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MEAT TENDERNESS GENETIC AND GENOMIC VARIATION SOURCES IN COMMERCIAL BEEF CATTLE

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ABSTRACT

To assess genetic group (GGR; *Bos indicus* [*Bi*], *Bos taurus* [*Bt*] and crosses [*BtxBi*]) and to confirm the calpain (CAPN316 and CAPN4751) and calpastatin (CAST-T1) single nucleotide polymorphism (SNP) effects on Warner–Bratzler shear force (WBSF), 196 animals under commercial conditions were analyzed. A model was fitted including the effect of GGR and considering residuals as adjusted WBSF (aWBSF). Another model was fitted to evaluate the SNP effect on aWBSF. Allele substitution effect (α) and combined favorable alleles in CAPN and CAST on aWBSF were evaluated. GGR showed a significant effect ($P < 0.0001$) on WBSF; *Bt* and *BtxBi* had the lower WBSF. CAPN316 showed significant effect on aWBSF with an $\alpha = -0.549$ kg. The combined effect of CAPN and CAST showed significant ($P < 0.0056$) reduction on aWBSF of 0.239 kg by favorable allele. The results remarked the importance of GGR and confirmed CAPN316 and combined effect of CAPN and CAST on prediction of meat tenderness.

PRACTICAL APPLICATIONS

Knowledge of main factors related to tenderness, as a key related factor to beef consumer satisfaction, would serve as a resource for commercial beef classification and management under slaughterhouse conditions. Confirmation on combined marker effects provides strong validation for marker-assisted management use of these technologies under industry conditions. Additionally, the presented results may be used as a reference for research in the beef industry aimed to provide improvement on beef tenderness to the final product.

INTRODUCTION

Beef quality is one of the main concerns in the bovine industry and, depending on the regional and country conditions, has many definitions (Hocquette and Gigli 2005). Yet, the most important concern is related to consumer satisfaction. Flavor, juiciness and, most importantly, tenderness are the main traits related to beef quality and consumer preference (Mintert *et al.* 2000).

In order to consistently produce quality meat products, the industry must have a clear understanding of the factors affecting meat quality variation (Warner *et al.* 2010). These factors may include environmental and genetic components. However, revealing the influence of these factors is a very difficult task to achieve mostly because of the complexity of beef quality traits, which are expensive and only possible to measure after slaughter (Gao *et al.* 2007; Van Eenennaam 2010). In addition, most of these traits have

moderate to low heritabilities (Johnston *et al.* 2003; Minick *et al.* 2004; Allan and Smith 2008).

To ease the difficulty in conventional genetic evaluation and improvement of beef quality traits, the use of genetic markers was suggested. In the last decades, the amount of information and reports with regard to the effect of some genetic markers on beef quality traits in different bovine breeds has been quite significant (Gao *et al.* 2007; Van Eenennaam *et al.* 2007; Allan and Smith 2008). The progress in genomic marker research has primarily let the search for quantitative trait loci and, then, the associated punctual marker variant, which, in some cases, is the causal mutation in the candidate gene affecting the trait (Gao *et al.* 2007). Calpain (CAPN; Page *et al.* 2004; White *et al.* 2005; Casas *et al.* 2006) and calpastatin (CAST; Barendse 2002) are two of the candidate genes with reported polymorphisms significantly associated with beef quality traits (i.e., tenderness); but regardless of their proposed direct use, unbiased and independent validation studies are needed to build confidence in marker technology and also as a potential source of data required to enable the integration of marker data into genetic management (Van Eenennaam *et al.* 2007).

The beef industry in Mexico is large and is associated with the nationwide agroecological regions conditioning beef production systems, processing and consumption. Annually, over 1.5 million calves are exported from Mexico to feedlots into the U.S.A., fluctuating year by year according to environmental incidences (e.g., drought). However, this trend has been changing in recent years and the Mexican beef industry is emerging as a beef exporter assisted by the transformation from carcass to boxed beef marketing system (Peel 2013).

In Mexico, a unique and explicit definition for the quality of beef does not exist, but attention has been paid to all those characteristics involved in beef industry that provide an extra value to its products (Mendez *et al.* 2009). However, to date the evidence to confirm and/or to validate the extensive use of genetic markers in beef quality management and improvement conditions is scarce (Bonilla *et al.* 2010).

The objectives of the present work were to assess the effect of genetic group (GGR) and to confirm the proposed effect of CAPN and CAST polymorphisms on tenderness of commercial beef in Mexico.

MATERIALS AND METHODS

Sample Origin and Management

A total of 196 animals from *Bos taurus* ($n = 40$) and *Bos indicus* ($n = 95$) background produced in Mexico were included in the study along with their crosses (*Bix*Bt*, $n = 61$). All animals had been concentrate fed (sorghum, corn and soybean-based diets plus vitamin and mineral premixes). Animals were slaughtered following the current commercial practices in Mexican slaughterhouses (TIF: Federal Inspection Type slaughterhouses) and then refrigerated at 0C for 24 h. Afterward, the trained personnel removed 2 inches of steaks (longissimus dorsi, 13th rib) from each selected carcasses, labelled and vacuum packed them before they were transported to the Meat Science Laboratory at the Faculty of Veterinary Medicine of Universidad Nacional Autónoma de México, Mexico City. The samples transported by road or air in insulated containers with coolant gels reached the laboratory within 8–10 h. Upon arrival, the samples were left to age for 14 days under refrigeration conditions (2–4C). Aged steaks were measured to determine the Warner–Bratzler shear force (WBSF) according to the AMSA Research Guidelines for Cookery, Sensory Evaluation, and Instrumental Tenderness Measurements of Meat (American Meat Science Association 2015). After cooking, the steaks were allowed to equilibrate at room temperature (20–25C) before we removed six to eight cores of 1.27 cm in diameter from each steak, parallel to the muscle fibre, with an automated coring device. Later, the cores were sheared perpendicularly to the muscle fibre, with a WBSF machine using a slice shear force blade from G-R Manufacturing (Manhattan, KS).

Genotyping

Micro-CAPN 316 (AF252504: CAPN316) and 4751 (AF248054: CAPN4751) (Parra-Bracamonte *et al.* 2007) and CAST T1 (AF159246: CAST-T1) loci (Casas *et al.* 2006) were analyzed and assessed on their association with beef tenderness. DNA was isolated from 5 g of lean meat using the commercial kit genomic DNA purification Wizard (Promega Corp., Madison, WI). For genotyping, markers CAPN316, CAPN4751 and CAST-T1 were analyzed using an allelic discrimination assay. Genotype assignment of each sample was carried out using the ABI Prism 7000 Real-Time Sequence Detection Software (Applied Biosystems, Foster City, CA), and was validated by comparison with control samples genotyped by sequencing.

Statistical Analysis

To assess the effect of GGR, a linear model including the fixed effect of sex of animal (ASX), age group (AGR) and days on feed (DOF) was fitted. The fitted model of WBSF adjustment was as follows:

$$Y_{ijkl} = \mu + ASX_i + AGR_j + DOF_k + GGR_l + \varepsilon_{ijkl}$$

where Y is the WBSF, μ is the general mean, ASX is the fixed effect of the *i*th ASX (bull or heifer), AGR is the fixed effect

of the *j*th AGR (<18 months, 18–26 months and >26 months of age), FMG is the fixed effect of the *k*th effect of DOF (<100 days, 100–150 days and >150 days of feeding regimen before slaughter), GGR is the fixed effect of the *l*th GGR (*B. indicus: Bi*, crossbred *B. taurus* × *B. indicus: BixBt* and *B. Taurus: Bt*) and ε is the random residual error. The significant effect of ASX, AGR and DOF is not discussed in the present work, and is used only to isolated genetic and, later on, genomic effects.

Genotypic and allelic frequencies of all loci were estimated. Hardy–Weinberg equilibrium (HWE) was tested and a genotypic linkage disequilibrium analysis was performed using GENEPOP ver. 4.2 (Rousset 2008). A correspondence analysis was used to determine the allelic distribution among GGRs identified in included samples analyzed using de CORRESP procedure of SAS 9.3 (SAS Institute Inc., Cary, NC).

From the first fitted linear model, the residuals were considered as adjusted WBSF (aWBSF) to be used for loci posterior analysis, including the individual loci effect in a linear model as fixed along with the random error. Dummy variables were created using the basis of theoretical favorable allele at candidate markers using 0, 1 or 2, accordingly, as the number of favorable alleles in the genotype. For all loci, the allelic substitution effect (α) was estimated as the pendant in a regression line model including the dummy genotypes (0, 1 and 2) as covariates. An additional analysis included the recoding of genotypes of CAPN316, CAPN4751 and CAST-T1; taking the number of favorable alleles as classified by Van Eenennaam *et al.* (2007); and fitting them in a regression analysis against aWBSF. All analyses were performed using the GLM and REG procedure of SAS 9.3 (SAS Institute Inc.).

RESULTS

Genotypic and allelic frequencies of the three studied loci are presented in Table 1. All loci were in genetic equilibrium. All loci comparison showed independent segregation in their genotypes ($P > 0.05$), except for CAPN316 and CAPN4751 that showed genotypic linkage disequilibrium ($P = 0.01$), indicating a nonindependent genotype segregation. Correspondence analysis among allele segregation of CAPN and CAST genetic markers showed a significant association ($P < 0.01$) of C alleles from *B. taurus* GGR samples (Fig. 1). In the same way, *BixBt* and *B. indicus* GGRs clustered closed together with G allele of CAPN316, and T alleles of CAPN4751 and CAST-T1, respectively.

The GGR showed a strong and highly significant effect on aWBSF ($P < 0.0001$). *B. taurus* and *BixBt* showed that the lower values of aWBSF ($P > 0.05$) are significantly different to the *B. indicus* ($P \leq 0.0005$; Table 2). As expected, the association analysis of GGRs showed that aWBSF is significantly higher for *B. indicus* beef cuts compared with *B. taurus* and even crossbred cattle.

TABLE 1. GENOTYPE AND ALLELIC FREQUENCIES OF CAPN AND CAST GENETIC MARKERS IN COMMERCIAL BEEF

	Frequencies						
	Genotypic			Allelic			HWE-P
Loci		*n*	*f*		*n*	*f*	
CAPN316	GG=	133	0.74	G=	308	0.86	0.7554
	GC=	42	0.23	C=	50	0.14	
	CC=	4	0.02				
CAPN4751	TT=	82	0.42	T=	252	0.65	0.8733
	TC=	88	0.45	C=	138	0.35	
	CC=	25	0.13				
CAST-T1	CC=	17	0.09	C=	108	0.28	0.4830
	CT=	74	0.38	T=	208	0.72	
	TT=	103	0.53				

CAPN, calpain; CAST, calpastatin; *f*, relative frequency; HWE-P, Hardy–Weinberg equilibrium *P* value.

For the polymorphism association evaluation, the CAPN316 locus showed significant effect on aWBSF ($P = 0.0316$), favoring a reduction in allelic substitution effect of more than 0.500 kg by favorable C alleles in genotype. Similarly, for CAPN4751, a significant trend was

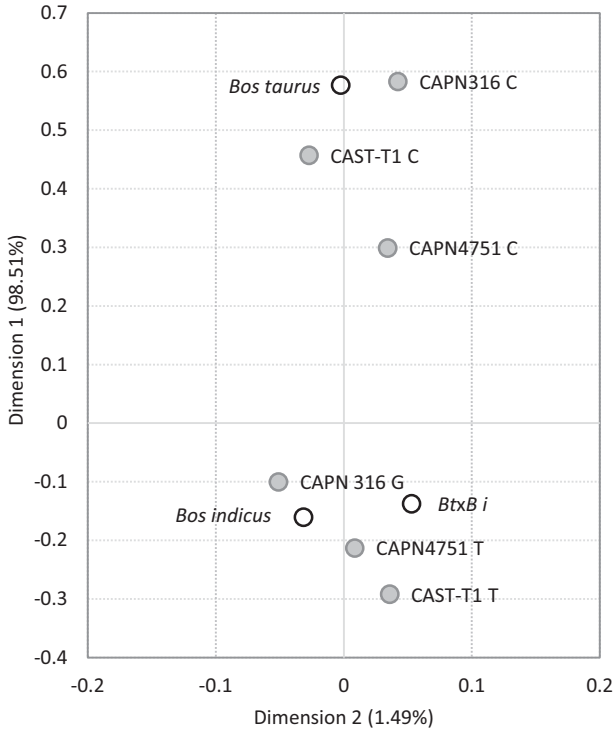

FIG. 1. CORRESPONDENCE ANALYSIS PLOT OF CAPN4751, CAPN316 AND CAST-T1 ALLELES BY GENETIC GROUP OF ANALYZED SAMPLES

TABLE 2. LEAST SQUARE MEANS ± SE OF INDIVIDUAL EFFECT OF GENETIC GROUP ($P < 0.0001$) ON WARNER–BRATZLER SHEAR FORCE (WBSF) OF COMMERCIAL BEEF

GGR	*n*	WBSF (kg)
Bos indicus	95	7.313 ± 0.202[b]
BixBt	61	5.935 ± 0.216[a]
Bos taurus	40	5.491 ± 0.294[a]

[a,b] Means with different letter are significantly different ($P < 0.01$).
GGR, genetic group; SE, standard error.

observed (Table 3), and the allelic substitution effect produced a significant reduction on aWBSF of more than 0.300 kg by favorable C allele. The combined theoretical favorable allele segregation (Fig. 2) showed a significant linear trend ($P = 0.0056$), in which pendant estimates showed a reduction of 0.239 ± 0.085 kg by segregating CAPN and CAST allele units. The homozygous combination of six favorable alleles was excluded from the analysis because of the low frequency observed ($n = 1$).

TABLE 3. LEAST SQUARE MEANS ± SE OF INDIVIDUAL EFFECTS OF CAPN316, CAPN4751 AND CAST T1 GENOTYPES ON ADJUSTED WARNER–BRATZLER SHEAR FORCE OF COMMERCIAL BEEF

Loci/genotype	*n*	aWBSF (kg)	α
CAPN316		*P = 0.0316*	
GG	133	0.130 ± 0.119[b]	–0.549 ± 0.207**
GC	42	–0.389 ± 0.212[ab]	
CC	4	–1.096 ± 0.288[a]	
CAPN4751		*P = 0.0940*	
TT	82	0.213 ± 0.152[b]	–0.316 ± 0.144*
TC	88	–0.123 ± 0.147[ab]	
CC	25	–0.404 ± 0.275[a]	
CAST-T1		*P* = 0.1972	
CC	17	0.552 ± 0.338	–0.235 ± 0.152
CT	74	0.021 ± 0.162	
TT	103	–0.145 ± 0.137	

* $P < 0.05$; ** $P < 0.01$.
[a,b] Means with different letter are significantly different ($P < 0.10$).
aWBSF, adjusted Warner–Bratzler shear force; SE, standard error.

DISCUSSION

Tenderness is one of the most important economic beef traits related to consumer acceptance and satisfaction. However, its improvement is conditioned to the difficulty and cost of measurement. As its heritability is moderate (Burrow *et al.* 2001), there are yet some important nongenetic and genetic factors to be identified and quantified in order to be used for selection and management of the best ranked animals. In consequence, the assessment of main factors as sources of variation for this trait would have important consequences in the profitability of the meat industry. Additionally, the discovery, development and validation of genomic indicators to assist selection and management may have a fundamental role along the productive chain. The present research had the objective to assess the effect of genetic factor and confirm the previously documented association effect of three single nucleotide polymorphisms (SNPs) in CAPN and CAST genes on the shear force value of commercial beef.

GGR Effect

Favorable allele frequencies of both, CAPN316 and CAPN4751, were related ($P < 0.05$) to the genetic grouping pattern of *B. taurus* classification. Conversely, crossbred and *B. indicus* animals had the higher frequencies of normal/unfavorable alleles. Linkage disequilibrium among these SNPs could partially explain this pattern; however, the HWE test suggested that this segregating association is perhaps not positively related to the selection of the favorable genotypes. Some works support the relative null and low fre-

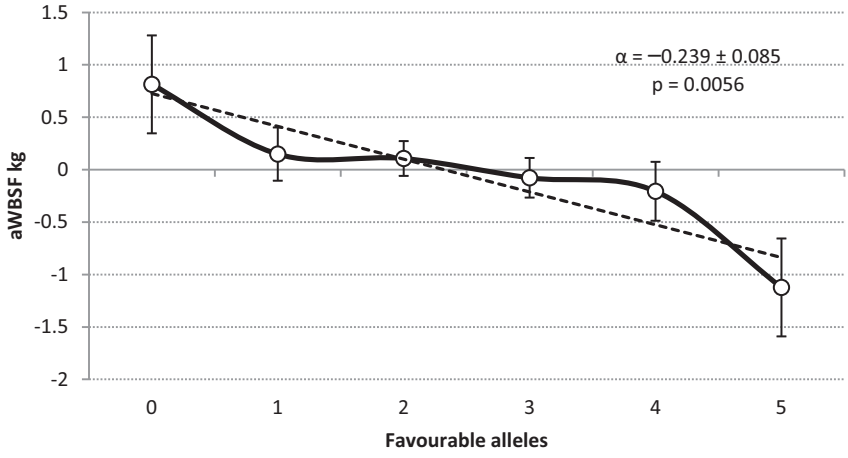

FIG. 2. LINEAR EFFECT OF THE NUMBER OF CALPAIN AND CALPASTATIN FAVORABLE ALLELES ON ADJUSTED WARNER–BRATZLER SHEAR FORCE OF COMMERCIAL BEEF

quencies of favorable alleles segregated by *B. indicus* and *B. indicus*-derived cattle (Parra-Bracamonte *et al.* 2007; Curi *et al.* 2009; Bonilla *et al.* 2010).

Meat from *B. taurus* cattle has been related to more tender beef compared with that from *B. indicus* animals (Crouse *et al.* 1993; O'Connor *et al.* 1997; Burrow *et al.* 2001). The present results suggested that *B. indicus* performance in aWBSF might have unfavorable grade if GGR is used as a classification criterion. Attention should be paid in this factor as an important proportion of *B. indicus* cattle come to feedlot from tropical production systems. A large proportion of the cattle raised in tropical and subtropical regions need the adaptability advantage of *B. indicus*-derived breeds, with the resulting increase in the toughness of meat as estimated in crossbred cattle with a 50% or higher zebu inheritance (Koohmaraie 1996). Delgado *et al.* (2005) reported that higher values of WBSF in the Central and South regions of Mexico are related to the most frequent used Zebu-type animals, and Rubensam *et al.* (1998) indicated that greater than 25% proportion of *B. indicus* inheritance may significantly and sustainably affect beef tenderness.

CAPN and CAST Effect

The genotypic association analysis confirmed two out of three previously reported associations. CAPN316 and CAPN4751 are well documented to have significant effect on objective traits of tenderness measurement. Morris *et al.* (2006) found a reduction of around 20% in average shear force as the effect of CAPN316 genotypes in *B. taurus* crosses. Van Eenennaam *et al.* (2007) performed a large validation assessment and proved the significant effect of CAPN genotypes on beef tenderness of several cattle breeds. Curi *et al.* (2009) indicated the potential use of CAPN4751 for selection of tenderness in Nellore cattle. Gill *et al.* (2009) reported a significant effect of CAPN316 genotypes on tenderness traits of Aberdeen Angus sired animals. Bonilla *et al.* (2010) performed the first association assessment between CAPN markers and tenderness in commercial meat in Mexico, and reported the significant association of CAPN316 genotypes on WBSF in 14-day-old beef cuts. The present report confirmed this association and additionally found a trending association for CAPN4751, supporting their utility for marker-assisted management for commercial beef cattle.

Even though CAST polymorphism showed a nonsignificant response on aWBSF, its combined effect along with favorable CAPN alleles confirmed a highly significant trend on shear force reduction of commercial beef; this trend agrees with the reported combined CAPN and CAST genetic marker validation assessment in several beef cattle breeds (Van Eenennaam *et al.* 2007). Recent research assessing CAST effects on slice shear force in crossbred and Angus cattle indicate strong improvement with favorable genotype, even with residual variance preventing the risk of tough beef, and strongly supporting its use for marker-assisted management or marketing of beef products (Tait *et al.* 2014a,b).

The combined effects of CAPN and CAST have been related to important economic returns. Weaber and Lusk (2010), by a simulation study, estimated that the selection strategy including genotypic information, in which bulls from upper 30% of genetic merit are selected each year, would result in increased profitability of $9.60 per head for feeder cattle and $1.23 per head for fed cattle in 20 years. Genotyping reduction costs and profitability evidence might open the possibility of considering marker-assisted selection or management as an actual option for beef tenderness selection and classification.

CONCLUSIONS

B. taurus and crossbred-derived beef have superior performance for tenderness. The CAPN316 genetic marker presented an equilibrated distribution in commercial beef and its effect support it as a potential tenderness predictor of 14-day-old commercial bovine meat. CAPN and CAST favorable polymorphisms might be used in combination as a prediction criterion for marker-assisted management in classification of commercial beef cuts.

The present results have important implications for the management of meat related to beef quality traits and improvement of value chain related to beef tenderness. The important individual effect detected for genetic grouping remarks the possibility of using these criteria as a slaughterhouse category to classify beef tenderness. In the same way, the individual marker effects proved its revisited importance for prediction of WBSF of longissimus dorsi beef cuts as good objective criterion for beef tenderness. It is important to consider that the utility of the present information is moderated by the current breeding goal of beef production systems in Mexico, which is mostly oriented toward beef volume production (Bonilla *et al.* 2010). However, perhaps in the near future, this supporting evidence, further validation and farmers' payment guaranteed for tender beef would generate new market niche creation involving genomic reliable indicators for the classification this important trait.

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