Breed Effects and Retained Heterosis for Growth, Carcass, and Meat Traits in Advanced Generations of Composite Populations of Beef Cattle[1,2]

K. E. Gregory*, L. V. Cundiff*, R. M. Koch†, M. E. Dikeman‡, and M. Koohmaraie*

*Roman L. Hruska U.S. Meat Animal Research Center, ARS, USDA, Clay Center, NE 68933; †Animal Science Department, University of Nebraska, Lincoln 68583-0908; and ‡Department of Animal Science and Industry, Kansas State University, Manhattan 66506-0201

ABSTRACT: Retained heterosis for growth, carcass, and meat traits was estimated in F_3 generation castrate male progeny in three composite populations 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 carcass weight, dressing percentage, fat thickness, and marbling score; for retail product, fat trim and bone percentages and weights at two levels of fat trim (8 and 0 mm); and for carcass lean, fat, and bone percentages and weights. Mean slaughter weight was 54.7 kg greater for the Simmental, Gelbvieh, and Charolais breeds than for the Limousin but did not differ ($P > .05$) from Limousin in retail product weight or carcass lean weight because of higher dressing percentage, lower fat trim percentage, and lower bone percentage of Limousin. The effects of dietary energy density were important ($P < .01$) for most traits. The interaction of breed group × dietary energy density generally was not important. Retained heterosis generally was significant for each composite population for weight of retail product, fat trim, bone, and carcass lean, fat, and bone. For percentage of retail product, fat trim, carcass lean, carcass fat, and chemical fat in the 9-10-11th rib cut, generally, heterosis was significant for composites MARC II and MARC III but not for composite MARC I (i.e., composites MARC II and MARC III had a lower percentage of retail product and carcass lean and a higher percentage of fat trim, carcass fat, and chemical fat in the 9-10-11th rib cut than the mean of contributing purebreds).

Key Words: Cattle, Heterosis, Breed Differences, Energy Intake, Growth Traits, Carcass Composition

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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). Furthermore, 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 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

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

Item			Composite population			
			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.

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* contributing breeds 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 growth, carcass, and meat traits of castrate males finished on two levels of dietary energy density, and 2) to estimate retention of combined individual and maternal heterosis in the F_3 generation for growth, carcass, and meat traits in *inter se*-mated composite populations 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 (i.e., Red Poll, Hereford, Angus, Limousin, Braunvieh, Pinzgauer, Gelbvieh, Simmental, and Charolais). 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 backcrossing to the four breeds of sire. Grade-up programs to these breeds started at the U.S. Meat Animal Research Center (MARC) in 1969 for Simmental, in 1970 for 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 to augment the Gelbvieh population in 1977 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 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 descended 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. Before 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%).

Immediately after assignment to treatment, animals were castrated. Animals were assigned to treatment on a random basis stratified by weight. 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.

Animals were kept on the backgrounding diet (2.69 Mcal of ME per kg of dry matter and 12.88% CP) for different periods in different years before changing to the finishing diet. Average ages when dietary energy density was changed to finishing diets by birth year were as follows: 1988, 319 d; 1989, 293 d; 1990, 264 d; and 1991, 212 d. Feed consumption data were recorded on a pen basis starting on the following dates for each year: 1988 on November 9 and in 1989, 1990, 1991 on December 4.

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. 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 weights were a single weight taken starting at 0700, after overnight access to feed and water. All steers were weighed at each slaughter date. Weights of steers slaughtered at the first three slaughter dates were approximately the same as weights of steers remaining in a pen.

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 longissimus muscle area were obtained and the right side of each carcass was returned to the MARC to obtain carcass cut-out and chemical composition data. For animals born in 1988, 1989, and 1990, limitations on carcass processing capability forced random sampling of sides for detailed cut-out and sensory data. Cut-out data were not obtained on a total of 65 carcasses in the 3 yr.

Carcasses were processed into wholesale cuts of round, loin, rib, chuck, plate, flank, and brisket plus

Table 2. Summary of *F*-statistics, residual mean squares, and least squares means for growth and cooler-measured carcass traits

Item	df or n	Initial wt, kg	Final wt, kg	ADG, kg	Carcass wt, kg	Dressing percentage, %
Analysis of variance						
Breed group (B)	11	64.45**	36.18**	11.86**	25.94**	34.66**
Sires/B[c]	295	785.50	2519.99	.02	1036.84	4.43
Feed level (F)	1	.00	163.92**	325.24**	217.80**	66.97**
Age of dam (A)	3	42.03**	8.23**	1.07	8.94**	2.06
Slaughter group (S)	3	.35	158.29**	5.27**	206.51**	56.26**
Year (Y)	3	124.94**	12.88**	21.72**	20.33**	17.58**
B × F	11	.61	.45	.93	.48	.70
B × S	33	.35	.32	.47	.53	1.30
F × Y	3	.33	3.80**	6.43**	4.03**	5.36**
F × S	3	.27	.97	1.42	.18	2.48
Regression						
Initial age, d	1	549.88**	99.01**	18.47**	99.03**	4.83**
Residual[c]	1,293	551.30	1811.96	.02	778.64	3.59
Least squares means						
μ	1,661	258	549	1.241	333	60.58
Breed group means						
Red Poll	114	250	525	1.170	315	59.98
Hereford	146	217	507	1.234	306	60.33
Angus	118	233	515	1.199	316	61.32
Limousin	142	241	519	1.184	330	63.43
Braunvieh	139	273	567	1.259	339	59.73
Pinzgauer	118	276	557	1.202	331	59.45
Gelbvieh	150	277	567	1.240	340	59.94
Simmental	127	274	581	1.316	348	59.79
Charolais	126	266	573	1.314	348	60.66
D.05[d]		10.7	19.2	.05	12.4	.81
MARC I F_3	178	265	563	1.274	345	61.24
MARC II F_3	148	274	573	1.275	347	60.48
MARC III F_3	155	254	543	1.226	329	60.56
D.05[e]		11.0	19.7	.06	12.7	.83

[a]Adj. fat = adjusted fat thickness at 12th rib, REA = area of longissimus muscle, Est. KPH = perirenal fat estimate.
[b]4.00–4.90 = slight; 5.00–5.90 = small.
[c]Sires within breed group and residual mean squares.
[d]D.05 is the approximate difference between means of parental breeds required for significance.
[e]D.05 is the approximate difference between means of all breed groups required for significance.
*P < .05.
**P < .01.

shank. Each wholesale cut was processed further by cutting into boneless steaks, roasts, lean trim, and fat trim to 8-mm fat trim, except that the dorsal and lateral vertebral processes in the short loin and dorsal vertebral processes and ribs were left in standing rib roasts. Lean trim was targeted to contain 20% fat and was adjusted to 20% based on chemical analysis of the lean trim. Further processing removed all subcutaneous and accessible intermuscular fat (0 mm 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 for determination of water and fat.

Retail product included trimmed (8- or 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 lean was calculated by summing the total of roasts and steaks trimmed to 0 mm of subcutaneous and accessible intermuscular fat and lean trim with all fat subtracted based on chemical analysis of the lean trim. Carcass fat was calculated as the sum of the physically removed perirenal, subcutaneous, and accessible intermuscular fat and mathematically removed fat from the lean trim based on chemical analysis. Carcass bone included all bone from the carcass. Three measures of composition resulted from these procedures: 1) retail product, fat trim, and bone;

Table 2 (*continued*). Summary of *F*-statistics, residual mean squares, and least squares means for growth and cooler-measured carcass traits

Adj. fat, cm[a]	REA, cm[2a]	Est. KPH, %[a]	Marbling score[b]	Percentage ≥ USDA Choice	Percentage ≥ USDA Select
99.64**	70.86**	18.40**	27.34**	23.84**	9.08**
.12	82.31	.46	.52	.25	.05
151.84*	14.33**	19.86**	88.98**	72.50**	7.31**
1.24	.92	1.10	1.02		
59.23**	38.58**	28.79**	29.61**	8.15**	6.51**
4.97**	8.65**	15.10**	16.05**	12.33**	1.06
5.81**	.92	1.31	.78	1.76	1.99*
1.83**	1.06	1.16	1.21	.91	2.00**
3.35**	1.08	5.18**	12.81**	7.44**	3.86**
1.26	.60	5.33**	.72	.91	.93
9.81	8.09**	12.90**	16.33**	20.20**	10.55**
.08	64.39	.35	.29	.17	.04
.654	78.1	2.77	4.97	.46	.95
.762	69.4	3.30	5.30	.71	1.00
1.158	67.9	2.41	5.21	.60	1.00
1.178	68.1	2.64	5.41	.77	1.00
.427	86.5	2.47	4.43	.14	.84
.464	85.2	2.79	4.84	.42	.94
.432	79.1	2.74	5.16	.55	.98
.360	83.7	2.68	4.53	.15	.85
.395	81.0	2.50	4.80	.34	.92
.370	80.6	2.80	4.71	.24	.96
.13	3.5	.26	.28	.19	.08
.587	83.5	2.94	4.79	.42	.91
.802	78.0	2.88	5.13	.57	1.00
.915	74.3	3.06	5.31	.65	.98
.14	3.6	.27	.28	.20	.09

2) carcass lean, fat, and bone; and 3) estimated lean, fat, and bone from the 9-10-11th and the wholesale rib.

Three longissimus muscle steaks, cut 2.5-cm thick from the 5 and 6th and from the 12th ribs, were frozen on d 9 after slaughter and were used for chemical determination of water and fat in the longissimus muscle, for shear force evaluation of the longissimus muscle. Sample preparation followed AMSA (1978) guidelines.

Analysis 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, age of dam, slaughter group, year of birth, interactions of breed group with feed level and with slaughter group, and 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. A second analysis deleted slaughter group as a main effect from the model and included days fed (linear and quadratic) in the model as a covariate. Interactions that were significant for any trait were included in the final analysis. Three-way interactions were assumed not to be important.

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. Retained heterosis 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 expectation 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 approximate 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 Tables 2, 3, 4, 5, 6, and 7. Differences among breed groups were important ($P < .01$) for all traits analyzed. The effects of dietary energy density (2.82 vs 3.07 Mcal of ME/kg of dry matter and 11.50% CP) were important ($P < .01$) for most traits analyzed. The effects of age of dam generally were important ($P < .01$) for most traits associated with weight but generally were not important ($P > .05$) for carcass composition traits. The effects of slaughter group and year were important ($P < .01$) for most traits analyzed. The interaction of breed group × dietary energy density generally was not significant; exceptions were adjusted carcass fat thickness, retail product percentage at 8 mm of fat trim, carcass lean percentage, and whole rib lean percentage. For these few exceptions, the earlier-maturing breed groups (i.e., Angus, Hereford, Red Poll, and MARC III) tended to have relatively more fat when fed the higher dietary energy density than the later-maturing breed groups (i.e., Charolais, Simmental, Braunvieh, Gelbvieh, Limousin, and MARC I). The interaction of breed group × dietary energy density was not significant for retail product weight or fat trim weight or for carcass lean or fat weight. A greater difference in response (B × E interaction) among breed groups to differences in dietary energy density was expected.

Generally, the interaction of breed group × slaughter group was not significant; the only exception was adjusted carcass fat thickness, which was not reflected

Table 3. Summary of *F*-statistics, residual mean squares, and least squares means for carcass composition (percentage)

Item	df or n	Retail product[a] 8 mm, %[b]	Retail product[a] 0 mm, %[c]	Fat trim 8 mm, %[b]	Fat trim 0 mm, %[c]	Bone 8 mm, %[b]	Bone 0 mm, %[c]
Analysis of variance							
Breed group (B)	11	120.0**	130.0**	122.3**	132.0**	69.8**	70.2**
Sires/B[d]	294	12.0	14.9	14.9	18.4	1.1	1.3
Feed level (F)	1	127.0**	135.4**	188.4**	192.2**	198.9**	192.8**
Age of dam (A)	3	1.8	1.8	1.5	1.6	.5	.6
Slaughter group (S)	3	52.3**	49.8**	60.6**	56.1**	31.9**	27.9**
Year of birth (Y)	3	18.0**	17.8**	16.3**	16.4**	4.8**	4.6**
B × F	11	2.0*	1.8	1.6	1.4	1.2	1.2
B × S	33	1.2	1.1	1.0	1.0	.8	.9
F × Y	3	9.2**	8.0**	9.6**	8.6**	4.4**	4.6**
F × S	3	1.7	1.7	1.3	1.2	2.0	1.9
Regression							
Initial age, d	1	32.0**	30.3**	40.8**	38.7**	29.3**	29.2**
Residual[d]	1,229	7.1	8.8	10.0	12.3	.9	1.0
Least squares means							
μ	1,596	70.7	65.8	15.3	18.9	14.0	15.2
Breed group means							
Red Poll	114	67.8	62.6	18.6	22.4	13.6	14.9
Hereford	132	66.0	60.1	20.8	25.5	13.2	14.4
Angus	117	67.1	61.5	20.0	24.4	12.9	14.1
Limousin	138	76.5	72.3	10.4	13.4	13.1	14.3
Braunvieh	137	71.9	67.3	12.9	16.1	15.1	16.5
Pinzgauer	119	71.5	66.8	13.7	17.0	14.8	16.1
Gelbvieh	147	74.2	70.0	11.3	14.2	14.5	15.8
Simmental	126	72.8	68.4	12.4	15.5	14.8	16.1
Charolais	124	73.2	68.7	11.9	15.0	14.9	16.2
D.05[e]		1.3	1.5	1.5	1.6	.4	.4
MARC I F_3	157	71.9	67.2	14.4	17.9	13.7	14.9
MARC II F_3	146	68.3	63.1	18.3	22.3	13.4	14.7
MARC III F_3	139	67.2	61.9	19.2	23.3	13.5	14.8
D.05[f]		1.4	1.5	1.5	1.7	.4	.4

[a]Retail product includes steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of lean trim.
[b]Subcutaneous and accessible intermuscular fat trimmed to 8 mm.
[c]All subcutaneous and accessible intermuscular fat removed.
[d]Sires within breed group and residual mean squares.
[e]D.05 is the approximate difference between means of parental breeds required for significance.
[f]D.05 is the approximate difference between means of all breed groups required for significance.
*$P < .05$.
**$P < .01$.

in the carcass composition data. Even at the extremes of the 63-d difference between slaughter group 1 and slaughter group 4 the difference among breed groups in response was less than expected. The interaction of dietary energy density × year generally was significant for weight and for carcass composition traits. This interaction was not significant for retail product weight and carcass lean weight. The interaction of dietary energy density × slaughter group generally was not significant; exceptions were estimated perirenal fat (KPH) percentage, fat trim weight at 8 mm of fat trim, and estimated separable lean percentage in 9-10-11th rib cut and in the whole rib.

A second analysis was conducted in which slaughter group was deleted as a main effect and days fed was included in the model as a covariate (linear and quadratic). These regressions are presented for relevant traits analyzed in Tables 8, 9, 10, 11, 12, and 13. The linear regressions on days fed were significant for most traits. The quadratic regressions generally were not significant. Exceptions were area of longissimus muscle (**REA**), cm^2, KPH percentage, marbling score, fat percentage in 9-10-11th rib cut, fat and water percentage in longissimus muscle and fat and water percentage in lean trim.

Differences Among Parental Breeds

Differences among parental breeds reported here include the sum of the additive direct and additive maternal genetic effects ($G^i + G^m$).

Live Weight and Carcass Traits Measured in the Cooler. Large differences were observed among breed groups in growth and carcass traits measured in the

Table 4. Summary of *F*-statistics, residual mean squares, and least squares means for carcass composition (weight)

Item	df or n	Retail product[a] 8 mm, kg[b]	Retail product[a] 0 mm, kg[c]	Fat trim 8 mm, kg[b]	Fat trim 0 mm, kg[c]	Bone 8 mm, kg[b]	Bone 0 mm, kg[c]
Analysis of variance							
Breed group (B)	11	86.2**	102.2**	69.4**	71.6**	82.7**	82.3**
Sires/B[d]	294	453.7	429.4	214.5	271.4	22.6	26.6
Feed level (F)	1	88.6**	64.4**	254.1**	264.4**	8.9**	11.4**
Age of dam (A)	3	7.0**	6.1**	4.2**	4.5**	8.2**	8.3**
Slaughter group (S)	3	111.4**	95.9**	117.1**	118.0**	79.3**	87.2**
Year of birth (Y)	3	19.8**	18.4**	17.8**	18.9**	21.4**	20.6**
B × F	11	.5	.5	1.6	1.5	1.0	1.0
B × S	33	.7	.8	1.1	1.0	.6	.7
F × Y	3	.7	.5	8.0**	7.3**	1.6	1.4
F × S	3	.7	.9	2.6*	2.4	.3	.3
Regression							
Initial age, d	1	71.2**	61.5**	75.0**	76.6**	38.2**	39.8**
Residual[d]	1,229	341.7	310.8	149.5	191.0	14.6	17.2
Least squares means							
μ	1,596	223.8	208.3	49.1	60.5	44.2	48.2
Breed group means							
Red Poll	114	202.5	187.1	56.4	67.9	40.7	44.4
Hereford	132	192.3	175.0	61.9	75.4	38.3	41.9
Angus	117	201.2	184.0	61.2	74.6	38.6	42.2
Limousin	138	239.8	226.5	33.3	42.6	41.0	44.7
Braunvieh	137	232.1	217.0	42.7	53.2	48.8	53.2
Pinzgauer	119	225.0	210.2	43.6	54.0	46.4	50.7
Gelbvieh	147	240.1	226.2	37.6	47.1	46.8	51.0
Simmental	126	239.3	224.5	42.2	52.4	48.5	52.9
Charolais	124	241.3	226.3	39.9	50.3	49.0	53.4
D.05[e]		8.2	8.0	5.7	6.4	1.8	2.0
MARC I F_3	157	236.4	220.6	47.9	59.4	45.0	49.1
MARC II F_3	146	225.6	208.2	61.2	74.4	44.3	48.4
MARC III F_3	139	210.6	193.7	61.5	74.4	42.4	46.3
D.05[f]	—	8.5	8.3	5.9	6.6	1.9	2.1

[a]Retail product includes steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of lean trim.
[b]Subcutaneous and accessible intermuscular fat trimmed to 8 mm.
[c]All subcutaneous and accessible intermuscular fat removed.
[d]Sires within breed group and residual mean squares.
[e]D.05 is the approximate difference between means of parental breeds required for significance.
[f]D.05 is the approximate difference between means of all breed groups required for significance.
*$P < .05$.
**$P < .01$.

cooler (Table 2). For initial weight, Herefords were lightest ($P < .05$) and Gelbvieh, Pinzgauer, Simmental, and Braunvieh were heaviest and did not differ ($P > .05$) from each other. Charolais approached the heaviest breed groups and Angus, Red Poll, and Limousin were intermediate. For final weight, Herefords were lightest but did not differ ($P > .05$) from Angus, Red Poll, and Limousin. Simmental, Charolais, Gelbvieh, and Braunvieh were heaviest but did not differ ($P < .05$) from each other, whereas Pinzgauer differed ($P < .05$) only from Simmental among the heavier breed groups. For ADG, Red Poll was lowest but was not different ($P > .05$) from Angus, Limousin, and Pinzgauer, whereas Simmental and Charolais were higher ($P < .05$) than all breed groups. For carcass weight, Herefords were lightest but did not differ ($P > .05$) from Red Poll and Angus; Simmental, Charolais, Gelbvieh, and Braunvieh were heaviest and did not differ ($P > .05$) from each other. Pinzgauer and Limousin were intermediate. For dressing percentage, Limousin was significantly higher than other breed groups; Angus and Charolais were intermediate. Differences in dressing percentage among other breed groups were relatively small even though some were significant. Adjusted fat thickness at the 12th rib ranged from .360 cm in Gelbvieh to 1.178 cm in Angus. Breeds ranked similarly in REA as for carcass weight except that Limousin was highest, but not significantly higher than Braunvieh and Gelbvieh. Differences among breed groups in estimated KPH percentage generally were small except that Red Poll had significantly higher KPH percentage than other breed groups. For marbling score, Limousin was lowest, but not lower than Gelbvieh. Angus was highest but not higher than Red Poll, Hereford, and Pinzgauer. Braunvieh, Simmental, and Charolais

Table 5. Summary of *F*-statistics, residual mean squares, and least squares means for carcass lean, fat, and bone (percentages and weights)

Item	df or n	Lean[a]		Fat[b]		Bone	
		%	kg	%	kg	%	kg
Analysis of variance							
Breed group (B)	11	133.8**	702.8**	134.7**	53.1**	70.2**	82.3**
Sires/B[c]	294	11.4	335.9	14.6	269.2	1.3	26.6
Feed level (F)	1	133.2**	68.6**	195.8**	284.6**	192.7**	11.4**
Age of dam (A)	3	1.9	6.1**	1.6	5.8**	.6	8.3**
Slaughter group (S)	3	50.7**	98.4**	57.2**	142.3**	27.9**	87.2**
Year of birth (Y)	3	16.6**	17.7**	15.4**	19.7**	4.6**	20.6**
B × F	11	1.8*	.5	1.4	1.3	1.2	1.0
B × S	33	1.1	.8	1.0	.9	.9	.7
F × Y	3	7.2**	.7	8.1**	7.0**	4.6**	1.4
F × S	3	1.7	.8	1.2	2.2	1.9	.3
Regression							
Initial age, d	1	29.0**	64.4**	38.2**	90.7**	29.2**	39.8**
Residual[c]	1,229	6.6	244.5	9.8	196.9	1.0	17.2
Least squares means							
μ	1,596	58.8	186.0	26.0	82.7	15.2	48.2
Breed group means							
Red Poll	114	56.0	167.2	29.1	87.9	14.9	44.4
Hereford	132	53.8	156.5	31.8	94.0	14.4	41.9
Angus	117	54.9	164.4	31.0	94.2	14.1	42.2
Limousin	138	64.6	202.4	21.1	66.8	14.3	44.7
Braunvieh	137	60.1	193.9	23.3	76.3	16.5	53.2
Pinzgauer	119	59.8	187.9	24.1	76.2	16.1	50.7
Gelbvieh	147	62.4	201.8	21.8	71.5	15.8	51.0
Simmental	126	61.1	200.6	22.8	76.2	16.1	52.9
Charolais	124	61.2	201.6	22.5	75.0	16.2	53.4
D.05[d]		1.3	7.1	1.5	6.3	.4	2.0
MARC I F_3	157	60.0	196.8	25.1	83.2	14.9	49.1
MARC II F_3	146	56.4	186.0	29.0	96.6	14.7	48.4
MARC III F_3	139	55.3	173.2	29.9	94.8	14.8	46.3
D.05[e]	—	1.4	7.3	1.5	6.6	.4	2.1

[a]Carcass lean includes steaks and roasts trimmed to 0 mm of fat cover plus fat free lean trim based on chemical analysis of lean trim.
[b]Carcass fat includes fat trim plus fat in the lean trim based on chemical analysis of lean trim.
[c]Sires within breed group and residual mean squares.
[d]D.05 is the approximate difference between means of parental breeds required for significance.
[e]D.05 is the approximate difference between means of all breed groups required for significance.
*$P < .05$.
**$P < .01$.

were intermediate in marbling score and were not different from each other.

Retail Product, Fat Trim, and Bone and Carcass Lean, Fat, and Bone (Percentage). Differences among parental breeds in retail product, fat trim, and bone percentage when retail product was trimmed to 8 and to 0 mm of fat are presented in Table 3. Mean differences between 8 and 0 mm of fat trim for retail product was 4.9%, for fat trim 3.6%, and for bone 1.2%. Differences in retail product percentage between the two trim levels tended to be less in breeds with lower fat (e.g., Limousin was 4.2%) than in breeds with more fat (e.g., Hereford was 5.9%). This was because the Limousin and similar breeds had less than 8 mm of fat cover on some cuts, and thus less fat was removed when trimmed to 0 mm. Limousin had the highest retail product percentage ($P < .05$) and lowest fat trim percentage but were not different ($P > .05$) from Gelbvieh in fat trim percentage and were similar ($P > .05$) to Angus and Hereford in bone percentage. Hereford, Angus, and Red Poll were similar ($P > .05$) in retail product, fat trim, and bone percentages. Consistent with the report of Koch et al. (1976), these results show that differences among breeds are considerably greater for fat trim percentage than for bone percentage. The range in fat trim percentage was 12.1% among breeds at 0-mm fat trim, whereas the range in bone percentage was 2.4% among breeds at 0-mm fat trim. When expressed on this basis, breed group differences in fat trim percentage were five times greater than breed group differences in bone percentage. The ranking of breeds for carcass lean and fat percentages (Table 5) are similar to rankings on retail product percentage and fat trim percentage. This was expected because lean trim was adjusted to 20% fat based on chemical analysis in

Table 6. Summary of *F*-statistics, residual mean squares, and least squares means for separable lean, fat, and bone percentages in the 9-10-11th rib cut and the whole rib

Item	df or n	9-10-11th rib cut composition			Whole rib composition		
		Lean, %[a]	Fat, %[b]	Bone, %	Lean, %[a]	Fat, %[b]	Bone, %
Analysis of variance							
Breed group (B)	11	136.0**	133.3**	32.1**	130.4**	125.3**	39.2**
Sires/B[c]	294	17.6	21.9	3.4	13.9	18.2	2.2
Feed level (F)	1	172.5**	240.0**	146.0**	211.1**	280.8**	187.9**
Age of dam (A)	3	1.5	.9	1.5	1.4	1.2	1.3
Slaughter group (S)	3	70.1**	61.5**	5.9**	80.6**	66.2**	5.2**
Year of birth (Y)	3	9.2**	6.4**	.4	6.1**	4.5**	.3
B × F	11	1.3	1.4	1.1	1.8*	1.7	.9
B × S	33	.9	.9	1.0	1.0	1.0	1.2
F × Y	3	4.3**	6.8**	5.8**	7.9**	9.8**	5.8**
F × S	3	3.4*	2.0	.4	3.7**	1.9	1.3
Regression							
Initial age, d	1	16.7**	26.9**	22.3**	24.2**	34.2**	26.4**
Residual[c]	1,229	11.0	15.9	2.3	8.1	12.1	1.5
Least squares means							
μ	1,596	55.8	27.0	17.2	60.6	24.1	15.3
Breed group means							
Red Poll	114	51.8	30.7	17.5	57.4	27.1	15.4
Hereford	132	48.9	35.1	16.0	54.4	31.2	14.3
Angus	117	50.7	33.0	16.3	56.1	29.5	14.4
Limousin	138	62.0	22.2	15.8	66.0	19.8	14.2
Braunvieh	137	58.0	23.6	18.4	62.2	21.4	16.4
Pinzgauer	119	57.4	24.1	18.5	62.0	21.6	16.4
Gelbvieh	147	59.8	22.4	17.8	64.1	19.9	16.0
Simmental	126	59.2	22.8	17.9	63.5	20.5	16.0
Charolais	124	59.8	22.4	17.8	64.1	19.8	16.1
D.05[d]		1.6	1.8	.7	1.4	1.6	.6
MARC I F_3	157	57.3	26.1	16.6	61.9	23.2	14.9
MARC II F_3	146	53.1	30.4	16.5	58.2	27.0	14.8
MARC III F_3	139	51.6	31.5	16.9	57.0	28.1	14.9
D.05[e]	—	1.7	1.9	.7	1.5	1.7	.6

[a]Separable lean includes steaks and roasts trimmed to 0 mm of fat cover plus fat free lean trim based on chemical analysis of lean trim.
[b]Separable fat includes fat trim plus fat in the lean trim based on chemical analysis of lean trim.
[c]Sires within breed group and residual mean squares.
[d]D.05 is the approximate difference between means of parental breeds required for significance.
[e]D.05 is the approximate difference between means of all breed groups required for significance.
*$P < .05$.
**$P < .01$.

determination of retail product and fat trim percentages.

Retail Product, Fat Trim, and Bone and Carcass Lean, Fat, and Bone (Weight). Differences among parental breeds in retail product, fat trim, and bone weight when retail product was trimmed to both 8 and 0 mm of fat are presented in Table 4. Parental breed differences in weight of carcass lean, fat, and bone are presented in Table 5. Retail product and carcass lean weight reflect differences among parental breeds in lean tissue growth rate. Limousin, Simmental, Charolais, and Gelbvieh were similar ($P > .05$) in retail product and carcass lean weight at 0 mm of fat. Even though the mean slaughter weight was 54.7 kg greater for the Simmental, Gelbvieh, and Charolais breeds than for the Limousin, the higher dressing percentage, higher retail product percentage, and smaller bone percentage of the Limousin resulted in no difference ($P > .05$) among the four breeds in retail product weight and carcass lean weight. The Hereford breed was lowest ($P < .05$) of all groups in retail product weight and in carcass lean weight, followed by Angus and Red Poll, which did not differ from each other ($P > .05$). The difference between the Braunvieh and Pinzgauer in retail product weight and in carcass lean weight approached significance, with the Braunvieh approaching the Simmental, Limousin, Charolais, and Gelbvieh.

Composition of 9-10-11th Rib Cut and Whole Rib and 9-10-11th Rib Cut Chemical Composition. Differences among parental breeds for estimated separable lean, fat, and bone percentages for 9-10-11th rib cut

Table 7. Summary of *F*-statistics, residual mean squares, and least squares means for shear force of longissimus muscle and fat (%) and water (%) in longissimus muscle, lean trim, and 9-10-11th rib cut

Item	df or n	Longissimus muscle: Shear force kg[a]	Longissimus muscle: Fat, %[b]	Longissimus muscle: H_2O, %[c]	Lean trim: Fat, %[b]	Lean trim: H_2O, %[c]	9-10-11th rib cut: Fat, %[b]	9-10-11th rib cut: H_2O, %[c]
Analysis of variance								
Breed group (B)	11	14.7**	31.7**	16.9**	89.8**	77.3**	110.8**	105.6**
Sires/(B)[d]	294	1.4	1.7	1.3	5.7	3.4	31.9	18.9
Feed level (F)	1	11.0**	42.4**	86.6**	97.0**	117.8**	178.7**	200.4**
Age of dam (A)	3	1.9	.3	.6	1.2	1.2	2.3	2.3
Slaughter group (S)	3	1.3	16.4**	13.4**	8.0**	6.6**	45.0**	44.6**
Year (Y)	3	44.6**	22.7**	25.1**	27.3**	23.0**	4.2**	5.8**
B × F	11	1.3	.6	.6	.8	1.0	1.4	1.4
F × S	33	.9	1.4	1.1	1.1	1.2	1.4	1.3
F × Y	3	5.0**	8.0**	6.2**	4.9**	5.0**	6.4**	6.3**
B × S	3	2.6*	2.2	1.2	.0	.1	.6	.6
Regressions								
Initial age, d	1	6.8**	28.7**	27.0**	28.5**	28.9**	29.0**	30.8**
Residual[d]	1,229	1.2	1.0	.9	4.4	2.7	23.5	14.0
Least squares means								
μ	1,596	5.1	4.0	73.6	21.0	60.9	33.1	51.7
Breed group means								
Red Poll	114	4.7	4.6	73.0	22.7	59.5	38.4	47.6
Hereford	132	5.1	4.5	73.3	23.7	59.1	40.1	46.4
Angus	117	4.5	4.8	73.1	23.6	59.2	40.1	46.4
Limousin	138	5.6	2.8	74.1	18.4	62.8	26.6	56.4
Braunvieh	137	5.1	3.7	73.8	19.8	61.7	29.9	54.1
Pinzgauer	119	4.5	4.2	73.4	21.1	60.7	30.8	53.4
Gelbvieh	147	5.8	3.2	74.2	18.6	62.7	27.7	55.8
Simmental	126	5.5	3.7	73.9	19.6	61.9	28.8	55.0
Charolais	124	5.2	3.4	74.0	19.1	62.4	28.0	55.6
D.05[e]		.4	.5	.4	.9	.7	2.2	1.7
MARC I	157	5.0	3.6	73.8	19.8	61.8	31.2	53.1
MARC II	146	5.1	4.3	73.3	22.2	60.0	36.3	49.3
MARC III	139	5.1	4.6	73.0	23.1	59.3	38.8	47.3
D.05[f]	—	.5	.5	.5	1.0	.7	2.3	1.7

[a]Shear force required to cut through a 1.27-cm core.
[b]Ether-extracted fat.
[c]Water determined by oven drying.
[d]Sires within breed group and residual mean squares.
[e]D.05 is the approximate difference between means of parental breeds required for significance.
[f]D.05 is the approximate difference between means of all breed groups required for significance.
*$P < .05$.
**$P < .01$.

Table 8. Least squares means for feed level and slaughter group for growth and cooler measured carcass traits

Item	No.	Initial wt, kg	Final wt, kg	ADG, kg	Carcass wt, kg	Dressing percentage, %	Adj fat, cm[a]	REA, cm2[a]	Est. KPH, %[a]	Marbling score[b]	Percentage ≥ USDA Choice	Percentage ≥ USDA Select
Overall mean	1,661	258	549	1.241	333	60.58	.654	78.11	2.77	4.97	.46	.95
Feed level[c]												
1	816	258	535**	1.180**	322**	60.17**	.560**	77.31**	2.70**	4.83**	.37**	.93**
2	845	258	564	1.302	344	60.98	.748	78.91	2.84	5.10	.56	.96
Slaughter group[d]												
1	360	258	512**	1.247**	305**	59.56**	.499**	75.47**	2.63**	4.76**	.39**	.90**
2	437	259	542	1.260	328	60.53	.619	81.58	2.69	4.90	.43	.95
3	452	257	559	1.234	339	60.70	.706	76.50	2.78	5.10	.50	.96
4	412	258	584	1.224	359	61.52	.793	78.89	3.02	5.10	.53	.97
Regressions												
Initial age, d	—	1.204**	.926**	-.001**	.607**	.009**	.002**	.050**	.005**	.005**	.003**	.001**
Days fed[e]												
Linear	—	—	1.05508**	-.00055**	.80738**	.03013**	.00476**	.02646*	.00716**	.00390**	.00238**	.00088**
Quadratic	—	—	-.00430	-.00002*	-.00252	-.00005	-.00002	-.00195**	.00014**	-.00008*	—	—

[a]Adj. fat = adjusted fat thickness at 12th rib, REA = area of longissimus muscle, Est. KPH = perirenal fat estimate.
[b]4.00–4.90 = slight; 5.00–5.90 = small.
[c]Feed level 1 and 2 = 2.82 or 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein.
[d]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.
[e]Estimated from a second analysis that deleted slaughter group as a main effect and included days fed in the model as a covariate.
*$P < .05$.
**$P < .01$.

Table 9. Least squares means for feed level and slaughter group for carcass composition (percentage)

Item	No.	Retail product[a] 8 mm, %[b]	Retail product[a] 0 mm, %[c]	Fat trim 8 mm, %[b]	Fat trim 0 mm, %[c]	Bone 8 mm, %[b]	Bone 0 mm, %[c]
Overall mean	1,596	70.7	65.8	15.3	18.9	14.0	15.2
Feed level[d]							
1	781	71.5**	66.8**	14.2**	17.6**	14.3**	15.6**
2	815	69.9	64.9	16.5	20.2	13.6	14.9
Slaughter group							
1	346	72.0**	67.2**	13.7**	17.2**	14.3**	15.6**
2	419	71.1	66.3	14.7	18.3	14.1	15.4
3	439	70.2	65.3	16.0	19.6	13.8	15.1
4	392	69.4	64.4	16.9	20.6	13.6	14.9
Regressions							
Initial age, d							
Linear	—	−.034**	−.036**	.045**	.049**	−.012**	−.012**
Days fed[e]							
Linear	—	−.04608**	−.04926**	.05864**	.06192**	−.01255**	−.01872**
Quadratic	—	.00003	.00003	−.00003	−.00004	.00000	.00001

[a]Retail product includes steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of lean trim.
[b]Subcutaneous and accessible intermuscular fat trimmed to 8 mm.
[c]All subcutaneous and accessible intermuscular fat removed.
[d]Feed level 1 and 2 = 2.82 or 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein.
[e]Estimated from a second analysis that deleted slaughter group as a main effect and included days fed in the model as a covariate.
*$P < .05$.
**$P < .01$.

and for the whole rib are presented in Table 6. Estimation of separable lean and fat percentage was calculated by partitioning the lean and fat in the lean trim based on chemical determination of fat in the lean trim. Fat percentage determined by chemical analysis of the lean trim from the entire carcass and fat percentage of the 9-10-11th rib cut and longissimus muscle are presented in Table 7.

Table 10. Least squares means for feed level and slaughter group for carcass composition (weight)

Item	No.	Retail product[a] 8 mm, kg[b]	Retail product[a] 0 mm, kg[c]	Fat trim 8 mm, kg[b]	Fat trim 0 mm, kg[c]	Bone 8 mm, kg[b]	Bone 0 mm, kg[c]
Overall mean	1,596	223.8	208.3	49.1	60.5	44.2	48.2
Feed level[d]							
1	781	219.2**	204.5**	43.9**	54.4**	43.8**	47.8**
2	815	228.6	212.1	54.4	66.5	44.5	48.6
Slaughter group							
1	346	210.3**	196.2**	40.3**	50.5**	41.8**	45.5**
2	419	221.5	206.3	46.2	57.2	43.9	47.9
3	439	226.2	210.2	51.8	63.5	44.4	48.5
4	392	237.4	220.3	58.1	70.6	46.5	50.9
Regressions							
Initial age, d							
Linear	—	.348**	.309**	.236**	.270**	.053**	.059
Days fed[e]							
Linear	—	.39003**	.34307**	.30330**	.34080**	.06625**	.07580**
Quadratic	—	−.00058	−.00054	.00004	−.00001	−.00011	−.00007

[a]Retail product includes steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of lean trim.
[b]Subcutaneous and accessible intermuscular fat trimmed to 8 mm.
[c]All subcutaneous and accessible intermuscular fat removed.
[d]Feed level 1 and 2 = 2.82 or 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein.
[e]Estimated from a second analysis that deleted slaughter group as a main effect and included days fed in the model as a covariate.
*$P < .05$.
**$P < .01$.

Table 11. Least squares means for feed level and slaughter group for carcass lean, fat, and bone (percentages and weights)

Item	No.	Lean[a] %	Lean[a] kg	Fat[b] %	Fat[b] kg	Bone[a] %	Bone[a] kg
Overall mean	1,596	58.8	186.0	26.0	82.7	15.2	48.2
Feed level							
1	781	59.6**	182.5**	24.8**	76.3**	15.6**	47.8**
2	815	58.0	189.5	27.1	89.1	14.9	48.6
Slaughter group							
1	346	60.0**	175.3**	24.4**	71.5**	15.6**	45.5**
2	419	59.2	184.2	25.4	79.3	15.4	47.9
3	439	58.3	187.8	26.6	86.0	15.1	48.5
4	392	57.6	196.9	27.5	94.1	14.9	50.9
Regressions							
Initial age, d							
Linear	—	−.031**	.281**	.043**	.299**	−.012**	.059**
Days fed[d]							
Linear	—	−.04366**	.30764**	.05633**	.37623**	−.01266**	.07588**
Quadratic	—	.00004	−.00043	−.00006	−.00012	.00001	−.00007

[a]Carcass lean includes steaks and roasts trimmed to 0 mm fat cover plus fat-free lean trim based on chemical analysis of lean trim.
[b]Carcass fat includes fat trim plus fat in the lean trim based on chemical analysis of lean trim.
[c]Feed level 1 and 2 = 2.82 or 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein.
[d]Estimated from a second analysis that deleted slaughter group as a main effect and included days fed in the model as a covariate.
*$P < .05$.
**$P < .01$.

Fat determined by chemical analysis in the 9-10-11th rib cut averaged 6.1% greater than estimated separable fat (Table 6) in the 9-10-11th rib cut. Differences between the two methods in each breed were highly associated with chemical fat in the longissimus muscle (Table 7). Differences between ether-extracted fat and estimated separable fat in the 9-10-11th rib cut by breed group were as follows: Red Poll 7.7%, Hereford 5.0%, Angus 7.1%, Limousin 4.4%, Braunvieh 6.3%, Pinzgauer 6.7%, Gelbvieh 5.3%,

Table 12. Least squares means for feed level and slaughter group for separable lean, fat and bone percentages in 9-10-11th rib cut and the whole rib

Item	No.	9-10-11th rib cut composition: Lean, %[a]	Fat, %[b]	Bone, %	Whole rib composition: Lean, %[a]	Fat, %[b]	Bone, %
Overall mean	1,596	55.8	27.0	17.2	60.6	24.1	15.3
Feed level[c]							
1	781	57.0**	25.4**	17.7**	61.7**	22.5**	15.8**
2	815	54.6	28.7	16.7	59.4	25.7	14.9
Slaughter group							
1	346	57.8**	24.7**	17.5**	62.4**	22.1**	15.5**
2	419	56.3	26.5	17.2	61.0	23.6	15.4
3	439	54.9	28.0	17.1	59.9	24.8	15.2
4	392	54.2	28.8	17.0	58.9	25.9	15.2
Regressions							
Initial age, d							
Linear	—	−.030**	.046**	−.016**	−.031**	.046**	−.014**
Days fed[d]							
Linear	—	−.05988**	.06733**	−.00744**	−.05547**	.06292**	−.00746**
Quadratic	—	.00040	−.00054*	.00014	.00018	−.00023	.00005

[a]Separable lean includes 0-mm fat trim steaks and roasts plus fat-free lean trim determined by chemical analysis of lean trim.
[b]Separable fat includes fat trim plus fat in lean trim determined by chemical analysis of lean trim.
[c]Feed level 1 and 2 = 2.82 or 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein.
[d]Estimated from a second analysis that deleted slaughter group as a main effect and included days fed in the model as a covariate.
*$P < .05$.
**$P < .01$.

Table 13. Least squares means for feed level and slaughter group for shear force of longissimus muscle and fat (%) and water (%) in longissimus muscle, lean trim, and 9-11 rib cut

Item	No.	Longissimus muscle: Shear force, kg[a]	Longissimus muscle: Fat, %[b]	Longissimus muscle: H_2O, %[c]	Lean trim: Fat, %[b]	Lean trim: H_2O, %[c]	9-10-11 rib cut: Fat, %	9-10-11 rib cut: H_2O, %[c]
Overall mean	1,596	5.1	4.0	73.6	21.0	60.9	33.1	51.7
Feed level[d]								
1	781	5.2**	3.8**	73.8**	20.4**	61.4**	31.3**	53.1**
2	815	5.0	4.1	73.3	21.5	60.4	34.8	50.3
Slaughter group								
1	346	5.1	3.9**	73.6**	21.0**	60.8**	30.9**	53.4**
2	419	5.1	3.7	73.8	20.7	61.2	32.3	52.3
3	439	5.2	4.0	73.5	20.8	61.0	33.9	51.0
4	392	5.0	4.2	73.3	21.4	60.7	35.2	50.1
Regressions								
Initial age, d								
Linear	—	-.006**	.012**	-.011**	.025**	-.020**	.058**	-.046**
Days fed[e]								
Linear	—	-.00019	.00148**	-.00998**	-.00612*	.00541*	.07565**	-.05975**
Quadratic	—	-.00009	.00026**	-.00028**	.00052**	-.00040**	-.00010	-.00004

[a]Shear force required to cut a 1.27-cm core.
[b]Ether-extracted fat.
[c]Water determined by oven drying.
[d]Feed level 1 and 2 = 2.82 or 3.07 Mcal of ME/kg of dry matter and 11.50% crude protein.
[e]Estimated from a second analysis that deleted slaughter group as a main effect and included days fed in the model as a covariate.
*$P < .05$.
**$P < .01$.

Simmental 6.0%, and Charolais 5.6%.

Effects of Dietary Energy Density and Slaughter Group on Growth, Carcass, and Meat Traits

Least squares means for growth and for carcass traits measured in the cooler are presented in Table 8. The effects of dietary energy density and slaughter group were significant for all traits analyzed except initial weight. In an alternative method for examining the effects of time on feed the linear regression on days fed was significant for all growth and cooler-measured carcass traits; the quadratic regression was significant only for ADG (kilograms), REA (square centimeters), KPH percentage, and marbling score.

The effects of dietary energy density and slaughter group were significant for retail product, fat trim, and bone percentages at both 8 and 0 mm of fat trim (Table 9). The effects of dietary energy density and slaughter group also were significant for carcass lean, fat, and bone percentages (Table 11). The linear regressions of carcass composition traits on days fed were important ($P < .01$); the quadratic regression was not significant for any trait.

The effects of dietary energy density and slaughter group on retail product, fat trim, and bone weights were significant at both 8 and 0 mm of fat trim (Table 10) and on carcass lean, fat, and bone weight (Table 11). Carcass lean was 7.0 kg greater, carcass fat was 12.8 kg greater, and bone was .8 kg greater at the higher dietary energy density. Thus, only 34% of the 20.6 kg increase in carcass lean, fat, and bone weight resulting from higher dietary energy density was accounted for by an increase in carcass lean weight. The linear regressions of all traits on days fed were important ($P < .01$); quadratic regressions were not important.

The effects of dietary energy density and slaughter group were significant for separable lean, fat, and bone percentages for both the 9-10-11th rib cut and for the whole rib (Table 12). The linear regressions of all traits on days fed were important ($P < .01$). The quadratic regression of separable fat percentage in the 9-10-11th rib cut on days fed was significant but was not significant for other traits.

Least squares means for shear force for 1.27-cm cores of longissimus muscle and fat and water percentages in the longissimus muscle, in the lean trim from the entire carcass, and in the 9-10-11th rib cut are presented in Table 13. The effects of dietary energy density were significant for all traits analyzed. The effects of slaughter group were significant for all traits except shear force. The significant effect of year on shear force (kilograms) of longissimus muscle resulted from a large increase in shear force for calves born in 1991. We do not have an explanation for this anomaly because procedures followed were the same as in previous years. The linear regression of all traits except shear force on days fed was significant; the quadratic regression was significant for all traits

Table 14. Effects of retained heterosis on growth and cooler-measured carcass traits

Linear contrast	Initial wt, kg	Final wt, kg	ADG, kg	Carcass wt, kg	Dressing percentage, %	Adj. fat, cm[a]	Est. REA, cm[a]	KPH, %[a]	Marbling score
Heterosis									
MARC I[b] minus purebreds	13.7**	20.8**	.031*	13.4**	.08	−.02	3.5**	.29**	−.03
MARC II[b] minus purebreds	23.2**	30.7**	.028†	19.2**	.13	.03	2.8**	.33**	.15**
MARC III[b] minus purebreds	10.4**	16.8**	.025†	11.9**	.29	.03	3.1**	.28**	.04
Mean heterosis									
Composites minus purebreds	15.8**	22.8**	.028**	14.8**	.17	.01	3.1**	.30**	.05

[a]Adj. fat = adjusted fat thickness at 12th rib, REA = area of longissimus muscle, Est. KPH = perirenal fat estimate.
[b]F_3 generation progeny.
†$P < .10$.
*$P < .05$.
**$P < .01$.

except shear force and fat and water percentages in the 9-10-11th rib cut.

Retained Heterosis

If retained heterosis is proportional to retained heterozygosity, the genetic expectation for retained heterosis is .76 H^i + .76 H^m for the mean of the three composite populations in F_3 generation progeny of F_2 generation dams (Table 1). For retained heterozygosity-retained heterosis relationships for other traits evaluated in this experiment, see Gregory et al. (1991a,b,c,d, 1992a,b,c).

Estimates of retained heterosis for growth traits and for cooler-measured carcass traits are presented in Table 14. For traits related to growth and size, retained heterosis generally was significant for each composite population and for the mean of the three composites. Retained heterosis was not observed for dressing percentage or adjusted fat thickness. Significant retained heterosis was observed for marbling score for composite MARC II but not for composites MARC I or MARC III or for the mean of the three composites.

Estimates of retained heterosis for retail product, fat trim, and bone percentages at 8 and 0 mm of fat trim are presented in Table 15. Estimates of retained heterosis for carcass lean, fat, and bone percentage are presented in Table 16. For composite MARC I, retained heterosis was not significant for retail product, fat trim, carcass lean, or carcass fat percentages but was significant for bone (less) percentage. For composite MARC II, retained heterosis was significant for retail product (less), fat trim (greater), and bone (less) percentages and for carcass lean (less), carcass fat (greater), and separable bone (less) percentages. For composite MARC III, retained heterosis was significant for retail product (less), fat trim (greater), carcass lean (less) and carcass fat (greater) percentages. There was no effect of retained heterosis on bone or separable bone percentages. For the mean of the three composites, retained heterosis was significant for retail product (less), fat trim (greater), and bone (less) percentages and for carcass lean (less), estimated separable fat (greater), and separable bone (less) percentages.

Estimates of retained heterosis for retail product, fat trim, and bone weight at 8 and 0 mm of fat trim are presented in Table 17. Estimates of retained heterosis for carcass lean, fat, and bone weights are presented in Table 16. For composite MARC I, retained heterosis was significant for retail product (greater), fat trim (greater), carcass lean (greater), and carcass fat (greater) weight but not for bone weight. For composites MARC II and MARC III and for the mean of the three composites, retained heterosis was significant for retail product (greater), fat trim (greater), bone (greater), carcass lean (greater), carcass fat (greater), and bone (greater) weight. Note that 62.6% of the 13.1-kg increase in combined retail product, fat trim, and bone weight

Table 15. Effects of retained heterosis on carcass composition (percentage)

Linear contrast	Retail product[a]		Fat trim		Bone	
	8 mm, %[b]	0 mm, %[c]	8 mm, %[b]	0 mm, %[c]	8 mm, %[b]	0 mm, %[c]
Heterosis						
MARC I[d] minus purebreds	–.098	–.111	.453	.490	–.354**	–.379**
MARC II[d] minus purebreds	–1.704**	–1.904**	2.111**	2.350**	–.407**	–.445**
MARC III[d] minus purebreds	–.895**	–.894*	.971**	.995*	–.076	–.101
Mean heterosis						
Composites minus purebreds	–.899**	–.970**	1.178**	1.278**	–.279**	–.308**

[a]Retail product includes steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of lean trim.
[b]Subcutaneous and accessible intermuscular fat trimmed to 8 mm.
[c]All subcutaneous and accessible intermuscular fat removed.
[d]F_3 generation progeny.
*P < .05.
**P < .01.

was retail product in composite MARC I, whereas the comparable value for the mean of MARC II and MARC III was 32.5% at 0 mm of fat trim (Table 17).

Estimates of retained heterosis for separable lean, fat, and bone percentages for the 9-10-11th rib cut and for the whole rib are presented in Table 18. For composite MARC I, retained heterosis was significant for bone (less) percentage in the 9-10-11th rib cut and in the whole rib but not for separable lean or separable fat percentages. For composite MARC II, retained heterosis was significant for separable lean (less), separable fat (greater), and bone (less) percentages in the 9-10-11th rib cut and in the whole rib. For composite MARC III, retained heterosis was not significant for any trait. For the mean of the three composites, retained heterosis was significant for separable lean (less), separable fat (greater), and bone (less) percentages for the 9-10-11th rib cut and for the whole rib.

Estimates of retained heterosis for shear force of longissimus muscle and for fat and water estimated by ether extraction and by oven drying in longissimus muscle and 9-10-11th rib cut are presented in Table 19. For composite MARC I, retained heterosis was not significant for any trait. For composite MARC II, retained heterosis was significant for fat (greater) and water (less) percentage in the longissimus muscle and for fat (greater) and water (less) percentage in the 9-10-11th rib cut. For composite MARC III, significantly greater shear force was required for the longissimus muscle of the composite than for the mean of the contributing purebreds. This anomaly is interpreted to result from chance because there is no biological basis for this observation. Significant retained heterosis was observed in composite MARC III for fat (greater) and water (less) percentage in the 9-10-11th rib cut but not for fat or water percentage in the longissimus muscle. For mean of the three composites, retained heterosis was significant for water (less) percentage in the longissimus muscle and for fat (greater) and water (less) percentages in the 9-10-11th rib cut.

General. Gregory and Cundiff (1980) presented results showing that the proportion of retained heterosis was not less than the proportion of retained heterozygosity in rotational crossbreeding, which suggested that heterosis in cattle can be accounted for by the dominance effects of genes. In a comparison of

Table 16. Effects of retained heterosis on carcass lean, fat and bone (percentage and weight)

Linear contrast	Lean[a] %	Lean[a] kg	Fat[b] %	Fat[b] kg	Bone %	Bone kg
Heterosis						
MARC I[c] minus purebreds	–.12	7.25**	.50	5.13**	–.38**	.74
MARC II[c] minus purebreds	–1.68**	5.19**	2.12**	12.59**	–.44**	1.38**
MARC III[c] minus purebreds	–.77*	4.25**	.87*	6.76**	–.10	1.48**
Mean heterosis						
Composites minus purebreds	–.86**	5.56**	1.16**	8.16**	–.31**	1.20**

[a]Separable lean includes steaks and roasts trimmed to 0 mm of fat cover plus fat-free lean trim based on chemical analysis of lean trim.
[b]Separable fat includes fat trim plus fat in lean trim estimated by chemical analysis of lean trim.
[c]F_3 generation progeny.
*P < .05.
**P < .01.

Table 17. Effects of retained heterosis on carcass composition (weight)

Linear contrast	Retail product[a]		Fat trim		Bone	
	8 mm, kg[b]	0 mm, kg[c]	8 mm, kg[b]	0 mm, kg[c]	8 mm, kg[b]	0 mm, kg[c]
Heterosis						
MARC I[d] minus purebreds	8.9**	8.2**	3.5**	4.2**	.7	.7
MARC II[d] minus purebreds	7.4**	5.7**	10.5**	12.1**	1.3**	1.4**
MARC III[d] minus purebreds	5.3**	4.6*	5.7**	6.4**	1.4**	1.5**
Mean heterosis						
Composites minus purebreds	7.2**	6.2**	6.6**	7.5**	1.1**	1.2**

[a]Retail product includes steaks and roasts plus lean trim adjusted to 20% fat based on chemical analysis of lean trim.
[b]Subcutaneous and accessible intermuscular fat trimmed to 8 mm.
[c]All subcutaneous and accessible intermuscular fat removed.
[d]F_3 generation progeny.
*$P < .05$.
**$P < .01$.

Table 18. Effects of retained heterosis on separable lean, fat, and bone percentages in 9-10-11th rib cut and the whole rib

Linear contrast	9-10-11th rib cut composition			Whole rib composition		
	Lean, %[a]	Fat, %[b]	Bone, %	Lean, %[a]	Fat, %[b]	Bone, %
Heterosis						
MARC I[c] minus purebreds	−.12	.52	−.40*	.01	.35	−.36**
MARC II[c] minus purebreds	−1.56**	2.08**	−.52**	−1.32**	1.76**	−.44**
MARC III[c] minus purebreds	−.54	.74	−.20	−.52	.75	−.23
Mean heterosis						
Composites minus purebreds	−.74**	1.11**	−.37**	−.60**	.95**	−.34**

[a]Separable lean includes 0 mm of fat trim steaks and roasts plus fat-free lean trim estimated by chemical analysis of fat in lean trim.
[b]Separable fat includes fat trim plus fat in lean trim estimated by chemical analysis of lean trim.
[c]F_3 generation progeny.
*$P < .05$.
**$P < .01$.

Table 19. Effects of retained heterosis on shear force of longissimus muscle and fat (%) and water (%) in longissimus muscle and 9-10-11th rib cut

Linear contrast	Longissimus muscle			9-10-11th rib cut	
	Shear force, kg[a]	Fat, %[b]	H_2O, %[c]	Fat, %[b]	H_2O, %[c]
Heterosis					
MARC I[d] minus purebreds	−.15	−.08	.01	.02	.01
MARC II[d] minus purebreds	−.12	.28*	−.27*	2.17**	−1.62**
MARC III[d] minus purebreds	.42**	.06	−.15	1.40**	−1.10**
Mean heterosis					
Composite minus purebreds	.05	.09	−.13*	1.20**	−.90**

[a]Shear force required to cut a 12.7-mm core.
[b]Ether-extracted fat.
[c]Water estimated by oven drying.
[d]F_3 generation progeny.
*$P < .05$.
**$P < .01$.

inter se-mated F_3 vs F_1 generation Hereford-Angus crosses, Koch et al. (1985) reported that heterosis retained was greater than expected based on retained heterozygosity for four growth-related traits (postweaning gain, final weight, carcass weight, and longissimus muscle area), equal to the expectation based on retained heterozygosity in six traits (day born, birth weight, calving ease, preweaning gain, weaning weight, and fat thickness), and less than expected based on retained heterozygosity in three traits (survival rate, pregnancy rate, and marbling score). Prior reports from this same experiment indicate that retention of heterosis is approximately proportional to retention of heterozygosity for most traits and generally support the hypothesis that heterosis in cattle can largely be accounted for by dominance effects of genes and likely is the result of recovery of accumulated inbreeding depression that has occurred in the separation of local landraces and the formation of breeds (Gregory et al., 1991a,b,c,d; 1992a,b,c).

For the traits reported in this paper, retained heterosis relative to the F_1 generation cannot be estimated. However, generally, high levels of heterosis were observed in the F_3 generation for traits associated with growth.

Implications

Large differences among breeds of cattle in lean tissue growth rate and in carcass composition provide an opportunity to use breed differences to meet a wide range of production and market requirements. Variations in dietary energy density may be used to alter lean tissue growth rate and deposition of carcass fat in a wide range of biological types of cattle. The effects of dietary energy density varying from 2.82 to 3.07 Mcal of ME/kg of dry matter do not differ greatly among breeds that vary from 21.1 to 31.8 carcass fat and from 53.8 to 64.6% carcass lean. Composite populations or breeds provide an opportunity to use breed differences to achieve and maintain optimum additive genetic (breed) composition for carcass composition traits and to use heterosis to increase lean tissue growth rate and(or) to increase rate of fat deposition.

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