

JOURNAL OF ANIMAL SCIENCE

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J Anim Sci 1998. 76:665-673.

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Adipose Tissue Partitioning of Limit-Fed Beef Cattle and Beef Cattle with Ad Libitum Access to Feed Differing in Adaptation to Heat

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ABSTRACT: We compared fat distribution and lipoprotein lipase (LPL) activity in steers differing in adaptability to the subtropics. Steers were fed a grain diet (3.13 Mcal ME/kg DM) at limited (150 kcal ME·kg^{-0.75}·d⁻¹; .23 kg ADG) or ad libitum levels for 140 d, then slaughtered. Sixteen British- (8 Angus, 8 Hereford; S), 16 Boran- (R), 16 Brahman- (B), and 16 Tuli- (T) cross steers from MARC III composite cows were used. Adipose tissue samples from perirenal, omental, and subcutaneous depots were analyzed for LPL activity. Carcass measurements including omental, external, and seam fat trim from 1/2 of the carcass were measured. Subcutaneous fat had greater ($P < .05$) LPL activity than fat from the other depots. Generally, there were no differences ($P > .05$)

in fat distribution for steers fed at limited levels. Means for ADG, slaughter weights, carcass weights, yield grades, and carcass lipid weights for S and B fed for ad libitum intake were greater ($P < .05$) than those for T and R. Marbling was greatest ($P < .05$) for S and did not differ ($P > .05$) for the other breeds with ad libitum intake. Factor analysis of fat depots for animals with ad libitum intake indicated that *Bos taurus* cattle differing in adaptation to heat deposited fat differently; S deposited greater ($P < .05$) proportions of carcass fat and T deposited greater ($P < .05$) proportions of internal fat. It seems that accumulation of internal fat is detrimental for ADG for *Bos taurus* cattle.

Key Words: Lipoprotein Lipase, Beef Cattle, Breeds, Heat, Adipose Tissue

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J. Anim. Sci. 1998. 76:665-673

Introduction

The distribution of muscle, bone, and fat is largely a function of maturity (Berg and Butterfield, 1976; Robelin, 1986). Most phenotypic conformational differences among cattle are due to differences in maturity, muscle and bone shape, and fat distribution (Berg, 1978). Animals within the same species and level of maturity have more variation in distribution of fat than in any other tissue (Berg and Butterfield, 1976). Variation in the deposition and distribution of fat may be specifically related to the utility for which an animal was developed or to climatic conditions that

existed in the different environments in which cattle breeds originated. Recently, tropically adapted *Bos taurus* (Tuli) and *Bos indicus* (Boran) cattle from Africa have been introduced into the United States. However, little is known about the site of fat accumulation for these genotypes. The objective of this study was to compare temperately adapted *Bos taurus* (Angus and Hereford) and tropically adapted *Bos indicus* (Brahman) breeds presently in the United States to these newly introduced genotypes to determine how animals differing in adaptation to heat varied in site of fat accumulation and in lipoprotein lipase (LPL) activity (an enzyme that affects adipocyte accumulation of fat by mobilization of free fatty acids from extracellular triglycerides) by depot site.

Materials and Methods

Sixteen British- (8 Angus and 8 Hereford), 16 Boran-, 16 Brahman-, and 16 Tuli-sired steers from MARC III composite cows (1/4 Angus, 1/4 Hereford, 1/4 Pinzaguier, 1/4 Red Poll) were fed a corn-based diet³ (3.13 Mcal ME/kg DM; 2.14 Mcal NE_m/kg DM;

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³Dry matter content of feed (percentage):Corn, dry rolled 83.8, corn silage 13.0, soybean meal, solvent extracted 2.56, limestone, ground .434, urea, .138, Ca₂(PO₄)₃ .040, vitamin A-D-E premix - 012, trace mineral premix .008, and Rumensin 80 (Elanco Animal Health, Indianapolis, IN) .010.

Received March 26, 1997.

Accepted September 21, 1997.

1.47 Mcal NE_g/kg DM; NRC, 1984) for 140 d at the USDA Meat Animal Research Center (MARC) at Clay Center, Nebraska. Steers were randomly allotted within breed to two feeding levels. The two treatments consisted of half of the animals being given ad libitum access to the above diet and the other half of the animals receiving the same diet on a limited-feed basis (150 kcal ME·kg^{-0.75}·d⁻¹). Individual metabolizable energy intake/day was determined with Calan-Broadbent electronic headgates. Feeding levels for the limited-feed group were adjusted according to animal weights taken every 14 d. Unshrunk weights were obtained for experimental animals at the beginning of the trial, every 14 d afterward, and the end of the trial. Average daily gain was obtained by regression. Hip height at the end of the feeding trial was also determined. None of the steers was implanted with any type of growth-promoting agent.

Slaughter and Sample Collection

Mean age at slaughter for limit-fed steers was 424 d (SD = 12.0 d), with a range of 20 d among sire breed means. For steers given ad libitum access to feed, mean age at slaughter was 422 d (SD = 10.9 d), with a range of 12 d among sire breed means.

Following slaughter, weights were recorded for hot carcass, omental fat, liver, washed gastrointestinal tract, offal (hide, head, tail, feet, empty gastrointestinal tract, internal organs), and external and seam fat trim excised from one side of the carcass. One side of the carcass was graded for quality and yield and degree of marbling (Traces⁰⁰ = 200; Slight⁰⁰ = 300; Small⁰⁰ = 400). Percentage of kidney, heart, and pelvic fat (**KPH**) was also estimated and fat thickness over the 12th rib was measured. The right side of the carcass was separated into lean tissue, adipose tissue, and bone. Adipose tissue was assumed to contain 13.14% water, 82.00% fat, 3.89% fat-free organic matter, .97% ash, and 7.92 Mcal NE/kg. Bone tissue was assumed to contain 35.79% water, 19.73% fat, 8.09% fat-free organic matter, 36.84% ash, and 2.92 Mcal NE/g (Ferrell and Jenkins, 1984). Lean tissue separated as described above was ground and mixed thoroughly. Triplicate samples from 5 kg of lean product were obtained from each 1/2 carcass and analyzed for percentage of carcass lipid by ether extract (AOAC, 1980). Offal was ground through a large grinder and mixed by two additional passes through the grinder. Percentage of offal lipid was also determined by ether extract of triplicate samples of the ground offal. Kilograms of KPH fat were calculated using the estimated KPH percentage × hot carcass weight. Kilograms of offal lipid and carcass lipid were calculated by multiplying the respective percentages from ether extract × kilograms of offal or hot carcass weight. Total lipid was the sum of weight of offal and carcass lipid.

Within 15 min after exsanguination, 10-g fat tissue samples were obtained from omental, perirenal, and

subcutaneous sites and frozen at -20°C for later analysis of LPL activity (McNamara et al., 1987). The omental sample was obtained from fat near the omasum, the perirenal sample from the kidney fat or "knob," and the subcutaneous sample from the rump region immediately dorsal to the tuber ischiadicum (above the pinbone). Data from one Brahman-sired steer fed the limited-feed ration were eliminated due to abscessed kidneys, and one Boran-sired steer given ad libitum access to feed was eliminated because a descended testicle was discovered at slaughter.

Enzyme Assays

Fat samples from omental, perirenal, and subcutaneous sites for enzyme assays were homogenized (PRO250, Pro Scientific, Monroe, CT) using the procedure of McNamara et al. (1987), except that samples were homogenized in 2× volume instead of 1× volume of buffer (1.56 M Tris-HCl, .1 M NaCl, 20% glycerol, pH 7.0). Following homogenization, samples were centrifuged at 530 × *g* for 5 min at 4°C; the fluid below the fat pad was pipetted into microcentrifuge tubes and recentrifuged at 6,200 × *g* for 5 min at 4°C. The cytosolic supernate was then filtered under vacuum through 1.6-μm glass filters (Fisher Scientific, Houston, TX) and frozen until assayed. Cytosolic protein of the homogenate was determined with a modified Lowry procedure (Lowry et al., 1951; Markwell et al., 1978), using BSA as standard.

The activity of total LPL enzyme was measured in duplicate at 37°C for 1 h (McNamara et al., 1982) in .25 mL of final volume containing 4 mM triolein, .8 μCi glycerol tri-[9-10-³H]oleate, .11 mg phosphatidylcholine, 130 μL .156 M Tris base (pH 8.6), .705 mg BSA in 20 μL .156 M Tris base, 50 μL homogenate, and 50 μL of heat-inactivated (60°C for 10 min) rat serum. Samples were preincubated for 30 min with rat serum before adding enzyme, or Tris base for blanks. After the 1-h incubation, free fatty acids (**FFA**) were extracted (Belfrage and Vaughn, 1969; McNamara et al., 1982), vortexed, and centrifuged at 1,500 × *g* for 30 min, and a 1-mL aliquot of the upper phase was added to 10 mL of scintillation fluid (Scintiverse-E, Sigma, St. Louis, MO) for counting (Packard Model 1600GR Analyzer, Downers Grove, IL). Enzyme activity was reported as nanomoles of FFA released per hour per milligram of adipose tissue cytosolic protein. Duplicate samples that differed from each other 20% or more or had negative counts after subtracting the blanks were reanalyzed. The LPL assay was found to be linear with time and amounts of protein used.

Statistical Analyses

The dependent variables of live slaughter weight, ADG, carcass weight, hip height, omental fat weight, liver weight, washed gastrointestinal tract weight, offal lipid weight, carcass lipid weight, fat trim

weight, total lipid weight, yield grade, marbling, KPH fat weight, percentage KPH, percentage carcass lipid, percentage offal lipid, and fat thickness over the 12th rib were analyzed with analyses of variance (ANOVA) with the model \hat{Y} = sire breed, ration, and sire breed \times ration as fixed main effects. Because of the difference in live weight and carcass weight between breeds in this trial and their influence on absolute kilograms of fat in depot sites, carcass lipid weight, total lipid weight, fat trim weight, omental fat weight, offal lipid weight, and KPH fat weight were also analyzed within ration with one-way ANOVA with sire breed as a fixed main effect and carcass weight as a continuous variable. Exploratory plots were linear when raw data for these variables were plotted against carcass weight. All animals with ad libitum intake were adjusted to a carcass weight of 287 kg, which was within the range observed for all sire breeds but was -21, -24, +31, and +20 kg different from the actual means observed for Brahman-, British-, Boran-, and Tuli-sired steers, respectively. Steers on the limited-feed ration were adjusted to a carcass weight of 207 kg, again within the range observed for all sire breeds, but -3, -15, +6, and +12 kg different from the means observed for Brahman-, British-, Boran-, and Tuli-sired steers, respectively. Average daily gain within ration was analyzed with one-way ANOVA with sire breed as a fixed main effect.

Because of among-variable autocorrelations for the carcass measurements collected and because fat measurements did not express equivalent variables and did not have the same units, factor analysis (SAS, 1988) was employed to identify independent orthogonal factors indicative of different currents of fat deposition. The principal axis method with varimax rotation was used (SAS, 1988). Factor analysis reduces metric-scaled data on a large number of variables to a smaller subset of independent uncorrelated variables, called factors, which capture as much information as possible from the original data set (Parasuraman, 1986). Because of the large differences between growth curves of breeds used in this study and the large nutritional effect imposed, cattle at the time of slaughter varied greatly in weight (range 309 to 574 kg slaughter weights). Consequently, the initial factor analysis reflected this large variation, and individual factors retained were dominated by weight characteristics. Therefore, subsequent factor analyses were conducted on the residuals from the model: \hat{Y} = carcass weight and total lipid weight. The residuals were used to characterize adipose tissue depot site differences among breeds without the confounding variation that existed for weight and total fatness. Variables included in the factor analysis were marbling, fat thickness over the 12th rib, omental fat weight, KPH fat weight, carcass lipid weight, offal lipid weight, yield grade, percentage KPH, percentage carcass lipid, dressing percentage, external and seam fat trim weight, and percentage offal lipid. Redundant varia-

Table 1. Rotated factor pattern of steer fatness measurements^a

Variable	Factor 1 ^a	Factor 2 ^b
Marbling residual	-.12569	.72406
Fat thickness residual	.12925	.70538
Omental fat residual	.76249	.23280
Estimated KPH ^c weight residual	.57922	.07487
Carcass fat residual	-.92923	.16816
Offal fat residual	.92912	-.16797

^aFactor analysis was performed on residuals from the analysis \hat{Y} = carcass weight and total fat. Rotated by Varimax procedure. Eigenvalue for factor 1 = 2.68 and for factor 2 = 1.14. Factor 1 explained 45% of cumulative variation of the data set and factor 2 explained 19%, for a total of 64% of total variation of the data set.

^bFactor 1 is characterized by internal fat; factor 2 is characterized by carcass fat.

^cKidney, heart, and pelvic fat.

bles indicated by similar scores in factor loading of residuals were yield grade, percentage KPH, percentage carcass lipid, dressing percentage, external and seam fat trim weight, and percentage offal lipid. These were eliminated and the factor analysis was performed again on the remaining variables. Table 1 presents the final rotated factor patterns. Factors 1 and 2 explained 64% of the communal variance (Table 1). Factor 1 was characterized by measurements of fatness in the body cavity as indicated by the large positive loadings for omental fat weight, offal lipid weight, and KPH fat weight, and by the large negative loading for carcass lipid weight. Factor 2 was characterized by measurements of fatness within the carcass as indicated by large positive loadings for marbling and fat thickness over the 12th rib. Factor scores for factors 1 and 2 for each animal were analyzed by ANOVA with sire breed, ration, and sire breed \times ration as fixed main effects. Within rations, factors were analyzed by one-way ANOVA with sire breed as a fixed main effect.

Analysis of LPL activities used ANOVA with fixed main effects of sire breed, ration, depot site, and sire breed \times ration \times depot site. Analysis of LPL activity within ration by ANOVA had sire breed, depot site, and sire breed \times depot site as fixed main effects.

Treatment means for all statistical models were separated using unprotected least significant difference tests.

The relationship of fat distribution (individual factors from the factor analysis) to growth rate was tested within dietary treatment group using simple linear regression and by ANOVA with the model \hat{Y} = sire breed, factor, sire breed \times factor.

Results and Discussion

Animal Description

Generally, differences between sire breeds for all variables were less for limit-fed animals than for those

Table 2. Hip height, live weight, and weight gains^a

Breed of sire	Hip height at slaughter, cm		Live weight at slaughter, kg		Gain, kg/d ^b	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^c	128.8 ± 1.3 ^{df}	129.9 ± 1.3 ^{ef}	384.3 ± 15.4 ^e	521.5 ± 15.4 ^d	.40 ± .05 ^e	1.28 ± .05 ^d
Tuli	125.6 ± 1.3 ^d	128.1 ± 1.3 ^{df}	330.6 ± 15.4 ^f	441.2 ± 15.4 ^g	.25 ± .05 ^f	.97 ± .05 ^g
Boran	127.9 ± 1.3 ^{df}	127.9 ± 1.4 ^{df}	344.2 ± 15.4 ^{ef}	431.6 ± 16.5 ^g	.34 ± .05 ^{ef}	1.01 ± .06 ^g
Brahman	131.7 ± 1.4 ^{ef}	133.5 ± 1.3 ^e	354.6 ± 16.5 ^{ef}	499.6 ± 15.4 ^d	.34 ± .06 ^{ef}	1.28 ± .05 ^d

^aLeast squares means ± SE from the model \hat{Y} = sire, ration, and sire × ration.

^bSire × ration interaction, P = .043.

^cBritish = four Angus and four Hereford within dietary treatment group.

^{d,e,f,g}Means within an item with different superscripts differ, P < .05.

given ad libitum access to feed. When fed for ad libitum consumption, all breeds attained similar hip heights at slaughter except Brahman-sired steers, which were taller than the African breeds (P < .05, Table 2). When rations were limited, only Brahman and Tuli hip heights were different, the former being taller (P < .05). British- and Brahman-sired steers had similar slaughter weights and ADG when fed for ad libitum intake and out-performed the African-sired steers, which were similar (P > .10, Table 2). When fed the limited ration, British-sired steers were heavier and had greater ADG than Tuli-sired steers (P < .05), but they were similar to the remaining breeds (P > .10, Table 2).

Carcass Measurements

Carcass weights (Table 3) generally followed the same trends observed in final slaughter weights, except that there were no differences (P > .10) observed for limit-fed steers.

Although there were no differences in liver weight for limit-fed steers (P > .10), British-sired steers on the ad libitum ration had greater liver weights (P < .05) than the other steers, which were similar (P > .10). British-sired steers on the limit-fed and ad libitum rations also had greater (P < .05) gastrointestinal tract weights than did the other steers, which were similar (P > .10).

When liver weight for limit-fed steers was expressed as a percentage of live weight, there were no

differences (P > .20) among sire breeds. Among steers with ad libitum intake, *Bos taurus* breeds were similar (P > .05) to each other (Table 4), as were *Bos indicus* breeds (P > .10). There was a tendency (P = .055) for British-sired steers to have greater liver percentages of live weight than Tuli-sired steers. Both *Bos taurus* breeds on the ad libitum ration also had a greater (P < .05) liver percentage of live weight than did Brahman-sired steers (Table 4). British-sired steers on the ad libitum ration also had a greater liver percentage of live weight than did Boran, and Boran and Tuli were similar (P > .10). Liver size increases with increased feed intake and accounts for a significant proportion of fasting energy expenditure (Ferrell et al., 1976). Similarly, smaller gastrointestinal tract sizes for *Bos indicus* cattle have been implicated in lower fasting heat production (Webster, 1991) and greater heat tolerance (Sprinkle et al., 1996).

Gastrointestinal tract weight of steers on the ad libitum ration expressed as a percentage of live weight responded similarly to liver weight (Table 4); *Bos taurus* cattle had greater (P < .05) percentages than Brahman-sired steers, and British-sired steers, had greater (P < .05) percentages than Boran, which was similar to Tuli (P > .05). On the limited-fed ration, British-sired steers had greater (P < .05) gastrointestinal tract percentages of live weight than did all the other steers, which were similar (P > .10).

Table 5 presents measurements of overall fatness for steers in the trial. Steers on the limited-feed ration

Table 3. Carcass, liver, and washed gastrointestinal tract (GIT) weights^a

Breed of sire	Carcass weight at slaughter, kg		Liver weight at slaughter, kg ^b		GIT weight, kg	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^c	221.8 ± 9.7 ^e	311.4 ± 9.7 ^d	3.5 ± .2 ^d	6.2 ± .2 ^f	22.0 ± 1.0 ^f	29.2 ± 1.0 ^d
Tuli	195.3 ± 9.7 ^e	267.2 ± 9.7 ^f	3.1 ± .2 ^d	4.9 ± .2 ^e	17.2 ± 1.0 ^e	23.7 ± 1.0 ^f
Boran	201.1 ± 9.7 ^e	255.6 ± 10.3 ^f	3.3 ± .2 ^d	4.5 ± .2 ^e	18.2 ± 1.0 ^e	21.3 ± 1.0 ^f
Braham	209.9 ± 10.3 ^e	308.1 ± 9.7 ^d	3.4 ± .2 ^d	5.1 ± .2 ^e	18.1 ± 1.0 ^e	23.9 ± 1.0 ^f

^aLeast squares means ± SE from the model \hat{Y} = sire, ration, and sire × ration.

^bSire × ration interaction, P = .003.

^cBritish = four Angus and four Hereford within dietary treatment group.

^{d,e,f}Means within an item with different superscripts differ, P < .05.

Table 4. Liver and gastrointestinal tract (GIT) components^a

Breed of sire	Liver, percentage of live weight ^b		GIT, percentage of live weight	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^c	.91 ± .03 ^f	1.19 ± .03 ^e	5.76 ± .16 ^e	5.59 ± .16 ^{ef}
Tuli	.95 ± .03 ^{dh}	1.11 ± .03 ^{eg}	5.22 ± .16 ^{dfg}	5.37 ± .16 ^{de}
Boran	.95 ± .03 ^{dh}	1.05 ± .03 ^{dg}	5.28 ± .16 ^{df}	4.93 ± .17 ^{dg}
Brahman	.97 ± .03 ^{df}	1.01 ± .03 ^{dh}	5.11 ± .17 ^{dg}	4.79 ± .16 ^g

^aLeast squares means ± SE from the model $\hat{Y} = \text{sire, ration, sire} \times \text{ration}$.

^bSire × ration interaction, $P = .0024$.

^cBritish = four Angus and four Hereford within dietary treatment group.

^{d,e,f,g,h}Means within an item with different superscripts differ, $P < .05$.

were unable to express any differences by breed ($P > .10$). When placed on the ad libitum ration, Brahman- and British-sired steers were similar ($P > .10$) and had fatter carcasses ($P < .05$) than African breeds, which were similar ($P > .10$). The fatter carcasses for British- and Brahman-sired steers was apparent for yield grade ($P < .05$) and carcass lipid ($P < .05$). Total lipid weight did not differ among British- and Brahman-sired steers ($P > .10$), nor among African-sired steers ($P > .10$; Table 5), but British-sired steers had greater total lipid than both African breeds ($P < .05$). Brahman-sired steers had greater total lipid weight than Boran and tended ($P = .053$) to have more than Tuli steers when fed for ad libitum intake. *Bos indicus* (Brahman crosses) and *Bos taurus* (British crosses) presently used in the United States responded differently to increased feeding levels than did *Bos taurus* (Tuli crosses) and *Bos indicus* (Boran crosses) from Africa in respect to average daily gain, yield grade, and carcass lipid weight (breed × ration interaction, $P = .027$). This interaction is probably due to relatively recent selection pressure for growth placed on British and Brahman cattle used in U.S. production systems.

When steers on the trial were statistically adjusted to similar carcass weights within dietary treatment group (data not presented) there were no differences in total lipid or carcass lipid weight ($P > .10$) for

steers fed for ad libitum intake. Among steers on the limited-feed ration adjusted to similar carcass weights, Boran steers had greater ($P < .05$) total lipid weight than did Brahman-sired steers (46.6 ± 2.3 vs 39.1 ± 2.5 kg) and also tended ($P = .053$) to have greater carcass lipid than Brahman-sired steers (27.0 ± 1.5 vs 22.5 ± 1.6 kg).

Sire breed was important ($P = .0001$) for marbling and fat trim ($P = .01$), as was the interaction of sire breed and ration for fat trim ($P = .028$, Table 6). Breed differences in marbling, rib eye fat thickness, and fat trim were only detected in the ad libitum feeding regimen. However, there was a trend ($P < .10$) for British steers to have greater marbling than the other sire breeds when limit-fed. For steers on the ad libitum ration, only British cattle attained mean marbling scores adequate for the Choice grade (Table 6; $P < .05$). Subcutaneous fat cover (as suggested by rib eye fat thickness over the 12th rib) was greater ($P < .05$) for British-sired steers than for the African breeds, which were similar ($P > .10$). Brahman-sired steers were similar ($P > .10$) to British-sired steers in respect to subcutaneous fat cover but only had greater ($P < .05$) subcutaneous fat than Boran-sired steers. In respect to fat trim for steers fed for ad libitum intake, British- and Brahman-sired steers were similar ($P > .10$) and had greater ($P < .05$) amounts than both African breeds, which were similar ($P > .10$). When

Table 5. Overall fatness^a

Breed of sire	Yield grade ^b		Carcass lipid, kg ^c		Total lipid, kg ^d	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^e	2.0 ± .2 ^g	3.4 ± .2 ^f	26.7 ± 2.4 ^g	50.7 ± 2.4 ^f	46.9 ± 4.1 ^h	89.7 ± 4.1 ^f
Tuli	1.9 ± .2 ^g	2.6 ± .2 ^h	21.8 ± 2.4 ^g	37.5 ± 2.4 ^h	38.0 ± 4.1 ^h	74.1 ± 4.1 ^{gi}
Boran	1.9 ± .2 ^g	2.6 ± .2 ^h	25.7 ± 2.4 ^g	37.8 ± 2.6 ^h	44.7 ± 4.1 ^h	68.4 ± 4.4 ⁱ
Brahman	1.9 ± .2 ^g	3.4 ± .2 ^f	23.1 ± 2.6 ^g	48.1 ± 2.4 ^f	40.2 ± 4.4 ^h	85.6 ± 4.1 ^{fg}

^aLeast squares means ± SE from the model $\hat{Y} = \text{sire, ration, and sire} \times \text{ration}$.

^bSire × ration interaction, $P = .049$.

^cSire × ration interaction, $P = .027$.

^dSire × ration interaction, $P = .057$.

^eBritish = four Angus and four Hereford within dietary treatment group.

^{f,g,h,i}Means within an item with different superscripts differ, $P < .05$.

Table 6. Marbling, rib eye fat thickness, and fat trim^a

Breed of sire	Marbling ^b		Rib eye fat thickness, cm ^c		Fat trim kg ^d	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^e	338 ± 16 ^{gh}	443 ± 16 ^f	.32 ± .14 ^h	1.54 ± .14 ^{fg}	12.1 ± 2.0 ^g	33.4 ± 2.0 ^f
Tuli	295 ± 16 ^g	369 ± 16 ^h	.32 ± .14 ^h	1.03 ± .14 ^{ij}	8.6 ± 2.0 ^g	26.0 ± 2.0 ^h
Boran	294 ± 16 ^g	329 ± 17 ^{gh}	.35 ± .14 ^h	.82 ± .15 ⁱ	10.4 ± 2.0 ^g	24.0 ± 2.1 ^h
Brahman	293 ± 17 ^g	349 ± 16 ^h	.27 ± .15 ^h	1.25 ± .14 ^{gj}	8.7 ± 2.1 ^g	34.4 ± 2.0 ^f

^aLeast squares means ± SE from the model $\hat{Y} = \text{sire, ration, and sire} \times \text{ration}$.

^bMarbling = Traces⁰⁰ = 200; Slight⁰⁰ = 300; Small⁰⁰ = 400.

^cSire × ration interaction, $P = 0.55$.

^dSire × ration interaction, $P = 0.28$.

^eBritish = four Angus and four Hereford within dietary treatment group.

^{f,g,h,i,j}Means within an item with different superscripts differ, $P < .05$.

the statistical model with carcass weight as a covariate was used, the differences in fat trim from external and seam fat depots for steers with ad libitum intake seemed to be due to carcass weight ($P = .0001$) rather than breed alone ($P = .9241$). For animals fed the limited ration and adjusted to a common carcass weight, there was a trend ($P = .1211$) for breed effects, with Boran-sired steers having greater ($P < .05$) fat trim than Brahman. Brahman- and British-sired steers in this trial weighed 60 to 90 and 10 to 50 kg more than Tuli and Boran steers on ad libitum and limited-feed rations, respectively.

Table 7 presents least squares means for the internal fat depots of KPH fat, omental fat, and offal lipid without adjusting steers to a common carcass weight. There were no breed differences for animals fed the limited-feed ration. The interaction of sire breed with dietary treatment tended to be important for omental fat ($P = .062$). The influence of sire breed was only important ($P = .002$) for omental fat, with British-sired steers having greater omental fat than Tuli and Boran ($P < .05$) and Brahman and Tuli having greater omental fat than Boran ($P < .05$). There was a trend ($P = .130$) for breed differences for offal lipid, with Boran-sired steers having less ($P < .05$) offal lipid than all the other breeds. The introduction of carcass weight as a covariate did not

change breed rankings for least squares means for KPH fat for steers on the ad libitum ration ($P > .10$), but there was a trend ($P = .068$) for Tuli-sired steers to have greater KPH fat than Brahman- and British-sired steers. Also, carcass weight had an influence ($P < .037$) on breed rankings for animals on the limited-feed ration. Brahman-sired steers on this ration adjusted to a common carcass weight had less KPH fat than did British- and Boran-sired steers ($P < .05$) and tended to have less KPH fat than did Tuli-sired steers ($P < .10$). Carcass weight was not important ($P > .05$) in considering offal lipid, but Tuli-sired steers on the ad libitum ration adjusted to a common carcass weight had greater ($P < .05$) offal lipid than did Brahman- and British-sired steers and tended to have greater offal lipid ($P < .10$) than Boran. Covariate adjustment of omental fat least squares means removed breed differences for animals fed for ad libitum intake and revealed a trend ($P < .10$) for Tuli to have greater omental fat than Brahman- and Boran-sired steers. When omental fat least squares means for steers on the limited-feed ration were adjusted to a common carcass weight ($P = .23$ for sire breed), it resulted in British steers having greater ($P < .05$) omental fat than Brahman steers. Using covariance analysis, a clearer pattern of fat deposition emerges. The net result of covariate adjustment of omental fat, KPH fat, and offal lipid by carcass weight was that smaller

Table 7. Internal fat depots^a

Breed of sire	KPH, kg ^b		Omental fat, kg ^c		Offal lipid, kg	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^d	3.0 ± .5 ^f	8.6 ± .5 ^e	16.7 ± 1.5 ^g	32.6 ± 1.5 ^e	20.2 ± 2.0 ^g	39.0 ± 2.0 ^e
Tuli	2.1 ± .5 ^f	8.4 ± .5 ^e	13.3 ± 1.5 ^g	27.6 ± 1.5 ^f	16.2 ± 2.0 ^g	36.7 ± 2.0 ^{ef}
Boran	2.8 ± .5 ^f	7.4 ± .6 ^e	14.4 ± 1.5 ^g	22.8 ± 1.6 ^h	19.0 ± 2.0 ^g	30.6 ± 2.1 ^h
Brahman	1.6 ± .6 ^f	8.4 ± .5 ^e	13.4 ± 1.6 ^g	29.3 ± 1.5 ^{ef}	17.0 ± 2.1 ^g	37.4 ± 2.0 ^{ef}

^aLeast squares means ± SE from the model $\hat{Y} = \text{sire, ration, and sire} \times \text{ration}$.

^bEstimated from USDA percentage kidney, heart, and pelvic fat (KPH) × carcass weight.

^cSire × ration interaction, $P = .062$.

^dBritish = four Angus and four Hereford within dietary treatment group.

^{e,f,g,h}Means within an item with different superscripts differ, $P < .05$.

Table 8. Factor 1 and factor 2 least squares means^a

Breed of sire	Factor 1, proportion of fat ^b		Factor 2, proportion of fat ^b	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^c	-0.14 ± .31 ^d	-0.28 ± .31 ^d	.18 ± .32 ^d	1.15 ± .32 ^e
Tuli	-0.06 ± .31 ^d	1.37 ± .31 ^e	.22 ± .32 ^d	.00 ± .32 ^d
Boran	-0.37 ± .31 ^d	.06 ± .34 ^d	-0.25 ± .32 ^d	-0.53 ± .34 ^d
Brahman	-0.30 ± .34 ^d	-0.31 ± .31 ^d	-0.20 ± .34 ^d	-0.67 ± .32 ^d

^aFrom the model $\hat{Y} = \text{sire} + \text{ration} + \text{sire} \times \text{ration}$.

^bFactor 1 is characterized by internal fat; Factor 2 is characterized by carcass fat. Sire \times ration interaction for Factor 1, $P = .064$.

^cBritish = four Angus and four Hereford within dietary treatment group.

^{d,e}Means within an item with different superscripts differ, $P < .05$.

Tuli-sired steers on the ad libitum ration seemed to have greater proportions of fat in these internal fat depots than did the other breeds and that Brahman-sired steers on the limited-feed ration seemed to have lesser proportions of internal fat than the British-sired steers.

Factor Analysis Least Squares Means

The information that was presented in Tables 5 to 7 is enhanced and clarified by factor least squares means presented in Table 8. Although the type of ration tended to be unimportant ($P = .063$) for factor 1 (body cavity fat), large differences existed among breeds ($P = .013$). Tuli-sired steers on the ad libitum ration had greater body cavity fat than all the other breeds (Table 8). There was a trend ($P = .064$) detected for a sire breed \times dietary treatment interaction, the largest effect being for Tuli-sired steers on the ad libitum ration (Table 8). Tuli-sired steers stored more fat internally than other breeds with ad libitum feeding. In this respect, they may function more like a dairy breed (Koch et al., 1976) than a beef breed. Because Tuli cattle were developed from indigenous cattle among southern African tribesmen (Rouse, 1970), they may have a history of functioning as a dual-purpose breed. Also, in a hot environment, it would not be an advantage to have substantial external fat due to the extra heat load this would entail (Byers and Carstens, 1991).

In factor 2 (characterized by measures of fatness within the carcass) analyses, there were no differences by ration ($P = .99$), but British-sired steers on the ad libitum ration had greater ($P < .05$) carcass fat than did any other breed (Table 8). This is further evidence that adds to an already substantial base (Marshall, 1994) to support the premise that British breeds accumulate increased amounts of external fat and marbling with improved rations.

Lipoprotein Lipase Activity

Although all animals in the trial were fed for 140 d, large variation existed in cumulative fat deposition among individual animals (Tables 2, 3, and 5 to 8). Cattle of different frame sizes have different growth

curves (Berg and Walters, 1983), and this affects the deposition of fat. The activity of LPL can be perceived as a "snapshot" within time during the finishing process. Animals that varied in maturity and patterns of fat deposition could also be expected to vary greatly in LPL activity within various fat depots. This was reflected by large coefficients of variation (exceeding 90%) observed for LPL activity. Only fat depot site was important ($P = .0002$) as a main effect.

As animals mature, rates of fat deposition in individual depots shift from internal to external fat depots (Ingle et al., 1972). Steers on the ad libitum ration in this experiment had the greatest LPL activity (nanomoles of free fatty acids released per hour per milligram of adipose tissue cystolic protein) in the subcutaneous fat depot (43.02 ± 5.87 ; $P < .05$) and similar ($P > .10$) rates of LPL activity in the omental (23.08 ± 5.87) and perirenal (15.23 ± 5.87) fat depots. Within sire breed, there were no differences in LPL activity ($P > .05$) by deposition site for steers from African sires given ad libitum access to feed. Lipoprotein lipase activity for British-sired steers with ad libitum feed intake was greater ($P < .05$) within the subcutaneous depot than in the perirenal and omental depot (Table 9). Subcutaneous LPL activity was greater ($P < .05$) than perirenal LPL activity for Brahman-sired cattle with ad libitum intake. Thus, LPL activity in the subcutaneous fat depot for the faster-growing Brahman- and British-sired steers seemed to accompany increased subcutaneous fat partitioning for these breeds (Table 6).

Subcutaneous LPL activity (33.85 ± 4.30) for animals on the limited-feed ration was greater ($P < .05$) than that observed for the perirenal fat depot ($P < .05$; 20.07 ± 4.30) and tended to be greater ($P < .10$) than that observed for the omental fat depot (22.92 ± 4.30). There was a weak trend ($P = .154$) for sire breed to influence LPL activity in limit-fed animals. Overall LPL activity for all fat depots was less ($P < .05$) for limit-fed Brahman-sired steers than for British- or Boran-sired steers (Table 9). When LPL activity by depot site was compared for the different breeds on the limited-feed ration (Table 9), Brahman-sired steers tended ($P < .10$) to have less LPL activity

Table 9. Lipoprotein lipase activity (LPL) by fat depot^a

Breed of sire	Subcutaneous LPL ^b		Omental LPL ^b		Perirenal LPL ^b	
	Limit-fed	Ad libitum	Limit-fed	Ad libitum	Limit-fed	Ad libitum
British ^c	34.16 ± 10.11 ^{efg}	53.01 ± 10.11 ^{def}	36.33 ± 10.11 ^{efg}	20.91 ± 10.11 ^{gh}	20.92 ± 10.11 ^{gh}	17.38 ± 10.11 ^{gh}
Tuli	25.04 ± 10.11 ^{fgh}	44.24 ± 10.11 ^{efh}	18.76 ± 10.11 ^{gh}	18.40 ± 10.11 ^{gh}	31.51 ± 10.11 ^{efg}	20.81 ± 10.11 ^{gh}
Boran	54.57 ± 10.11 ^{de}	34.13 ± 10.81 ^{efg}	20.47 ± 10.11 ^{gh}	19.36 ± 10.81 ^{gh}	17.20 ± 10.11 ^{gh}	11.07 ± 10.81 ^g
Brahman	21.64 ± 10.81 ^{gh}	40.69 ± 10.11 ^{efh}	16.10 ± 10.81 ^{gh}	33.66 ± 10.11 ^{efg}	10.67 ± 10.81 ^g	11.64 ± 10.11 ^g

^aLeast squares means ± SE from the model $\hat{Y} = \text{sire, ration, depot site, and sire} \times \text{ration} \times \text{depot site}$.

^bLPL activity is expressed as nanomoles of free fatty acids released per hour per milligram of adipose tissue cystolic protein.

^cBritish = four Angus and four Hereford within dietary treatment group.

^{d,e,f,g,h}Means with different subscripts within row or column differ, $P < .05$.

in the perirenal depot than did Tuli. In the subcutaneous fat depot, Boran-sired steers had greater LPL activity than Brahman ($P < .01$) and Tuli ($P < .05$) and tended to have greater LPL activity than British-sired steers ($P < .10$). Within breed (Table 9), the response of subcutaneous LPL activity above that of perirenal and omental LPL activity was minimal ($P > .10$) for animals fed the limited-feed ration, except for Boran-sired steers ($P < .01$).

Lambs fed maintenance-level rations have been shown to have nondetectable LPL activity in subcutaneous depots, as opposed to much greater activity for animals fed a finishing ration (Haugebak et al., 1974). Animals with lesser maintenance requirements may be able to express an advantage in increased subcutaneous LPL activity.

Boran cattle are a humped breed of *Bos indicus* origin descended from the Shorthorn Zebu cattle that were introduced into Africa about 700 A.D. and are about 150 (female) to 300 kg (male) smaller than the American Brahman (Rouse, 1970). The greater subcutaneous LPL activity we observed for Boran-sired steers on the limited-feed ration in this experiment may have been a function of the lesser maintenance requirements that have been reported for *Bos indicus* cattle (Frisch and Vercoe, 1984) and the smaller size of the African *Bos indicus* cattle. This could allow a greater portion of ME intake to be partitioned for subcutaneous fat deposition compared to *Bos taurus* and the larger *Bos indicus* cattle and could be advantageous with the restricted ration.

Influence of Fat Partitioning on Average Daily Gain

The deposition of fat internally may be an advantage in energy retrieval (Byers and Schelling, 1988) and heat tolerance for Tuli-sired cattle but may be a disadvantage in growth rate (Solis et al., 1988). Tuli-sired steers on the ad libitum ration had the greatest proportion of internal fat (Table 8) and lesser ADG (Table 2) than British- and Brahman-sired steers. The relationship of internal fat (factor 1) or carcass fat (factor 2) to ADG was not important ($r^2 < .03$) for steers with ad libitum intake.

The relationship of internal fat to ADG is more apparent with animals on the limited-feed ration

(Figure 1). The simple linear regression of ADG against factor 1 showed that internal fat accounted for 11% of the variation in ADG for animals on the limited-feed ration, with ADG being reduced .05 kg for each unit change in internal fat. However, breed response differed among animals in this experiment, and a significant ($P < .05$) sire breed \times factor 1 interaction was detected. The two *Bos taurus* breeds had negative slopes for ADG, and those of the *Bos indicus* crosses had positive slopes (Figure 1). Among the *Bos taurus* breeds, British-sired steers reduced ADG twice as much as Tuli steers with each unit

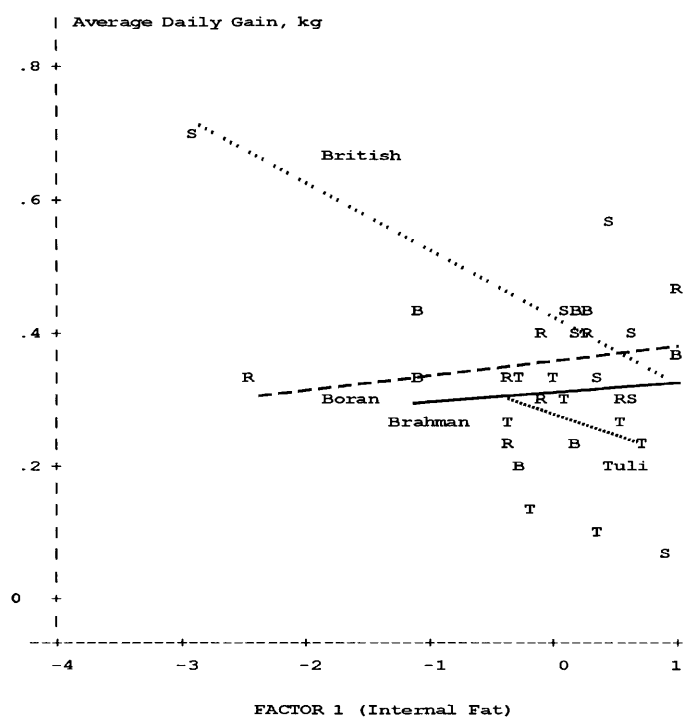


Figure 1. Average daily gain for steers on limited-feed ration and the relationship to internal fat. Symbol of sire: S = British; B = Brahman; R = Boran; T = Tuli. Regression lines from the model $\hat{Y} = \text{sire, factor 1, sire} \times \text{factor 1}$; $R^2 = .50$; mean square error = .011. Regression equation for British = $.385 - .118 (\text{factor 1})$; Tuli = $.246 - .057 (\text{factor 1})$; Boran = $.353 + .030 (\text{factor 1})$; Brahman = $.256 + .008 (\text{factor 1})$.

change in internal fat (-.12 vs -.06 kg). Among the *Bos indicus* breeds, Boran-sired steers were able to gain about four times as much as Brahman-sired steers with each unit change in internal fat (.03 vs .008 kg). The positive slopes observed for internal fat in Figure 1 for *Bos indicus* crosses may be related to the lesser maintenance requirements that have been observed for these breeds (Frisch and Vercoe, 1984). The relationship of ADG to carcass fat for animals on the limited-feed ration was minimal ($r^2 < .004$).

In an environment with surplus energy available, the influence of internal fat may have a lesser effect on ADG, but in a more limited environment internal fat may be a detriment to increased ADG, especially for British cattle. Breeds of cattle that have a propensity to deposit fat internally with improved rations (Tuli) may do so at the expense of ADG. Internal fat may be more expensive to deposit (Solis et al., 1988) and maintain (Thompson et al., 1983). However, dual-purpose animals may deposit fat in these expensive depots, which allows them to benefit from the relative ease of tissue mobility during nutritional deprivation. Byers and Schelling (1988) suggested that internal fat is more readily mobilized than subcutaneous fat due to the greater vascularity of internal fat.

Implications

The site of adipose tissue deposition may be related to heat adaptation for some breeds of cattle. Heat-adapted Tuli-sired cattle deposited fat internally, and cool-season-adapted British cattle deposited fat in the carcass. For *Bos indicus* cattle, reduced gastrointestinal tract sizes may be more important in terms of heat adaptation. Internal fat may be a more expensive fat depot to deposit and maintain. Subcutaneous lipoprotein lipase activity for animals fed the limited ration was greatest for Boran-sired steers and may be related to maintenance requirements.

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