

Evaluation of Beef Carcass and Palatability Traits and Prediction of Tenderness in A Cross of *Bos Indicus* × *Bos Taurus* Cattle**

Jong Joo Kim* and Jerry Taylor¹

Animal Science Department, Texas A&M University, College Station, TX 78743, USA

ABSTRACT : Steers and heifers (N=490) were produced between 1991 and 1996 by reciprocal fullsib backcross and F₁ crosses from Angus and Brahman to compare characteristics of carcass and palatability traits between *Bos indicus* and *Bos taurus* inheritance. Carcasses of ¾Angus were heavier, fatter (p<0.05), more tender and higher in other palatability attributes (p<0.01) than those of ¾Brahman. Reciprocal effects of parental cross breeds were found on some traits. Within ¾Brahman inheritance group, Brahman sired progeny produced heavier and fatter carcasses with better palatability (p<0.05) than progeny with Brahman as a dam breed. Estimates of heritability were intermediate to high in most carcass and palatability traits. Genetic correlations of tenderness with marbling score (MARB), sarcomere length (SARC), fragmentation index (FRAG) and calpastatin activity (CALP) were moderate to high, suggesting potential use of the tenderness-influencing factors as indirect selection criteria to improve palatability attributes. MARB and SARC that were best predictors of tenderness explained 3.07 to 5.85% and 4.32 to 8.24% of variation in tenderness, respectively. However, there was no tenderness-influencing factor to dominantly explain large portion of variation in tenderness. (*Asian-Aust. J. Anim. Sci.* 2001. Vol 14, No. 11 : 1621-1627)

Key Words : Beef Cattle, Carcass, Palatability, Reciprocal Effect, Genetic Correlation, Tenderness Prediction

INTRODUCTION

Crossbreeding between *Bos taurus* and *Bos indicus* cattle has been widely practiced in subtropical regions due to merits of heterosis and breed complementarity for reproduction, growth and carcass traits. The advantages on production efficiency of crossbreeding programs using *Bos indicus* breeds, i.e., Brahman, in semitropical and tropical regions have been well demonstrated (Cole et al., 1963; Crockett et al., 1979). However, beef carcasses with high percentage of *Bos indicus* inheritance were less fat, heavy and tender, and more variable in tenderness (Crouse et al., 1989; Shackelford et al., 1991a).

In the last decade rapid developments in molecular technology enabled to find genes or economic trait loci with non-Mendelian inheritance or genomic imprinting effects influencing growth and carcass traits in livestock (Cockett et al., 1996; de Koning et al., 2000; Imumorin, 2000). Reciprocal effects on birth or preweaning traits when using Brahman or *Bos indicus* breeds as sires were also demonstrated (Baker et al., 1989; Thallman et al., 1992).

Beef carcass merit influences consumer acceptability and among palatability traits, tenderness is the main factor

of consumer satisfaction on meat. However, consistency in meat tenderness and earlier classification of meat according to its quality (thus degree of tenderness) with high precision are the primary concern in U.S. beef industry (Koochmaria et al., 1995).

The objectives of this study were 1) to compare effects on beef carcass characteristics and meat palatability due to differences of *Bos indicus* (Brahman) and *Bos taurus* (Angus) inheritances and inheritance patterns in paternal lines, 2) to estimate variance components of heritability, genetic and phenotypic correlations among those traits, and 3) to determine prediction of tenderness.

MATERIALS AND METHODS

Resource family structure and phenotypes

Steers and heifers (N=490) were produced between 1991 and 1996 by reciprocal fullsib backcross and F₁ crosses from Angus (A) and Brahman (B) by embryo transfer, which were randomly assigned to and reared by Brahman × Hereford crossbred recipient dams. Five cross types of parental breeds were classified as (AB, BA) × A, A × (AB, BA), (AB, BA) × B, B × (AB, BA) and (BA) × (AB). The numbers of families for the five crosses were 6, 8, 7, 7 and 2, respectively, with average 15 progeny per family. The progeny were raised at similar conditions from birth at the Texas A&M Agricultural Experiment Station at Angleton, weaned at approximately seven months of age, backgrounded on pasture for an average of 215 days and fed for 150 days on a corn-based finishing diet. Cattle then were shipped to the Rosenthal Meat Science and Technology Center in College Station, weighed, slaughtered

** This paper was presented at 6th World Congress on Genetic Applied to Livestock Production on January 15, 1998 at University of New England, Armidale, Australia.

* Address reprint request to Jong-Joo Kim, Dept of Genetics, Faculty of Veterinary Medicine, University of Liege, 20 Bd de Colonster, B43. 4000 Liege, Belgium. Tel: +32-4-366-4538, Fax: +32-4-366-4122, E-mail: JJKim@ulg.ac.be

¹ GenomicFX, L.P., 12024 Vista Parke Dr., Austin, Texas 78726, USA.

and chilled 24 h at 2°C.

Quality grade (QG) and Yield grade (YG) factors were measured at the 12-13th rib and included marbling score (MARB), actual and adjusted fat thickness (ACF, ADF), ribeye area (REA), kidney, pelvic and heart fat (KPH), slaughter weight (SWT), hot carcass weight (HCWT), and dressing percentage (DP). Warner-Bratzler shear force (WBSF) at 14 days postmortem was completed (AMSA, 1994). A trained meat descriptive attribute sensory panel evaluated overall tenderness (OTEND), juiciness (JUIC), and flavor intensity (FLAV) on two steaks for each animal (AMSA, 1994). Sarcomere length (SARC) at 24 h postmortem was evaluated as defined by Cross et al. (1981). Calpastatin activity (CALP) at 24 h postmortem was evaluated as defined by Harris (1994), and fragmentation index (FRAG) was measured.

Statistical analyses

Data were analysed by general linear model (GLM) procedures (SAS, 1985), and the mixed model was

$$Y = X\beta + Zu + e,$$

where Y is a vector of observations with length N, β is an unknown vector containing appropriate fixed effects (year-season of birth, sex, cross of sire and dam breeds) and covariates (weaning age and days on feed), u is a vector of random effects (family nested within cross of sire and dam breed), X and Z is known incidence matrices relating observations in Y to parameters in β and u, respectively, and e is a random vector of residuals. The random effect of families within cross of parental breeds was fitted to test cross effects of sire and dam breeds. Reciprocal effects were evaluated within progeny groups of $\frac{3}{4}$ Angus or $\frac{3}{4}$ Brahman breeds by linear contrasts, in which families within each cross were also fitted as a random effect.

Variance components for heritability, genetic and phenotypic correlations were estimated by use of an Animal Model using the MTDFREML program of Boldman et al. (1993). The same fixed effects and covariates were included as in the GLM model. Variance components were estimated for each combination of four traits (MARB, OTEND, WBSF and each other trait). When converged values of the variance components were the same as starting values with norm difference smaller than 1.D-9, global maximum was considered to be reached.

To determine best predictors of tenderness traits, forward regression analyses were performed using WBSF and OTEND as dependent variables and MARB, SARC, FRAG, ADF and CALP as independent variables across breed, within $\frac{3}{4}$ Angus or $\frac{3}{4}$ Brahman breed. In these analyses year-season effect of birth or other fixed and random effects as in the GLM model were accounted for before regression analyses were performed. In each forward regression step, the best independent variable with at least

statistical significance of $p < 0.1$ was included in the model.

RESULTS AND DISCUSSION

Effects of parental breed cross types

The analyses of variance under the GLM model indicated that year-season of birth and families within cross type of sire and dam breeds were significant sources of variation for all traits ($p < 0.01$) except MARB, JUIC and FLAV. Effects of parental breed cross type were also significant ($p < 0.1$) for all traits except DP (data are not shown).

Table 1 shows least squares means of parental breed cross type, statistical significance on the differences between $\frac{3}{4}$ Angus and $\frac{3}{4}$ Brahman progeny, and reciprocal effects within $\frac{3}{4}$ Angus and $\frac{3}{4}$ Brahman progeny. Most carcass and palatability traits differed between $\frac{3}{4}$ Angus and $\frac{3}{4}$ Brahman progeny. Angus crosses ($\frac{3}{4}$) were heavier (for SWT and HCWT, $p < 0.05$), fatter (for ACF, ADF and KPH, $p < 0.05$), had higher leanness (for REA, $p < 0.01$), lower WBSF values ($p < 0.01$) and higher MARB, OTEND, FLAV and JUIC values ($p < 0.01$). This indicates that $\frac{3}{4}$ Angus inheritance produces higher palatability characteristics than $\frac{3}{4}$ Brahman. These results were consistent with other reports, in which more than half or increasing the percentage of *Bos indicus* inheritance decreases carcass weight, fat thickness, marbling, tenderness and other palatability traits (Crouse et al., 1989; Whipple et al., 1990; Johnson et al., 1990; Shackelford et al., 1991a; Sherbeck et al., 1995).

Also SARC and CALP, main factors of postmortem tenderization (Koochmaraie, 1996), were longer and lower, respectively ($p < 0.01$) in carcasses of $\frac{3}{4}$ Angus progeny (table 1), which supports higher attributes to tenderness in $\frac{3}{4}$ Angus carcasses. However, there were no significant differences of DP, YG and FRAG between carcasses of the two different inheritance groups ($p > 0.05$). FRAG, a measure of degree of muscle fiber integrity, has been assumed to be related to postmortem tissue degradation, and reported to be associated with tenderness (Crouse et al., 1989; Whipple et al., 1990; Johnson et al., 1990; Shackelford et al., 1991b). Thus it was unexpected not to observe difference in FRAG between the two groups that had dissimilar tenderness characteristics in this study. One thing to note is, however, that reciprocal effect on FRAG within $\frac{3}{4}$ Angus carcasses was found such that FRAG values of $F_1 \times A$ and $A \times F_1$ carcasses were averaged out, so as not to differ from the FRAG values estimated in $\frac{3}{4}$ Brahman carcasses (table 1).

Estimated values of carcass and palatability traits of ($F_1 \times F_1$) progeny were generally in the middle range between those of $\frac{3}{4}$ Angus and $\frac{3}{4}$ Brahman carcass groups (table 1). Those values were not significantly different from either values of $\frac{3}{4}$ Angus or $\frac{3}{4}$ Brahman group (data are not

Table 1. Least squares means of cross types of parental breeds and linear contrasts among the crosses for beef carcass and palatability traits

Trait ^a	Cross least squares means ^b					Linear contrasts ^f			Overall means	CV ^j	Model R ²
	F ₁ ^c × A ^d	A × F ₁	B ^e × F ₁	F ₁ × B	F ₁ × F ₁	1 ^g	2 ^h	3 ⁱ			
SWT	497	489	479	453	459	*	ns	ns	490	9.2	0.54
HCWT	319	315	309	288	297	**	ns	*	316	10.0	0.58
MARB	480	467	363	359	405	**	ns	ns	415	17.4	0.54
QG	707	715	653	649	686	**	ns	ns	683	5.8	0.51
FRAG	222	209	213	216	229	ns	*	ns	218	8.6	0.40
DP	64.2	64.1	64.5	63.6	64.1	ns	ns	ns	64.2	2.6	0.34
REA	78.3	76.8	70.7	70.6	75.7	**	ns	ns	76.4	10.2	0.45
ACF	1.19	1.15	1.05	0.84	0.99	**	ns	*	1.12	35.8	0.39
ADF	1.32	1.32	1.25	1.05	1.16	*	ns	*	1.31	28.6	0.48
KPH	2.49	2.37	2.26	2.13	2.39	**	ns	ns	2.31	22.3	0.28
YG	3.07	3.07	3.22	2.83	2.72	ns	ns	**	3.12	19.6	0.34
OTEND	5.70	5.95	5.26	4.84	5.34	**	ns	*	5.48	12.5	0.56
WBSF	3.54	3.33	3.93	4.18	3.77	**	ns	ns	3.56	26.7	0.31
JUIC	5.44	5.75	5.33	5.20	5.28	**	**	ns	5.46	10.4	0.30
FLAV	5.49	5.58	5.45	5.29	5.49	**	*	**	5.51	4.5	0.52
SARC	1.76	1.77	1.73	1.70	1.75	**	ns	ns	1.75	5.2	0.27
CALP	2.00	1.95	2.14	2.48	2.33	**	ns	*	2.23	23.9	0.36

^a SWT, slaughter weight (kg), HCWT, hot carcass weight (kg), MARB, marbling scores (400 = Slight⁰⁰; 500 = Small⁰⁰), QG, USDA quality grade, FRAG, fragmentation index, DP, dressing percentage (%), REA, ribeye area (cm²), ACF, actual fat thickness at the 12-13th rib (cm), ADF, adjusted fat thickness at the 12-13th rib (cm), KPH, kidney, pelvic and heart fat (%), YG, USDA yield grade, OTEND, overall tenderness by sensory panel (8 = extremely tender; 1 = extremely tough), WBSF, Warner-Bratzler shear force at 14 days postmortem (kg), JUIC, juiciness (8 = extremely juicy, 1 = extremely dry), FLAV, flavor intensity (8 = extremely intense, 1 = extremely bland), SARC, sarcomere length (μm) at 24 hr postmortem, CALP, calpastatin activity per gram of muscle at 24 h postmortem.

^b The first letter indicates sire breed and the latter dam breed.

^c F₁, Angus × Brahman or Brahman × Angus. ^d A, Angus. ^e B, Brahman. ^f ns, nonsignificant, *, p<0.05, **, p<0.01.

^g 1, test Ho: ¼Angus = ¼Brahman. ^h 2, test Ho: (F₁×A)=(A×F₁). ⁱ 3, test Ho: (F₁×B)=(B×F₁). ^j CV, coefficient of variation × 100.

shown).

Reciprocal effects were found on some traits within ¼Angus or ¼Brahman inheritance. Compared to ¼Angus group, the reciprocal effects were observed in much more traits (HCWT, ACF, ADF, YG, OTEND, FLAV and CALP, p<0.05) within ¼Brahman group. Furthermore, those estimated values indicate that Brahman sired progeny produced heavier and fatter carcasses with better palatability than progeny with Brahman as dam breed. These results were consistent with the differences between carcasses of ¼Angus and ¼Brahman. Results of reciprocal effects for other traits without statistical significance within the ¼Brahman group were also generally consistent with the differences between carcasses of ¼Angus and ¼Brahman.

It is well demonstrated that maternal heterosis and maternal direct effect did not strongly influence postweaning or carcass traits (Gregory et al., 1987; Comerford et al., 1988; Arthur et al., 1989; De Rouen et al., 1992). Most current genetic evaluations in livestock are based on the Mendelian genetic model that assumes equal contribution of each parent to their progeny inheritance.

However, some non-Mendelian effects on birth and preweaning traits were found in crosses of *Bos indicus* × *Bos taurus* cattle, in which *Bos indicus* sired progeny were heavier at birth, weaning and yearling ages than progeny with *Bos indicus* dams (Baker et al., 1989; Thallman et al., 1992). Thallman et al. (1992) explained possible genetic mechanisms on the reciprocal effects, i.e., mitochondrial inheritance, genomic imprinting, X-linked inheritance with non-random X-chromosome inactivation, Y-linked inheritance, maternal transmission of non-genetic ova cytoplasmic components and maternal effect of ovary, oviduct and uterus of donor cow on embryo prior to transfer of the embryo on day 7.

In recent years, genes or quantitative trait loci (QTL) with non-Mendelian mode of gene action were found in livestock. Among them were included callipyge locus on ovine muscular hypertrophy with polar overdominance effects (Cockett et al., 1996), IGF2 locus on porcine muscularity with paternal imprinting effects (Jeon et al., 1999; Nezer et al., 1999) and QTL on porcine body composition and bovine birth and growth traits with paternal or maternal imprinting effects (de Koning et al.,

2000; Imumorin, 2000). Systematic searches and identification of QTL with Mendelian or non-Mendelian effects will unravel the genetic mechanisms in those complex traits that are polygenic and interacted with environmental factors. Thus, identification of the QTL or genes and utilisation in marker assisted selection will allow the design of more efficient breeding schemes (Kim and Park, 2001).

Heritabilities, genetic and phenotypic correlations

Estimates of heritability (h^2) for most carcass and palatability traits were intermediate to high, except for JUIC and FLAV ($h^2=0.03$ in table 2). These results were consistent with other reports in which heritabilities of fatness traits, WBSF, MARB, REA, CALP were generally estimated intermediate to high (Koch et al., 1982; Arnold et al., 1991; Gregory et al., 1994; Shackelford et al., 1994; Wulf et al., 1996). The low estimates of h^2 for JUIC and FLAV, measures of palatability attributes, were also consistent with the reports of Wulf et al. (1996), and Gregory et al. (1995) where the heritabilities estimated in purebreds were 0.06 and 0.08, respectively.

Magnitudes of genetic correlations (r_g) of tenderness traits (OTEND and WBSF) and MARB with other carcass and palatability traits were generally intermediate to high (table 2). Some genetic correlations among tenderness, other palatability traits and tenderness influencing factors were estimated high; -0.93 between OTEND and WBSF, 1.00 for FLAV with OTEND and MARB, -0.59 between FRAG and OTEND, and -0.95, 0.68 and -0.67 for CALP with OTEND, WBSF and MARB, respectively. Results from other reports were similar to the estimates in this study; $r_g=-0.98$ and -1.00 between OTEND and WBSF (Gregory et al., 1994; Gregory et al., 1995, respectively), 0.81 and 0.63 between FLAV and OTEND (Gregory et al., 1994; Gregory et al., 1995, respectively), -1.14 between CALP and OTEND (Wulf et al., 1996), 0.50 and 1.08 between CALP and WBSF (Shackelford et al., 1994; Wulf et al., 1996, respectively), and -0.75 between CALP and MARB (Wulf et al., 1996). However, Miller et al. (1996) reported small estimate of genetic correlation between CALP and WBSF ($r_g=0.16$) in a half-blood *Bos indicus*-influenced population.

Moderate or high genetic associations of MARB, FRAG, CALP and SARC with tenderness traits indicate that these tenderness-influencing factors are good candidates as indirect selection criteria to improve palatability attributes. However, the candidate factors should be chosen such that antagonism with other growth or carcass traits of economic value does not exist or is minimal if it exists.

Most estimates of phenotypic correlations (r_p) among carcass and tenderness traits were lower than those of genetic correlations (table 2). These results were consistent with other reports (Koch et al., 1982; Gregory et al., 1994;

Table 2. Within breed heritability, genetic and phenotypic correlation estimates among beef carcass and palatability traits

Trait	h^{2a}	OTEND ^b	WBSF ^b	MARB ^b
SWT	0.64	0.31	-0.12	0.63
	0.69	0.12	-0.08	0.29
HCWT	0.54	0.42	-0.43	0.58
	0.57	0.16	-0.12	0.27
DP	0.39	-0.10	-0.20	-0.20
	0.41	0.08	-0.06	0.07
ACF	0.25	0.36	-0.57	0.29
	0.31	0.16	-0.13	0.27
ADF	0.34	0.09	-0.40	0.12
	0.34	0.14	-0.14	0.25
KPH	0.30	0.38	-0.35	0.22
	0.37	0.18	-0.07	0.21
REA	0.49	0.55	-0.63	0.49
	0.51	0.16	-0.14	0.17
YG	0.23	0.04	-0.11	0.14
	0.23	0.12	-0.09	0.23
QG	0.63	0.42	-0.32	0.90
	0.94	0.26	-0.14	0.86
OTEND	0.49	-	-0.93	0.42
	0.47	-	-0.58	0.23
WBSF	0.17	-0.93	-	-0.37
	0.18	-0.58	-	-0.15
JUIC	0.03	0.43	-0.23	0.58
	0.01	0.40	-0.22	0.13
FLAV	0.03	1.00	-0.34	1.00
	0.02	0.35	-0.18	0.27
MARB	0.78	0.42	-0.37	-
	0.79	0.23	-0.15	-
SARC	0.25	0.42	-0.12	0.12
	0.26	0.32	-0.16	0.08
FRAG	0.42	-0.59	0.47	0.48
	0.42	-0.19	0.13	0.35
CALP	0.42	-0.95	0.68	-0.67
	0.42	-0.30	0.10	-0.15

^aUpper and lower values of heritabilities were estimated by single and multiple trait analyses, respectively.

^bUpper and lower values are genetic and phenotypic correlation estimates, respectively.

Gregory et al., 1995; Miller et al., 1996; Wulf et al., 1996). Estimates of phenotypic correlations of WBSF with MARB, SARC, FRAG and CALP were -0.15, -0.16, 0.13 and 0.10, while those of OTEND with the four traits were 0.23, 0.32, -0.19 and -0.30, which is consistently higher than the estimates for WBSF. This indicates that the four tenderness-influencing factors explain better phenotypic variance in OTEND than in WBSF. However, small magnitudes of these phenotypic correlations suggest that the four tenderness-influencing factors are poor predictors of beef tenderness in this cross population of Angus and Brahman.

Table 3. Regression coefficients of tenderness-influencing factors on tenderness measures across breed, within ¼ Angus and ¼ Brahman after accounting for year-season effect of birth

	OTEND ^b				WBSF ^c			
	Predictors ^a	β value ^d	Partial R ²	Model R ²	Predictors	β value ^d	Partial R ²	Model R ²
Across breed	SARC	2.240**	0.0824	0.50	MARB	-0.003**	0.0432	0.24
	MARB	0.002**	0.0352		FRAG	0.012**	0.0325	
	FRAG	-0.010**	0.0365		SARC	-1.270**	0.0161	
	CALP	-0.220**	0.0146		ADF	-0.200 [†]	0.0060	
	ADF	0.150 [†]	0.0045					
		Σ 0.1732				Σ 0.0918		
¼ Angus	MARB	0.001**	0.0307	0.44	MARB	-0.002**	0.0585	0.30
	SARC	0.980*	0.0225		CALP	0.240 [†]	0.0151	
	FRAG	-0.007*	0.0157		SARC	-1.140 [†]	0.0149	
	ADF	0.210 [†]	0.0122					
		Σ 0.0811				Σ 0.0885		
¼ Brahman	SARC	2.910**	0.0697	0.60	SARC	-2.610**	0.0432	0.34
	CALP	-0.390**	0.0357		FRAG	0.018*	0.0242	
					ADF	-0.520**	0.0340	
		Σ 0.1054				Σ 0.1014		

^a The predictors were included in tenderness equation models in that order by forward regression analyses. MARB, marbling scores, FRAG, fragmentation index, SARC, sarcomere length (µm) at 24 h postmortem, CALP, calpastatin activity per gram of muscle at 24 h postmortem, ADF, adjusted fat thickness at the 12-13th rib (cm).

^b OTEND, overall tenderness by sensory panel. ^c WBSF, Warner-Bratzler shear force at 14 days postmortem (kg).

^d [†] p<0.1, * p<0.05, ** p<0.01.

Prediction of tenderness

The best 1- to 5-variables for prediction of WBSF and OTEND after accounting for year-season effect of birth are shown in table 3. MARB accounted for the highest amount of variation in WBSF across breed, within ¼Angus breed, and in OTEND within ¼Angus breed. Partial R² for MARB ranged between 3.07% and 5.85%. SARC accounted for the highest amount of variation in WBSF within ¼Brahman breed, and in OTEND across breed and within ¼Brahman breed. Partial R² for SARC ranged between 4.32% and 8.24%. FRAG was the second variable to enter the WBSF equations across breed and within ¼Brahman breed, and CALP was the second variable to enter the WBSF and OTEND equations within ¼Angus and ¼Brahman breeds, respectively.

Associations of the five predictors with tenderness have been well demonstrated in Hawkins et al. (1987) for FRAG, Whipple et al. (1990) for CALP, Dikeman (1996) for ADF and MARB, and Koohmaraie (1996) for SARC. In some reports, significant amount of variation in tenderness was due to the predictors; 44% of variation in WBSF and OTEND by CALP (Whipple et al., 1990) and 26.4% of variation in WBSF by FRAG (Hawkins et al., 1987). The amount of variation (5% to 10%) due to MARB in Dikeman (1996) and Jones and Tatum (1994) was comparable to the results in this study. However, the tenderness-influencing factors included in the tenderness equations were not good predictors, because total variations of tenderness explained by the predictors were around or less than 10% except for that (17.32%) of OTEND across breed (table 3). The

amounts of variation were even smaller (<5%) when effects of cross type, family nested within parental breed cross type, sex, weaning age and days on feed were additionally accounted for (data are not shown). Small contribution of those predictors to explaining tenderness was expected partly due to low phenotypic correlations (table 2).

As there was no factor among the predictors to dominantly explain a large portion of variation in meat tenderness, and as there is still large portion of variation unexplained by factors fitted in the GLM model (model R² =0.56, 0.31 for OTEND and WBSF, respectively in table 1), other sources in broad categories of genetics and environments should be considered to determine best combination of predictors of meat tenderness. Among them are included factors relating to breed, feeding, slaughter and postmortem processing conditions.

ACKNOWLEDGEMENTS

This research was financially supported by the support of the Texas Agricultural Experiment station, a grant from the Beef Industry Council of the National Livestock and Meat Board and by USDA.NRICGP grants 94-37205-1224 and 95-37205-2273.

REFERENCES

- AMSA. 1994. Research guidelines for cookery, sensory evaluation and instrumental tenderness measurements of fresh meat. American Meat Science Association, Chicago, IL.

- Arnold, J. W., J. K. Bertrand, L. L. Benyshek and C. Ludwig. 1991. Estimates of genetic parameters for live animal ultrasound, actual carcass data and growth traits in beef cattle. *J. Anim. Sci.* 69:985-992.
- Arthur, P. F., M. Makarechian, M. A. Price and R. T. Berg. 1989. Heterosis, maternal and direct effects in double-muscled and normal cattle: II. Carcass traits of young bulls. *J. Anim. Sci.* 67:911-919.
- Baker, J. F., C. E. Dorn and G. A. Rohrer. 1989. Evaluation of direct genetic and maternal effects on birth weight and gestation length. *Tex. Agr. Exp. Sta. Tech. Rep.* 89:1-25.
- Boldman, K. G., L. A. Kriese, L. D. Van Vleck and S. D. Kachman. 1993. A manual for use of MTDFREML. USDA, Agriculture Research Service, Clay Center, Nebraska.
- Cockett, N. E., S. P. Jackson, T. D. Shay, D. Nielsen, R. D. Green and M. Georges. 1996. Polar overdominance at the ovine callipyge locus. *Science* 273:236-238.
- Cole, J. W., C. B. Ramsey, C. S. Hobbs and R. S. Temple. 1963. Effects of type and breed of British, Zebu and dairy cattle on production, palatability and composition. I. Rate of gain, feed efficiency and factors affecting market value. *J. Anim. Sci.* 22:702-707.
- Comerford, J. W., L. L. Benyshek, J. K. Bertrand and M. H. Johnson. 1988. Evaluation of performance characteristics in a diallel among Simmental, Limousin, Polled Hereford and Brahman beef cattle. II. Carcass traits. *J. Anim. Sci.* 66:306-316.
- Crockett, J. R., F. S. Baker, Jr., J. W. Carpenter and M. Koger. 1979. Postweaning, feedlot and carcass characteristics of calves sired by Continental, Brahman and Brahman-derivative sires in subtropical Florida. *J. Anim. Sci.* 49:900-907.
- Cross, H. R., R. L. West and T. R. Dutton. 1981. Comparison of methods for measuring sarcomere length in beef *Semiteminosus* muscle. *Meat Sci.* 5:261-266.
- Crouse, J. D., L. V. Cundiff, R. M. Koch, M. Koohmaraie and S. C. Seideman. 1989. Comparisons of *Bos indicus* and *Bos taurus* inheritance for carcass beef characteristics and meat palatability. *J. Anim. Sci.* 67:2661-2668.
- De Koning, D. J., A. P. Rattink, B. Harlizius, J. A. M. van Arendonk, E. W. Brascamp and M. A. M. Groenen. 2000. Genome-wide scan for body composition in pigs reveals important role of imprinting. *Proc. Natl. Acad. Sci. USA* 97:7947-7950.
- De Rouen, S. M., D. E. Franke, T. D. Bidner and D. C. Blouin. 1992. Direct and maternal genetic effects for carcass traits in beef cattle. *J. Anim. Sci.* 70:3677-3685.
- Dikeman, M. E. 1996. The relationship of animal leanness to meat tenderness. *Proc. Annu. Recip. Meat Conf.* 49:87-101.
- Gregory, K. E., D. D. Dearborn, L. V. Cundiff and R. M. Koch. 1987. Maternal heterosis and grandmaternal effects in beef cattle: postweaning growth and carcass traits. *J. Anim. Sci.* 65:1180-1194.
- Gregory, K. E., L. V. Cundiff, R. M. Koch, M. E. Dikeman and M. Koohmaraie. 1994. Breed effects, retained heterosis, and estimates of genetic and phenotypic parameters for carcass and meat traits of beef cattle. *J. Anim. Sci.* 72:1174-1183.
- Gregory, K. E., L. V. Cundiff and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. *J. Anim. Sci.* 73:1920-1926.
- Harris, J. J. 1994. Growth, composition and palatability of calf- and yearling-fed cloned steers. Ph. D. Thesis, Texas A&M University, College Station, Texas, USA.
- Hawkins, R. R., G. W. Davis, J. K. Gable, Jr. and C. B. Ramsey. 1987. Fragmentation index as an early postmortem predictor of beef tenderness. *J. Anim. Sci.* 64:171-176.
- Imumorin, I. 2000. Quantitative trait loci mapping of genomic imprinting effects in *Bos taurus* × *Bos indicus* cattle. Ph. D. Thesis, Texas A&M University, College Station, Texas, USA.
- Jeon, J.-T., Ö. Carlborg, A. Törnsten, E. Giuffra, V. Amarger, P. Chardon, L. Andersson-Eklund, K. Andersson, I. Hansson, K. Lundström and L. Andersson. 1999. A paternally expressed QTL affecting skeletal and cardiac muscle mass in pigs maps to the IGF2 locus. *Nat. Genet.* 21:157-158.
- Johnson, D. D., R. D. Huffman, S. E. Williams and D. D. Hargreave. 1990. Effects of percentage Brahman and Angus breeding, age-season of feeding and slaughter end point on meat palatability and muscle characteristics. *J. Anim. Sci.* 68:1980-1986.
- Jones, B. K. and J. D. Tatum. 1994. Predictors of beef tenderness among carcasses produced under commercial conditions. *J. Anim. Sci.* 72:1492-1501.
- Kim, J. J. and Y. I. Park. 2001. Current status of quantitative trait locus mapping in livestock species. *Asian-Aust. J. Anim. Sci.* 14(4):587-596.
- Koch, R. M., L. V. Cundiff and K. E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. *J. Anim. Sci.* 55:1319-1329.
- Koohmaraie M., T. L. Wheeler and S. D. Shackelford. 1995. Beef tenderness: regulation and prediction. *CSIRO Meat '95 Proc.* pp. 4A-1-4A-20.
- Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization processes of meat. *Meat Sci.* 43:S193-S201.
- Miller, R. K., J. F. Taylor, J. O. Sanders, D. K. Lunt, S. K. Davis, J. W. Turner, J. W. Savell, F. Kallel, J. Ophir and R. E. Lacey. 1996. Methods for improving meat tenderness. *Proc. Annu. Recip. Meat Conf.* 49:106-113.
- Nezer, C., L. Moreau, B. Brouwers, W. Coppieters, J. Detilleux, R. Hanset, L. Karim, A. Kvasz, P. Leroy and M. Georges. 1999. An imprinted QTL with major effect on muscle mass and fat deposition maps to the IGF2 locus in pigs. *Nat. Genet.* 21:155-156.
- SAS. 1985. SAS User's Guide: Statistics (Version 5 Ed.) SAS Inst. Inc., Cary, NC.
- Shackelford, S. D., M. Koohmaraie, M. F. Miller, J. D. Crouse, and J. O. Reagan. 1991a. An evaluation of tenderness of the longissimus muscle of Angus by Hereford versus Brahman crossbred heifers. *J. Anim. Sci.* 69:171-177.
- Shackelford, S. D., M. Koohmaraie, G. Whipple, T. L. Wheeler, M. F. Miller, J. D. Crouse and J. O. Reagan. 1991b. Predictors of beef tenderness: Development and verification. *J. Food Sci.* 56:1130-1135.
- Shackelford, S. D., M. Koohmaraie, L. V. Cundiff, K. E. Gregory, G. A. Rohrer and J. W. Savell. 1994. Heritabilities and

- phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield, and growth rate. *J. Anim. Sci.* 72:857-863.
- Sherbeck, J. A., J. D. Tatum, T. G. Field, J. B. Morgan and G. C. Smith. 1995. Feedlot performance, carcass traits, and palatability traits of Herford and Herford×Brahman steers. *J. Anim. Sci.* 73:3613-3620.
- Thallman, R. M., J. O. Sanders and J. F. Taylor. 1992. Non-Mendelian genetic effects in reciprocal cross Brahman × Simmental F₁ calves produced by embryo transfer. *Tex. Agri. Exp. Sta., College Station, Beef Cattle Research in Texas.* PR-5053:8-14.
- Whipple, G., M. Koochmaraie, M. E. Dikeman, J. D. Crouse, M. C. Hunt and R. D. Klemm. 1990. Evaluation of attributes that affect longissimus muscle tenderness in *Bos taurus* and *Bos indicus* cattle. *J. Anim. Sci.* 68:2716-2728.
- Wulf, D. M., J. D. Tatum, R. D. Green, J. B. Morgan, B. L. Golden and G. C. Smith. 1996. Genetic influences on beef longissimus palatability in Charolais- and Limousin-sired steers and heifers. *J. Anim. Sci.* 74:2394-2405.