel tenderness scores and tended to be associated with breed group rankings for sensory panel tenderness scores.

Differences in Feed Level and in Slaughter Group

The higher level of energy density resulted in higher ($P < .01$) 12th rib adjusted fat thickness, higher ($P < .01$) score for marbling, greater ($P < .01$) percentage of longissimus muscle fat, greater ($P < .01$) percentage of fat in the 9-10-11th rib, less ($P < .01$) shear force, greater ($P < .01$) sensory panel evaluation of flavor intensity, and lower ($P < .01$) percentage of retail product (Table 3). The lack of significance of breed group × feed level interaction for all traits except 12th rib adjusted fat thickness is noted because we expected an interaction (Table 2). There was no effect of energy density on tenderness and juiciness scores as evaluated by the sensory panel.

The effect of slaughter group was significant for 12th rib adjusted fat thickness. The difference between slaughter groups averaged .10 cm and ranged from .08 to .12 cm. The effect of slaughter group on marbling score was significant; however, there was no difference ($P > .05$) in marbling score between slaughter groups 3 and 4. The effect of slaughter group also was significant on percentage of longissimus fat. The decrease observed in percentage of longissimus fat between slaughter groups 1 and 2 is not consistent with the marbling scores and percentage of fat in the 9-10-11th rib cut for slaughter groups 1 and 2 and is likely accounted for by sampling error. The effect of slaughter group on percentage of fat in the 9-10-11th rib cut was significant and averaged 1.42% between slaughter groups. The effect of slaughter group on shear force was not significant. The effects of slaughter group on sensory panel scores were significant for tenderness and flavor but not for juiciness. For sensory panel scores for tenderness and flavor, slaughter group 1 was favored over slaughter groups 2, 3, and 4. The lack of significance for breed group × slaughter group interaction for all traits except 12th rib adjusted fat thickness is noted and was not expected (Table 2). The effects of slaughter group on percentage of retail product were significant and averaged about 1% between slaughter groups.

Retained Heterosis

The effects of retained heterosis were not significant for any trait in composite MARC I (Table 4). For composite MARC II, the effects of retained heterosis were significant for marbling score (.16), percentage of longissimus fat (.29), percentage of 9-10-11th rib fat (2.28%), sensory panel flavor score (.08), and percentage of retail product (−1.904). For composite MARC III, the effects of retained heterosis were significant for percentage of 9-10-11th rib fat (1.37), shear force (.44 kg), sensory panel tenderness score (−.24), and percentage of retail product (−.894). The agreement in retained heterosis for shear force and sensory panel tenderness score suggests that the difference between composite MARC III and the mean of the parental breeds is real. It is noted that two of the parental breeds of MARC III (e.g., Red Poll and Pinzgauer) were among the lowest in shear force value and among the highest in tenderness evaluated by sensory panel. Sampling error contributing to these parental breed means for shear force value and sensory panel score for tenderness could result in the values observed for retained heterosis for these traits. Sampling error of steaks is unlikely because shear force (kilograms) and sensory panel tenderness scores were evaluated on different steaks from the longissimus muscle. For the mean of the three composite populations, the effects of retained heterosis were significant only for percentage of 9-10-11th rib fat and for percentage of retail product.

Table 3. Effects of feed level and slaughter group on meat traits

Item	No.	Adj. fat, cm[a]	Marbling score[b]	Longissimus muscle fat, %	Fat 9-10-11th rib cut, %	Shear force, kg[c]	Sensory panel: Tenderness[d]	Sensory panel: Juiciness[e]	Sensory panel: Flavor[f]	Retail product, % 0 mm of fat trim
Overall mean	1,599	.65	4.97	3.96	33.01	5.09	5.07	5.17	4.87	65.8
Feed level[g]										
1	783	.56**	4.84**	3.78**	31.27**	5.19**	5.05	5.17	4.80**	66.8**
2	816	.75	5.11	4.14	34.75	4.99	5.10	5.17	4.95	64.9
Slaughter group[h]										
1	347	.50**	4.78**	3.89**	30.82**	5.08	5.16*	5.13	4.92*	67.2**
2	419	.62	4.91	3.69	32.24	5.13	5.09	5.17	4.84	66.3
3	439	.70	5.10	4.05	33.88	5.15	5.02	5.20	4.86	65.3
4	394	.80	5.11	4.22	35.08	4.99	5.02	5.18	4.87	64.4
Regression										
Initial age, d	—	.00136**	.00442**	.01117**	.04856**	–.00498**	.00214	.00188*	–.00001	–.36**

[a]Subcutaneous fat at 12th rib.
[b]4.00 to 4.90 = slight; 5.00 to 5.90 = small.
[c]Shear force required to cut a 1.27-cm core.
[d]4 = slightly tough; 5 = slightly tender; 8 = extremely tender.
[e]4 = slightly dry; 5 = slightly juicy; 8 = extremely juicy.
[f]4 = slightly bland; 5 = slightly intense; 8 = extremely intense.
[g]Feed level 1 and 2 = 2.82 Mcal of ME or 3.07 Mcal of ME/kg dry matter and 11.50% crude protein.
[h]Animals were serially slaughtered at four end points with 20, 21, or 22 d between slaughter dates and 63 d between first and fourth slaughter dates.
*$P < .05$.
**$P < .01$.

Table 4. Effect of retained heterosis on carcass and meat traits

Item	Adj. fat, cm[a]	Marbling score[b]	Longissimus muscle fat, %	Fat 9-10-11th rib cut, %	Shear force, kg[c]	Sensory panel			Retail product, % 0 mm of fat trim
						Tenderness[d]	Juiciness[e]	Flavor[f]	
Linear contrasts									
Heterosis									
MARC I[a] minus purebreds	−.03	−.04	−.08	.05	−.15	.16	.00	.01	−.111
MARC II[a] minus purebreds	.03	.16*	.29*	2.28**	−.16	.02	−.02	.08*	−1.904**
MARC III minus purebreds	.03	.03	.04	1.37**	.44**	−.24**	−.07	−.02	−.894*
Mean heterosis									
All composites									
Composites minus purebreds	.01	.05	.08	1.23**	.04	−.02	−.03	.02	−.970**

[a]Subcutaneous fat at 12th rib.
[b]4.00 to 4.90 = slight; 5.00 to 5.90 = small.
[c]Shear force required to cut a 1.27-cm core.
[d]4 = slightly tough; 5 = slightly tender; 8 = extremely tender.
[e]4 = slightly dry; 5 = slightly juicy; 8 = extremely juicy.
[f]4 = slightly bland; 5 = slightly intense; 8 = extremely intense.
*$P < .05$.

Genetic and Phenotypic Parameters

Estimates of genetic (**rg**) and phenotypic (**rp**) parameters are presented in Table 5.

Phenotypic Correlations. Adjusted fat at the 12th rib was relatively important in accounting for variation in percentage of 9-10-11th rib fat (R^2 = .29). Variation in marbling score accounted for 40% of the variation in percentage of longissimus muscle fat and 18% of the variation in 9-10-11th rib fat. Variation in marbling score accounted for only 5, 3, and 4%, respectively, of the variation in shear force and sensory panel evaluation of tenderness and juiciness, and only 1% of the variation in flavor. Thus, these results suggest that marbling score in cattle slaughtered at an average age of 437 d following a standard feeding regimen has very low predictive value for end-use properties (e.g., tenderness, juiciness, and flavor) of individual beef carcasses. This is in agreement with the results of Campion et al. (1975). The phenotypic correlations of percentage of longissimus muscle fat with percentage of fat in the 9-10-11th rib cut and with palatability attributes were similar to the phenotypic correlations of marbling score with the same traits. Variation in shear force accounted for 32% of the variation in sensory panel evaluation of tenderness (Table 5).

Estimates of Heritability. Estimates of heritability (h^2) of 12th rib adjusted fat thickness (.30), marbling score (.52), percentage of longissimus fat (.47), and percentage of retail product (.50) are in general agreement with prior estimates (Koch et al., 1982). However, the estimate of heritability of percentage of fat in the 9-10-11th rib cut (.28) is lower than was expected based on the report of Koch et al. (1982). The estimate of heritability of shear force (.12) was lower than that reported by Koch et al. (1982). This lower h^2 for shear force suggests that shear force was likely measured with low precision. The h^2 for sensory panel evaluations of tenderness, juiciness, and flavor generally were low, suggesting that differences were evaluated with low precision. However, the h^2 for sensory panel tenderness score (.21) was higher than h^2 for shear force (.12) (Table 5).

Genetic Correlations. Generally, estimates of genetic correlations (**rgs**) were much higher than estimates of phenotypic correlations (**rps**). Even though marbling score may have low predictive value for palatability attributes of individual carcasses, the high rgs between marbling score and percentage longissimus muscle fat with shear force suggest that marbling score may have potential for use as an indirect selection criterion to reduce shear force. The rg of marbling score with longissimus fat was .96 ± .06. The rg of marbling score with 12th rib adjusted fat (.32) was lower than that reported by Cundiff et al. (1964). The rg of marbling score with percentage of fat in 9-10-11th rib cut (.65) is in closer agreement with the report of Cundiff et al. (1964) for marbling score with other measures of fatness. The rg of marbling with percentage of retail product (−.56) reveals a high genetic antagonism between these traits. However, the rgs of percentage of retail product with shear force and sensory panel evaluations of tenderness, juiciness, and flavor were low.

The high rg with low standard error between marbling score and percentage of longissimus muscle

Table 5. Genetic and phenotypic parameters among carcass and meat traits of cattle[abc]

Item	Adj. fat, cm[a]	Marbling score	Longissimus muscle fat, %	Fat 9-10-11th rib cut, %	Shear force, kg	Sensory panel: Tenderness	Sensory panel: Juiciness	Sensory panel: Flavor	Retail product, (%) 0 mm fat trim
Adj. fat, cm	**.30 ± .09**	.24	.26	.54	-.06	.05	.10	.10	-.56
Marbling score	.32 ± .16	**.52 ± .10**	.63	.43	-.23	.19	.20	.12	-.42
Longissimus fat, %	.28 ± .17	.96 ± .06	**.47 ± .09**	.46	-.23	.16	.20	.12	-.47
9-10-11th rib fat, %	.71 ± .14	.65 ± .13	.65 ± .13	**.28 ± .09**	-.16	.13	.14	.12	-.77
Shear force, kg	-.35 ± .34	-1.00 ± .45	-.93 ± .44	-.05 ± .33	**.12 ± .08**	-.57	-.19	-.23	.15
Tenderness	.30 ± .25	.34 ± .19	.34 ± .20	.06 ± .26	-.98 ± .74	**.21 ± .08**	.60	.16	-.11
Juiciness	.45 ± .23	.28 ± .18	.41 ± .18	.33 ± .23	-.96 ± .53	.91 ± .14	**.24 ± .08**	-.06	-.14
Flavor	.31 ± .45	.34 ± .38	.48 ± .43	-.14 ± .45	-1.00 ± 1.00	.81 ± .60	1.00 ± .86	**.06 ± .08**	-.14
Retail product, 0 mm of fat trim	-.76 ± .28	-.56 ± .19	-.55 ± .20	-.90 ± .35	.22 ± .26	-.14 ± .22	-.31 ± .21	.02 ± .38	**.50 ± .10**

[a]Heritabilities (h^2) on diagonal (boldface type).
[b]Genetic correlations (rgs) below diagonal.
[c]Phenotypic correlations (rps) above diagonal.

fat (.96 ± .06) and the relatively high h^2 and low standard error for both marbling score and percentage of longissimus fat (i.e., .52 ± .10 and .47 ± .09) suggests that each was measured with relatively high precision. The low h^2 for shear force (.12 ± .08) and the high rgs with high standard errors of shear force with marbling score and with longissimus fat (−1.00 ± .45 and −.93 ± .44) suggests relatively low precision in measuring shear force. Further evidence is the generally higher standard errors of rgs involving shear force relative to standard errors of rgs involving other traits (Table 5).

Correlations Among Breed Group Means. Correlations among breed group means for carcass and meat traits are presented in Table 6. Marbling score and percentage of longissimus muscle fat were highly correlated with shear force (− .80 and −.74) and with sensory panel scores for tenderness and juiciness (range from .65 to .92). The correlation of marbling score with sensory panel flavor was .61. The correlation between marbling score and percentage of longissimus fat was .99.

These values reflect high correlations among breed group means for both marbling score and percentage of longissimus fat at the 12th rib with palatability attributes. However, high correlations were observed among breed group means for marbling score and percentage of longissimus fat with other measures of fat (e.g., adjusted fat at 12th rib [.81 and .82] and percentage of fat in 9-10-11th rib [.92 and .93]). The correlations of marbling score and percentage longissimus fat with percentage of retail product (0 mm of fat trim) were −.94 and −.95. Percentage of retail product generally was negatively associated with palatability attributes. There seems to be limited opportunity to select among breeds to achieve high levels of marbling and high levels of fat in the longissimus muscle simultaneously with achieving a high percentage of retail product in the carcass.

The optimum resolution of the problem resulting from the generally high genetic association between favorable carcass composition and less favorable palatability attributes may be to form composite breeds (Table 2), with breed contributions organized to achieve an optimum balance between favorable carcass composition and desirable palatability attributes at optimum slaughter weights.

Implications

Large differences exist among breeds for carcass composition and significant differences exist among breeds in longissimus muscle palatability attributes. Both within and among breeds, there is a positive genetic association between traits that reflect fatness and palatability attributes. Furthermore, there is a high genetic correlation between intramuscular fat

Table 6. Correlation coefficients among breed group means for carcass and meat traits

Item	Shear force, kg	Sensory panel			Adj. fat, cm	Marbling score	Longissimus muscle fat, %	Fat 9-10-11th rib cut, %
		Tenderness	Juiciness	Flavor				
Sensory panel								
Tenderness	−.95**							
Juiciness	−.82**	.79**						
Flavor	−.86**	.75**	.55					
Adj. fat, %	−.49	.54	.82**	.17				
Marbling score	−.80**	.72**	.92**	.61*	.81**			
Longissimus muscle fat, %	−.74**	.65*	.92**	.55	.82**	.99**		
Fat 9-10-11th rib cut, %	−.60*	.56	.86**	.35	.95**	.92**	.93**	
Retail product								
0 mm of fat trim, %	.62*	−.55	−.87**	−.37	−.91**	−.94**	−.95**	−.98**

*P < .05.
**P < .01.

(i.e., marbling) and other measures of carcass fat. The optimum resolution of the genetic antagonism between favorable carcass composition and less favorable palatability attributes may be to form composite breeds, with breed contributions organized to achieve an optimum balance between favorable carcass composition and desirable palatability attributes at optimum slaughter weights.

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