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Production and processing studies on calpain-system gene markers for tenderness in Brahman cattle: 2. Objective meat quality[1]

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ABSTRACT: Effects and interactions of calpain-system tenderness gene markers on objective meat quality traits of Brahman (*Bos indicus*) cattle were quantified within 2 concurrent experiments at different locations. Cattle were selected for study from commercial and research herds at weaning based on their genotype for calpastatin (*CAST*) and calpain 3 (*CAPN3*) gene markers for beef tenderness. Gene marker status for μ-calpain (*CAPN1–4751* and *CAPN1–316*) was also determined for inclusion in statistical analyses. Eighty-two heifer and 82 castrated male cattle with 0 or 2 favorable alleles for *CAST* and *CAPN3* were studied in New South Wales (NSW), and 143 castrated male cattle with 0, 1, or 2 favorable alleles for *CAST* and *CAPN3* were studied in Western Australia (WA). The cattle were backgrounded for 6 to 8 mo and grain-fed for 117 d (NSW) or 80 d (WA) before slaughter. One-half the cattle in each experiment were implanted with a hormonal growth promotant during feedlotting. One side of each carcass was suspended from the Achilles tendon (AT) and the other from the pelvis (tenderstretch). The M. longissimus lumborum from both sides and the M. semitendinosus from the AT side were collected; then samples of each were aged at 1°C for 1 or 7 d. Favorable alleles for one or more markers reduced shear force, with little effect on other meat quality traits. The size of effects of individual markers varied with site, muscle, method of carcass suspension, and aging period. Individual marker effects were additive as evident in cattle with 4 favorable alleles for *CAST* and *CAPN3* markers, which had shear force reductions of 12.2 N ($P < 0.001$, NSW) and 9.3 N ($P = 0.002$, WA) in AT 7 d aged M. longissimus lumborum compared with those with no favorable alleles. There was no evidence (all $P > 0.05$) of interactions between the gene markers, or between the hormonal growth promotant and gene markers for any meat quality traits. This study provides further evidence that selection based on the *CAST* or *CAPN3* gene markers improves meat tenderness in Brahman cattle, with little if any detrimental effects on other meat quality traits. The *CAPN1–4751* gene marker also improved beef tenderness without affecting other objective meat quality traits in heterozygous cattle compared with homozygotes for the unfavorable allele.

Key words: calpain, calpastatin, cattle, genetic marker, meat quality, shear force

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INTRODUCTION

Genomic technologies have underpinned the discovery and use of gene markers in livestock. Certain gene markers can identify cattle with better performance for commercial traits including meat tenderness (Barendse, 2002; Page et al., 2002; White et al., 2005; Barendse et al., 2008). The 4 gene markers for tenderness are lo-

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cated in the calpain-calpastatin enzyme complex that regulates the rate of protein degradation in the live animal (Koohmaraie et al., 2002). Activity of calpains accelerates protein degradation, whereas calpastatin activity acts as an inhibitor. As discussed by Koohmaraie et al. (2002), the rate of protein degradation postmortem affects the eating quality of meat. Variation in calpastatin abundance affects postmortem aging rates in different muscles (Ouali and Talmant, 1990; Geesink et al., 1992).

Several management and genetic factors affect protein degradation rates in the live animal, with subsequent effects on meat quality. Hormonal growth promotants (**HGP**) operate via synthetic and degradative pathways and can result in tougher meat (Dunshea et al., 2005; Watson, 2008). Gerken et al. (1995) showed that HGP implantation increased calpastatin activity. The calpain-calpastatin system is also implicated in the ability of *Bos indicus* cattle to perform in adverse environments, and *B. indicus* have greater calpastatin activity and tougher meat than *Bos taurus* cattle (Shackelford et al., 1995; Ferguson et al., 2001).

Hence, it is important to understand the magnitude of the effects of gene marker on tenderness and whether they interact with other factors that influence the calpain-calpastatin axis, or whether the effects are simply additive. This experiment was designed to examine mechanisms by which gene markers work and potential interactions with management and processing practices. This paper reports effects of gene markers on beef quality. The effects of gene markers on production and carcass characteristics are reported by Cafe et al. (2010).

MATERIALS AND METHODS

The use of animals and the procedures performed in this study were approved by the Industry & Investment New South Wales (**NSW**) Orange Agricultural Institute Animal Ethics Committee, Commonwealth Scientific and Industrial Research Organisation (**CSIRO**) Rockhampton Animal Experimentation Ethics Committee, and the Department of Agriculture and Food, Western Australia (**WA**) Animal Ethics Committee.

Tenderness Gene Markers

Cattle were tested for 4 commercially available gene markers for beef tenderness at the laboratories of CSIRO Livestock Industries, Brisbane, Queensland. The 4 markers were SNP within genes controlling the calpain proteolytic system. The markers relate to the genes calpastatin (***CAST***, *CAST:c.2832A > G*; Barendse, 2002), calpain 3 (***CAPN3***, *CAPN3:c.1538+225G > T*; Barendse et al., 2008), and 2 in μ-calpain: CAPN1–4751 (***CAPN1–4751***, *CAPN1:g.6545C > T*; White et al., 2005) and CAPN1–316 (***CAPN1–316***, *CAPN1:c.947C > G*; Page et al., 2002). For each marker, the alleles differ in their effects on meat tenderness, and the favorable allele is associated with more tender meat, although it is not known whether any of the SNP are causal. The favorable alleles are A at *CAST*, G at *CAPN3*, C at *CAPN1–4751*, and the forward strand C at *CAPN1–316*. The number of favorable alleles (0, 1, or 2) for each marker is used in this paper to designate the genotype of cattle for each marker.

Experimental Designs

Two concurrent experiments were conducted, one at Industry & Investment NSW Agricultural Research and Advisory Station, Glen Innes, NSW (29°44′ S, 151°42′ E, altitude 1,057 m; n = 163 cattle) and one at the WA Department of Agriculture and Food Vasse Research Station near Busselton, WA (33°45′ S, 115°21′ E, altitude 25 m; n = 143). The Brahman cattle were selected for experimental groups based on their genotype for the *CAST* and *CAPN3* tenderness gene markers.

The experimental design for the NSW herd was composed of favorable alleles for *CAST* (0 or 2) × favorable alleles for *CAPN3* (0 or 2) × HGP treatment (with or without HGP during feedlot finisheding) × sex (heifer or castrated male) × method of carcass side suspension (Achilles or tenderstretch) × aging period (1 or 7 d aging). The experimental design in WA was composed of castrated male cattle with favorable alleles for *CAST* (0, 1, or 2) × favorable alleles for *CAPN3* (0, 1, or 2) × HGP treatment (with and without HGP during feedlot finished) × method of carcass side suspension (Achilles or tenderstretch) × aging period (1 or 7 d aging).

In designing the experiment, standard power calculations were performed on the design using the critical points of the normal distribution (Snedecor and Cochran, 1967). These calculations identified that samples sizes of 164 and 173 would detect marker effects that explain 6.6 and 6.1%, respectively, of the residual variance in shear force at a 5% significance threshold with a 90% power. The numbers of animals by sex, gene marker, and HGP status at each site are detailed in Cafe et al. (2010) and in the tables of results.

Cattle Management and Slaughter

The cattle and their management at both sites during the experiment are described in detail by Cafe et al. (2010). In summary, weaner Brahman cattle were sourced from research and commercial herds (n = 12 herds) in NSW, WA, and Queensland. At both sites, cattle were pasture-fed for 6 to 8 mo, then feedlot-finished for 80 d in WA and 117 d in NSW. Some of the selected steers in the WA herd appeared to contain a small proportion of *B. taurus* content, which was visually assessed and accounted for in the statistical analyses [see Statistical Analyses subsection of Materials and Methods, and Cafe et al. (2010)].

Cattle from each site were transported to the respective abattoirs the day before slaughter. At each site, one-half of the cattle were slaughtered on each of 2 kill

dates, with no mixing of pens during transport or lairage. Each animal was slaughtered by captive bolt stunning and exsanguination, and standard AUS-MEAT carcasses were prepared (AUS-MEAT, 2007) and split into 2 sides. Electrical stimulation of the carcasses was limited to that necessary for the hide removal process at both sites, plus immobilization during exsanguination in WA. The right sides were resuspended by the pelvis [tenderstretch suspension method, Thompson (2002)], and both sides were placed together in the same chillers.

Temperature and pH of the LM adjacent to the 12th rib were measured on the left side of each carcass at regular intervals from approximately 45 min postmortem until the majority of carcasses had reached pH 6. The postmortem change in carcass pH and temperature as a function of time were modeled using the equation:

$$y_t = a_u + (a_i - a_u)e^{-k \cdot t},$$

where y_t is pH or temperature at time t, a_i is the initial carcass pH or temperature, a_u is the ultimate pH or temperature, k is the exponential rate of pH or temperature decline, and t is the time postmortem. The parameters of the pH/time equation were estimated using nonlinear procedures (SAS Inst. Inc., Cary, NC) and used to predict for each carcass the time taken to reach pH 6, and the temperature at which pH 6 was reached.

Carcass sides were chilled overnight then quartered between the 10th and 11th ribs. Sides were graded according to Meat Standards Australia procedures (Meat Standards Australia, 2009) no less than 20 min after quartering.

Objective Beef Quality

The M. longissimus lumborum (**LLM**) and M. semitendinosus (**STN**) were removed from the Achilles suspended (**AT**) sides and the LLM removed from the tenderstretched (**TS**) sides during bone-out (average 28 h postmortem in NSW, and 20 h postmortem in WA). The LLM were sliced into 3 pieces and the STN into 2 pieces before each piece was individually vacuum packaged. One piece of each muscle was frozen at −20°C (1 d aged) immediately after bone-out, and 1 piece was aged at 1°C for a further 6 d (7 d aged) before being frozen at −20°C. Samples were transported to the laboratory using commercial frozen transport and were stored at −20°C until thawed for analyses.

Sample preparation and measurement of texture (shear force and compression), cooking loss, and intramuscular fat percentage (determined by near infrared spectrophotometry) were performed as described by Perry et al. (2001a). Briefly, samples were thawed and cooked in individual plastic bags in a 70°C water bath for 60 min, then stored overnight at 1°C before being prepared for textural analysis. Textural measurements were made on a Lloyd Instruments LRX Materials Testing Machine fitted with a 500N load cell (Lloyd Instruments Ltd., Hampshire, UK), and the mean of 6 measurements was recorded for shear force and compression. Each of these measurements was made on samples from the AT and TS sides for the LLM, whereas only shear force, compression, and cooking loss were determined for the STN from the AT side. Measurement of sarcomere length was conducted on the AT suspended LLM in the NSW herd, also as described by Perry et al. (2001a). All objective meat quality measurements were carried out at the Meat Science Laboratory at the University of New England, Armidale, NSW, Australia.

Statistical Analyses

Statistical analyses were conducted by fitting Linear Mixed Models using the REML methodology (Robinson, 1987; Genstat, VSN International Ltd., Hemel Hempstead, UK). Experimental sites (WA and NSW) were analyzed separately due to the differences in experimental design. Measurement for each muscle, carcass suspension method, and days aged were analyzed as separate traits due to differing residual variances. Fixed effects included in the final model were the marker genotypes, HGP treatment, and for the NSW herd, sex. Random effects in the models were property of origin, backgrounding replicate, feedlot replicate, slaughter group within slaughter day, and the first-order interactions between *CAST* × *CAPN3,* HGP × *CAST,* HGP × *CAPN3*, and (NSW experiment only) sex × HGP. For the WA experiment, estimated percentage *Bos indicus* content was also included in the analyses as a covariate [see Sources of Cattle subsection of Experimental Procedures and Cafe et al. (2010)], but did not have a significant effect (all $P \geq 0.06$) on any measured variables. Carcass pH was included as a covariate in the final model for meat quality analyses. In the NSW herd, the number of animals with 2 favorable alleles for the *CAPN1–4751* marker was small (n = 8). To avoid undue influence on estimates of means, the main effect of this marker was fitted for 0 and 1 favorable allele, with an additional fixed covariate used to model the difference between 2 and 1 favorable alleles. This difference was never significant (all $P \geq 0.11$) except for cooking loss in AT 7 d aged STN ($P = 0.06$); hence, results are reported in Table 4 only for 0 and 1 favorable alleles of *CAPN1–4751.* A significance level of $P < 0.05$ and a tendency level of $P < 0.10$ were used for main effects and interactions.

RESULTS

Effects of Site: Abattoir Processing

Differences in processing conditions were evident between the NSW and WA abattoirs at which cattle from the 2 sites were slaughtered. Notably, there were

Table 1. Processing characteristics for carcasses of cattle in the New South Wales (NSW) and Western Australia (WA) experiments[1]

Variable	NSW	WA
n	164	143
Carcass wt, kg	244 ± 32	243 ± 25
Time to pH 6, h	7.6 ± 12.9	1.5 ± 0.6
Temperature at pH 6, °C	21.1 ± 7.6	35.8 ± 3.2
pH at grading[2]	5.49 ± 0.05	5.57 ± 0.09
Loin temperature at grading, °C	7.2 ± 0.9	11.2 ± 1.0

[1]Values are mean ± SD.
[2]Meat Standards Australia grading (Meat Standards Australia, 2009) conducted 23.5 h after slaughter in NSW and 17.5 h after slaughter in WA.

differences between the postmortem temperature/pH declines of carcasses. Indices of the differences in processing conditions are presented in Table 1. In WA, carcasses showed a very rapid pH decline reaching pH 6 at 1.5 h postmortem at a temperature of 35.8°C. By comparison, carcasses in NSW had a much slower pH decline and reached pH 6 at 7.5 h postmortem at a temperature of 21.1°C.

At MSA grading the day after slaughter [average 23.5 h (NSW) and 17.5 h (WA) postmortem], the NSW carcasses were about 3°C cooler and had a slightly lesser pH than the carcasses in WA. Mean sarcomere length in AT suspended LLM was 1.89 μm (SD = 0.12 μm) for the NSW cattle.

Effects of Gene Markers

CAST Marker. The effects of the *CAST* marker on objective meat quality traits are presented in Table 2. In NSW, cattle with 2 favorable *CAST* alleles had 2.0 N less shear force ($P = 0.048$) in TS 1 d aged LLM and a tendency for a decreased shear force (by 2.1 N, $P = 0.06$) and compression (by 0.6 N, $P = 0.07$) in TS 7 d aged LLM than those with no favorable *CAST* alleles.

In WA, significant improvements in shear force for cattle with 2 vs. 0 favorable alleles were evident for TS 1 d aged (5.6 N less shear force, $P = 0.032$) and 7 d aged (4.2 N, $P = 0.038$) LLM, and AT 7 d aged (7.9 N, $P < 0.001$) LLM. There was also a significant difference due to *CAST* alleles in AT 1 d aged STN (3.5 N, $P = 0.039$). In all cases the shear force for cattle with 1 favorable allele was intermediate. In WA, *CAST* was also associated with differences in cooking loss. For the AT 7 d aged and TS 1 d aged LLM, cattle with 2 favorable alleles had less (all $P < 0.036$) cooking loss than those with 0 or 1 favorable alleles. In TS 7 d aged LLM and AT 7 d aged STN, the cattle with 2 favorable alleles had less (all $P < 0.027$) cooking loss than those with 1 favorable allele, and those with 0 favorable alleles were intermediate.

Table 2. Least squares means for effects of number of favorable alleles of the calpastatin marker on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) and Western Australia (WA) experiments

	NSW				WA				
Variable	0[1]	2[1]	SED	*P*-value	0[1]	1[1]	2[1]	SED	*P*-value
n	66	88			41	51	51		
Shear force, N									
AT 1 d aged LLM	81.4	78.9	2.71	0.36	52.3	52.0	51.2	2.33	0.62
AT 7 d aged LLM	74.9	70.1	4.09	0.24	54.4^{b}	48.9^{ab}	46.5^{a}	1.93	<0.001
TS 1 d aged LLM	48.0	46.0	1.01	0.048	56.0^{b}	53.1^{ab}	50.4^{a}	2.59	0.032
TS 7 d aged LLM	47.0	44.9	1.12	0.06	47.9^{b}	46.8^{ab}	43.7^{a}	1.93	0.038
AT 1 d aged STN	56.0	56.0	0.99	0.99	56.9^{b}	53.8^{ab}	53.4^{a}	1.69	0.039
AT 7 d aged STN	56.1	55.0	0.99	0.24	51.0	49.5	49.0	2.04	0.35
Compression, N									
AT 1 d aged LLM	19.8	19.7	0.36	0.71	19.3	19.3	18.6	0.50	0.16
AT 7 d aged LLM	19.4	19.1	0.37	0.47	19.4	19.4	18.3	1.08	0.34
TS 1 d aged LLM	18.2	17.8	0.31	0.18	17.7	18.0	17.2	0.46	0.16
TS 7 d aged LLM	17.9	17.3	0.31	0.07	19.5	18.8	18.5	0.62	0.11
AT 1 d aged STN	24.3	24.4	0.60	0.93	23.4	23.3	23.2	0.70	0.78
AT 7 d aged STN	24.8	24.3	0.88	0.54	23.0	22.6	21.6	0.66	0.11
Cooking loss, %									
AT 1 d aged LLM	26.3	26.3	0.55	0.95	28.1	28.3	27.9	0.36	0.43
AT 7 d aged LLM	27.4	27.5	0.82	0.88	28.2^{b}	28.4^{b}	27.4^{a}	0.28	<0.001
TS 1 d aged LLM	21.5	21.3	1.02	0.88	26.2^{b}	26.6^{b}	25.2^{a}	0.55	0.036
TS 7 d aged LLM	23.7	23.7	0.34	0.88	27.5^{ab}	28.0^{b}	27.1^{a}	0.34	0.024
AT 1 d aged STN	23.8	24.1	0.27	0.38	24.1	24.5	24.4	0.34	0.54
AT 7 d aged STN	24.8	25.2	0.28	0.21	24.0^{ab}	24.6^{b}	23.5^{a}	0.41	0.027
LLM IMF, %	2.1	1.8	0.22	0.13	2.0	1.9	2.3	0.17	0.12

[a,b]Within a row for the WA experiment, means with different superscripts differ ($P < 0.05$).
[1]Number of favorable alleles.

Table 3. Least squares means for effects of number of favorable alleles of the calpain 3 marker on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) and Western Australia (WA) experiments

	NSW				WA				
Variable	0[1]	2[1]	SED	*P*-value	0[1]	1[1]	2[1]	SED	*P*-value
n	88	71			36	60	47		
Shear force, N									
AT 1 d aged LLM	78.1	78.9	3.01	0.78	50.9	53.2	51.3	3.97	0.92
AT 7 d aged LLM	77.0	69.6	2.30	0.002	50.2	50.8	48.8	2.03	0.51
TS 1 d aged LLM	46.7	45.9	1.17	0.54	52.2	55.2	51.8	2.61	0.88
TS 7 d aged LLM	46.1	45.5	0.77	0.47	46.5	47.2	44.7	3.34	0.61
AT 1 d aged STN	57.1	56.5	1.00	0.56	56.5	54.0	53.7	1.70	0.12
AT 7 d aged STN	57.6	56.2	0.94	0.13	50.0	50.0	49.5	2.03	0.81
Compression, N									
AT 1 d aged LLM	19.7	19.2	0.35	0.13	19.4	18.7	19.0	0.51	0.45
AT 7 d aged LLM	19.5	18.7	0.35	0.019	18.9	19.3	18.8	0.53	0.83
TS 1 d aged LLM	18.0	18.2	0.77	0.81	17.9	17.7	17.4	0.45	0.29
TS 7 d aged LLM	17.6	17.2	0.28	0.15	18.9	18.9	18.9	0.65	0.99
AT 1 d aged STN	24.4	24.6	0.82	0.78	23.8	23.5	22.6	0.71	0.12
AT 7 d aged STN	24.8	24.1	0.74	0.35	22.6	22.2	22.4	0.68	0.83
Cooking loss, %									
AT 1 d aged LLM	26.5	26.0	0.49	0.83	28.3	28.0	28.0	0.37	0.53
AT 7 d aged LLM	27.8	27.1	0.75	0.40	27.9	28.1	27.9	0.29	0.93
TS 1 d aged LLM	21.5	20.9	0.72	0.44	25.6	26.6	25.9	0.41	0.45
TS 7 d aged LLM	23.7	23.9	0.36	0.55	27.4	27.6	27.7	0.34	0.34
AT 1 d aged STN	24.2	23.9	0.25	0.30	24.6	24.4	24.1	0.37	0.24
AT 7 d aged STN	25.4	25.0	0.28	0.13	24.2	24.0	24.0	0.46	0.68
LLM IMF, %	1.9	2.0	0.20	0.69	2.2	2.1	1.9	0.23	0.30

[1]Number of favorable alleles.

CANP3 Marker. The effects of the *CAPN3* marker on objective meat quality traits are presented in Table 3. In NSW, cattle with 2 favorable alleles for the *CAPN3* marker had 7.4 N less shear force ($P = 0.002$) for AT 7 d aged LLM and less compression (by 0.8 N, $P = 0.019$) in AT 7 d aged LLM than cattle with 0 favorable alleles.

CAPN1 Markers. The effects of the *CAPN1–4751* marker on objective meat quality traits are presented in Table 4. In NSW, cattle with 1 favorable allele for *CAPN1–4751* had 2.0 N less shear force ($P = 0.019$) in TS 7 d aged LLM, and 2.1 N less shear force ($P = 0.037$) in AT 1 d aged STN than cattle with no favorable alleles. There was also a tendency toward reduced shear force (by 1.4 N, $P = 0.07$) for TS 1 d aged LLM. Compression was less (by 0.6 N, $P = 0.030$) for TS 7 d aged LLM, and cooking loss was reduced (by 0.5%, $P = 0.049$) for AT 1 d aged STN in cattle with 1 compared with 0 favorable *CAPN1–4751* alleles. There was a tendency toward less cooking loss (by 1.1%, $P = 0.06$) in AT 7 d aged STN in cattle with 2 compared with 1 favorable *CAPN1–4751* allele. In WA, cattle with 1 favorable allele for *CAPN1–4751* had 3.8 N less shear force ($P = 0.001$) for AT 7 d aged STN than those with 0 favorable alleles.

The effects of the *CAPN1–316* marker on objective meat quality traits are presented in Table 5. In NSW, cattle with 1 favorable allele for *CAPN1–316* had 11.2 N greater ($P = 0.008$) shear force in AT 7 d aged LLM than cattle with 0 favorable alleles; however, this effect was not evident in WA. In WA, cattle with 1 favorable allele for *CAPN1–316* had 1.3 N less ($P = 0.032$) compression in AT 7 d aged LLM than those with 0 favorable alleles. The WA cattle with 1 favorable allele for the *CAPN1–316* marker had 0.7% greater ($P = 0.041$) cooking loss in AT 7 d aged STN compared with cattle with 0 favorable alleles.

Combined Effects of the Markers. The markers had an additive effect on shear force at 7 d aging in the LLM and STN muscles, with no interactions evident between *CAST* and *CAPN3* for any of the meat quality traits. The extremes in genotypes with adequate numbers of animals represented to allow for meaningful comparisons in both experiments were 0_0 vs. 2_2 favorable alleles for *CAST_CAPN3* (Table 6). The reduction in shear force in cattle with 4 favorable alleles compared with those with none was greatest in AT 7 d aged LLM in NSW (12.2 N, $P < 0.001$) and WA (9.3 N, $P = 0.002$). The reduction in shear force due to the favorable alleles was also significant for TS 1 and 7 d aged LLM in NSW ($P = 0.007$ and 0.015, respectively) and tended ($P = 0.05$) to be significant for TS 7 d aged LLM in WA. The 4 favorable alleles also resulted in a significant reduction ($P = 0.013$) in shear force in AT 1 d aged STN in WA and tended ($P = 0.05$) to reduce shear force in AT 7 d aged STN in NSW compared with no favorable alleles.

Table 4. Least squares means for effects of number of favorable alleles of the μ-calpain (*CAPN1–4751*) marker[1] on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) and Western Australia (WA) experiments

	NSW				WA				
Variable	0[2]	1[2]	SED	*P*-value	0[2]	1[2]	2[2]	SED	*P*-value
n	89	67			68	62	13		
Shear force, N									
AT 1 d aged LLM	80.3	76.7	2.76	0.19	50.8	50.4	54.2	3.00	0.33
AT 7 d aged LLM	75.1	71.6	2.47	0.16	50.5	46.8	52.6	2.47	0.45
TS 1 d aged LLM	47.0	45.6	0.78	0.07	52.0	51.1	56.3	3.03	0.23
TS 7 d aged LLM	46.8	44.8	0.82	0.019	47.1	45.7	45.5	2.49	0.58
AT 1 d aged STN	57.9	55.8	1.00	0.037	53.8	53.6	56.7	2.19	0.26
AT 7 d aged STN	57.1	56.6	1.01	0.65	52.3[b]	48.7[a]	48.5[a]	1.65	0.001
Compression, N									
AT 1 d aged LLM	19.5	19.4	0.37	0.71	19.0	18.9	19.4	0.65	0.58
AT 7 d aged LLM	19.4	18.8	0.37	0.11	19.0	19.2	18.9	0.66	0.86
TS 1 d aged LLM	18.2	18.0	0.31	0.43	17.8	17.7	17.5	0.58	0.70
TS 7 d aged LLM	17.7	17.1	0.30	0.03	19.1	18.6	19.2	0.64	0.88
AT 1 d aged STN	24.8	24.2	0.50	0.25	22.8	23.9	23.2	0.91	0.69
AT 7 d aged STN	24.3	24.6	0.54	0.67	23.1	22.3	21.9	0.87	0.25
Cooking loss, %									
AT 1 d aged LLM	26.3	26.2	0.27	0.88	28.1	28.0	28.2	0.42	0.94
AT 7 d aged LLM	27.7	27.4	0.27	0.63	28.1	27.9	28.0	0.37	0.84
TS 1 d aged LLM	21.1	21.4	0.40	0.51	26.1	26.0	26.0	0.52	0.77
TS 7 d aged LLM	23.7	23.9	0.35	0.73	27.7	27.6	27.3	0.40	0.39
AT 1 d aged STN	24.3	23.8	0.27	0.049	24.2	24.5	24.4	0.44	0.68
AT 7 d aged STN	25.3	25.2	0.28	0.59	24.4	23.9	23.8	0.41	0.17
LLM IMF, %	1.9	2.0	0.12	0.36	2.1	1.9	2.3	0.23	0.43

[a,b]Within a row for the WA experiment, means with different superscripts differ ($P < 0.05$).

[1]Small number of cattle with 2 favorable alleles at both sites. Results for 2 favorable alleles not presented for NSW (n = 8) and no effects significant (all $P \geq 0.06$). See Statistical Analyses section of Materials and Methods for detailed description of analyses.

[2]Number of favorable alleles.

The effect of the *CAST_CAPN3* marker combination on the other meat quality traits was smaller than the effect on shear force. In NSW there was a 1.1 N reduction in compression ($P = 0.030$) in AT 7 d aged LLM and a 1.0 N reduction in compression ($P = 0.013$) in TS 7 d aged LLM in cattle with 4 favorable alleles compared with those with no favorable alleles. There were also tendencies toward a reduction of 0.8% ($P = 0.07$) in cooking loss for AT 7 d aged LLM in WA and a reduction in intramuscular fat percentage (**IMF**) of 0.3% ($P = 0.05$) in NSW in cattle with 4 favorable alleles.

In NSW, numbers of cattle with extreme genotypes were sufficient to provide a meaningful comparison between those with 0_0_0 (n = 22) and 2_2_1 (n = 17) favorable alleles for the 3 markers, *CAST_CAPN3_CAPN1–4751*, respectively. The reduction in shear force in the cattle with 5 favorable alleles compared with those with none was greatest in AT 7 d aged LLM (15.8 N, $P < 0.001$). The reduction in shear force due to the 5 favorable alleles was also significant for TS 1 and 7 d aged LLM (4.3 N, $P = 0.001$ and 4.6 N, $P < 0.001$). The AT 7 d aged STN tended to have decreased shear force for the cattle with the 5 favorable alleles compared with those with none (by 3 N, $P = 0.06$). In WA, numbers of animals with the extreme genotypes for *CAST_CAPN3_CAPN1–4751* were small, with only 4 animals representing the 0_0_0 genotype and 7 animals representing the 2_2_1 genotype. Comparison between these small groups was consistent with NSW results; 5 favorable alleles resulted in a reduction in shear force of 13.0 N in AT 7 d aged LLM ($P < 0.001$), of 7.3 N in TS 7 d aged LLM ($P = 0.039$), of 6.6 N in AT 1 d aged STN ($P = 0.031$), and of 6.0 N in AT 7 d aged STN ($P = 0.023$) compared with no favorable alleles.

Effects of HGP

The effects of HGP treatment on objective meat quality traits are presented in Table 7. In NSW, the HGP treatment increased shear force in AT 1 d aged LLM by 8.2 N ($P = 0.007$), and in TS suspended LLM aged for 1 and 7 d by 3.5 ($P = 0.009$) and 3.4 N ($P = 0.002$), respectively. In WA, the HGP treatment increased shear force in AT 7 d aged LLM by 6.3 N ($P < 0.001$), and in TS 1 d aged LLM by 4.5 N ($P = 0.021$), and tended to increase shear force in AT 1 d aged LLM (by 6.0 N, $P = 0.07$). The HGP treatment increased compression in TS suspended LLM aged for 1 or 7 d by 0.9 ($P = 0.015$) and 1.2 N ($P = 0.035$), respectively, and reduced compression in AT 7 d aged STN by 1.2 N ($P = 0.049$). The HGP treatment increased cooking loss in the AT 7 d aged STN (by 0.8%, $P = 0.007$), and

Table 5. Least squares means for effects of number of favorable alleles of the μ-calpain (*CAPN1–316*) marker on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) and Western Australia (WA) experiments

	NSW				WA			
Variable	0[1]	1[1]	SED	*P*-value	0[1]	1[1]	SED	*P*-value
n	149	15			120	22		
Shear force, N								
AT 1 d aged LLM	76.4	80.6	4.70	0.37	53.9	49.7	2.75	0.13
AT 7 d aged LLM	67.7	78.9	4.14	0.008	51.3	48.6	2.32	0.26
TS 1 d aged LLM	46.7	45.9	1.35	0.56	52.7	53.6	2.76	0.77
TS 7 d aged LLM	45.4	46.2	1.39	0.60	46.7	45.6	2.36	0.66
AT 1 d aged STN	56.9	56.7	1.69	0.92	55.2	54.2	2.01	0.62
AT 7 d aged STN	56.7	57.1	1.71	0.81	50.2	49.5	1.51	0.67
Compression, N								
AT 1 d aged LLM	19.4	19.5	0.63	0.93	19.4	18.8	0.59	0.29
AT 7 d aged LLM	18.8	19.5	0.62	0.27	19.7	18.4	0.62	0.032
TS 1 d aged LLM	18.4	17.9	0.53	0.35	17.9	17.4	0.53	0.35
TS 7 d aged LLM	17.4	17.5	0.49	0.80	19.1	18.8	0.58	0.67
AT 1 d aged STN	24.3	24.7	0.85	0.70	23.8	22.8	0.83	0.24
AT 7 d aged STN	24.6	24.3	0.94	0.72	22.5	22.3	0.79	0.77
Cooking loss, %								
AT 1 d aged LLM	26.4	26.0	0.46	0.37	28.1	28.0	0.38	0.77
AT 7 d aged LLM	27.7	27.2	0.45	0.32	28.0	27.9	0.35	0.79
TS 1 d aged LLM	21.9	20.6	0.68	0.05	25.7	26.4	0.48	0.18
TS 7 d aged LLM	24.2	23.4	0.60	0.17	27.7	27.5	0.38	0.67
AT 1 d aged STN	23.8	24.3	0.45	0.29	24.4	24.3	0.40	0.83
AT 7 d aged STN	25.3	25.2	0.49	0.76	23.7	24.4	0.38	0.041
LLM IMF, %	1.9	2.0	0.21	0.90	2.0	2.1	0.21	0.69

[1]Number of favorable alleles.

Table 6. Least squares means for combined effects of number of favorable alleles of the calpastain (*CAST*) and calpain 3 (*CAPN3*) markers on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) and Western Australia (WA) experiments

	NSW				WA			
Variable	0_0[1]	2_2[1]	SED	*P*-value	0_0[1]	2_2[1]	SED	*P*-value
n	38	41			9	16		
Shear force, N								
AT 1 d aged LLM	81.0	79.4	3.65	0.66	51.4	50.7	3.49	0.84
AT 7 d aged LLM	78.6	66.4	3.26	<0.001	54.7	45.4	2.88	0.002
TS 1 d aged LLM	48.2	45.4	1.04	0.007	54.8	48.6	3.71	0.10
TS 7 d aged LLM	47.3	44.6	1.09	0.015	48.2	42.3	2.97	0.05
AT 1 d aged STN	56.3	55.7	1.32	0.66	58.7	52.4	2.53	0.013
AT 7 d aged STN	56.9	54.3	1.32	0.05	51.5	49.1	2.28	0.29
Compression, N								
AT 1 d aged LLM	20.1	19.4	0.49	0.18	19.7	18.6	0.75	0.14
AT 7 d aged LLM	19.8	18.7	0.50	0.030	19.3	18.1	0.78	0.14
TS 1 d aged LLM	18.1	17.9	0.41	0.59	18.0	16.9	0.67	0.14
TS 7 d aged LLM	18.1	17.1	0.39	0.013	19.5	18.5	0.73	0.17
AT 1 d aged STN	24.1	24.4	0.66	0.74	23.8	22.5	1.05	0.19
AT 7 d aged STN	24.9	23.8	0.72	0.14	23.1	21.6	1.01	0.14
Cooking loss, %								
AT 1 d aged LLM	26.7	26.2	0.36	0.16	28.3	27.8	0.52	0.30
AT 7 d aged LLM	27.3	27.3	0.36	0.99	28.1	27.3	0.42	0.07
TS 1 d aged LLM	21.8	21.0	0.53	0.18	25.8	25.1	0.60	0.27
TS 7 d aged LLM	23.6	23.9	0.47	0.57	27.3	27.3	0.47	0.88
AT 1 d aged STN	23.9	23.9	0.36	0.94	24.4	24.1	0.53	0.61
AT 7 d aged STN	25.0	25.0	0.37	0.90	24.3	23.6	0.54	0.21
LLM IMF, %	2.0	1.7	0.16	0.05	2.1	2.1	0.26	0.98

[1]Number of favorable alleles for markers *CAST_CAPN3*.

Table 7. Least squares means for effects of hormonal growth promotant (HGP) status on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) and Western Australia (WA) experiments

	NSW				WA			
Variable	No HGP	HGP	SED	*P*-value	No HGP	HGP	SED	*P*-value
n	83	81			71	72		
Shear force, N								
AT 1 d aged LLM	74.4	82.6	2.98	0.007	48.8	54.8	3.25	0.07
AT 7 d aged LLM	71.5	75.1	3.79	0.34	46.8	53.1	1.64	<0.001
TS 1 d aged LLM	44.6	48.1	1.31	0.009	50.9	55.4	1.89	0.021
TS 7 d aged LLM	44.1	47.5	1.05	0.002	44.5	47.8	2.73	0.23
AT 1 d aged STN	56.3	57.4	1.63	0.52	54.7	54.8	1.38	0.95
AT 7 d aged STN	57.1	56.6	0.92	0.58	49.1	50.5	1.03	0.17
Compression, N								
AT 1 d aged LLM	19.1	19.7	0.60	0.31	18.9	19.2	0.41	0.47
AT 7 d aged LLM	18.9	19.4	0.50	0.28	18.4	19.7	0.88	0.16
TS 1 d aged LLM	17.9	18.3	0.84	0.60	17.2	18.1	0.37	0.015
TS 7 d aged LLM	17.2	17.7	0.29	0.11	18.3	19.5	0.61	0.035
AT 1 d aged STN	24.7	24.2	0.75	0.50	23.4	23.2	0.57	0.70
AT 7 d aged STN	24.6	24.3	0.83	0.76	23.0	21.8	0.54	0.049
Cooking loss, %								
AT 1 d aged LLM	26.1	26.4	0.45	0.44	28.2	28.0	0.26	0.49
AT 7 d aged LLM	27.3	27.6	0.43	0.60	27.9	28.0	0.23	0.70
TS 1 d aged LLM	20.9	21.5	1.23	0.65	26.2	25.9	0.45	0.61
TS 7 d aged LLM	23.8	23.8	0.35	0.87	27.3	27.9	0.30	0.06
AT 1 d aged STN	24.1	24.0	0.25	0.54	24.1	24.6	0.27	0.07
AT 7 d aged STN	25.1	25.4	0.26	0.26	23.6	24.4	0.31	0.007
LLM IMF, %	2.0	1.8	0.18	0.29	2.3	1.8	0.18	0.008

tended to increase cooking loss in TS 7 d aged LLM (by 0.6%, $P = 0.06$) and AT 1 d aged STN (by 0.5%, $P = 0.07$), and reduced ($P = 0.008$) IMF% in WA.

Effects of Sex in the NSW Herd

The effects of sex on objective meat quality traits in the NSW herd are presented in Table 8. In 7 d aged meat the heifers had greater shear force than steers in AT suspended LLM by 14.3 N ($P < 0.001$), in TS suspended LLM by 4.5 N ($P = 0.008$), and in AT suspended STN by 3.3 N ($P = 0.003$). Heifers tended to have greater shear force in AT 1 d aged STN (by 3.1 N, $P = 0.06$). Heifers also had greater compression than steers in TS 7 d aged LLM by 0.7 N ($P = 0.019$) and in AT 7 d aged STN by 2.3 N ($P = 0.003$). Heifers had less cooking loss than steers for TS 1 d aged LLM ($P = 0.035$) and greater cooking loss than steers for AT 7 d aged STN ($P = 0.006$). Heifers had significantly shorter sarcomere lengths in the AT suspended LLM than steers (1.87 vs. 1.95 μm; SED = 0.028 μm; $P = 0.007$).

DISCUSSION

In combination, the calpain system gene markers for tenderness had significant effects on shear force in Brahman cattle in the present study, but few effects on other meat quality traits. Cattle of favorable genotype for the markers had reduced shear force compared with those with unfavorable genotype, particularly after aging. The combined effects of favorable alleles for *CAST* and *CAPN3* markers resulted in reductions in shear force of up to 12.2 N after 7 d of aging. The size of this effect is greater than the minimum shear force difference of approximately 5 N at which consumers can detect differences in tenderness (Huffman et al., 1996). The effect of the individual markers varied with site, muscle, method of carcass suspension, and aging period. There was no evidence of interactions between the gene markers, or between the HGP and gene markers, for any of the meat quality traits assessed in the study.

The findings of the present study and those of Cafe et al. (2010) are important because they suggest there are few adverse effects due to the calpain system gene markers on production, carcass, and beef quality-related characteristics. Although meat tenderness is one of the most important contributors to consumer satisfaction with beef (Mullen et al., 2006; King et al., 2009), improved tenderness and a reduction in the variability of meat tenderness at the expense of other economically important traits is unlikely to be acceptable to beef producers.

The experiment was primarily designed to study effects of *CAST* and *CAPN3* genotypes, and the animals were selected to provide a balanced design for these 2 markers. Additionally, we attempted to balance for *CAPN1–4751* genotype; however, this proved difficult due to the low frequency of animals with 2 favorable al-

Table 8. Least squares means for effects of sex on shear force, compression, and cooking loss in Achilles (AT) and tenderstretch (TS) suspended M. longissimus lumborum (LLM) and Achilles suspended M. semitendinosus (STN) aged for 1 or 7 d, and intramuscular fat (IMF) content of LLM, in cattle in the New South Wales (NSW) experiment

Variable	Heifers	Steers	SED	*P*-value
n	82	82		
Shear force, N				
AT 1 d aged LLM	82.3	74.7	5.93	0.20
AT 7 d aged LLM	80.5	66.2	3.77	<0.001
TS 1 d aged LLM	46.7	45.9	1.71	0.66
TS 7 d aged LLM	48.1	43.5	1.68	0.008
AT 1 d aged STN	58.4	55.3	1.66	0.06
AT 7 d aged STN	58.5	55.2	1.10	0.003
Compression, N				
AT 1 d aged LLM	20.1	18.8	0.86	0.13
AT 7 d aged LLM	19.6	18.6	0.66	0.13
TS 1 d aged LLM	18.2	18.0	0.45	0.80
TS 7 d aged LLM	17.8	17.1	0.31	0.019
AT 1 d aged STN	25.0	24.0	0.69	0.17
AT 7 d aged STN	25.6	23.3	0.77	0.003
Cooking loss, %				
AT 1 d aged LLM	26.3	26.2	0.56	0.77
AT 7 d aged LLM	27.6	27.3	0.39	0.52
TS 1 d aged LLM	20.4	22.0	0.75	0.035
TS 7 d aged LLM	23.8	23.7	0.38	0.81
AT 1 d aged STN	24.1	24.0	0.31	0.68
AT 7 d aged STN	25.6	24.9	0.26	0.006
LLM IMF, %	2.1	1.8	0.21	0.11

leles for *CAPN1–4751*. Likewise, the favorable *CAPN1–316* genotype was only represented by 1 animal, which we removed from the analyses. Hence, within the present study, the results for the *CAST* and *CAPN3* markers are likely to be more reliable for the 3 genotypes within each of these markers (that is, for 0, 1, and 2 favorable alleles), whereas the results for *CAPN1–4751* are likely to be more reliable for animals with 0 or 1 favorable alleles only.

There were large differences between the 2 sites in the rate of pH and temperature decline of the carcasses during abattoir processing. The rate of decline to rigor (pH 6) and the temperature at which this point is reached can affect muscle fiber shortening, and the activity of the calpain-system, which will affect the initial tenderness and aging potential of meat (Thompson et al., 2006). The carcasses from the WA herd experienced a rapid pH decline, with pH 6 reached at a carcass temperature of 35.8°C. The carcasses from the NSW herd experienced a much slower pH decline, with pH 6 reached at a carcass temperature of 21.1°C. However, sarcomere lengths in the AT-suspended LLM of cattle in the NSW herd were in the normal range for samples analyzed by the same laboratory, indicating that cold-shortening did not occur (Park et al., 2008). Associated with these different processing conditions were differences between the sites in 1 d shear force, in the improvement in shear force with aging, and in the effectiveness of TS in reducing shear force, particularly in the LLM. Most notably, cattle in NSW had greater shear force than the cattle in WA after 1 d aging, and aging for 7 d resulted in a marked improvement in shear force in NSW but little change in WA. The TS-suspension method also resulted in a large reduction in LLM shear force compared with Achilles suspension in NSW, but aging of the TS-suspended LLM for 7 d resulted in little further reduction in shear force. By contrast, TS had little effect on LLM shear force in WA after 1 d aging, whereas shear force was reduced by TS of the LLM after 7 d aging. Although the STN showed some tenderization after 7 d aging in WA, there was little improvement in NSW. In relation to factors that may have influenced beef quality before slaughter, the cattle at both sites were managed similarly for 11 mo before slaughter, although the NSW cattle were transported for longer from the feedlot to the abattoir, and there was little difference in growth or carcass characteristics between the cattle at the 2 sites (Cafe et al., 2010).

Hence, it is likely that the different processing conditions resulted in differences between sites in the postmortem tenderization process in the carcasses. This may be explained using the principle that the tenderization process begins at or near rigor (pH 6). In the WA carcasses, tenderization would have started sooner after death, and more importantly, at a greater carcass temperature, accelerating the rate of tenderization (Simmons et al., 2008; Thomson et al., 2008). As a result, a large difference in shear force was observed between the 2 sites at 1 d postmortem, which diminished after further aging but was still large.

The consistency of the combined effect of the gene markers in the 2 experiments despite the substantial differences between the 2 sites in the processing conditions is an important finding. The greatest effect at both sites was in the AT-suspended LLM that was aged for 7 d. Cattle with the most favorable combination of alleles (4 favorable alleles) had a 16% reduction in shear force compared with those with 0 favorable alleles in NSW, and a 17% reduction in shear force in WA. In the TS LLM aged for 7 d, the net effect of the favorable alleles was a reduction in shear force of 8% in NSW and 12% in WA. Despite the above findings, there were differences in the size of effects of individual markers between the sites. In WA, the *CAST* marker had the greatest effect on shear force, whereas *CAST*, *CAPN3*, and *CAPN1–4751* had a similar magnitude of effects in NSW. These differences in specific effects of individual markers may be due to the different processing conditions at the 2 sites, but could be due to other factors such as differences between the 2 experiments in power to detect more specific effects.

The present study does not provide any supporting evidence that genetic selection for the favorable tenderness markers would have any large detrimental effects on other meat quality traits. The favorable SNP tended to have positive effects on compression, although these effects rarely reached statistical significance. Also, the *CAST* marker showed some association with cooking loss in WA, although the favorable allele was associated with reduced cooking loss, which is not considered detrimental to meat quality. Furthermore, there were no significant associations between the markers and IMF, and there was no evidence of any interactions between the HGP and the tenderness markers on shear force or the other meat quality traits. In this regard, the HGP increased shear force of the LLM in Brahman cattle, but had no effect on shear force in the STN, which is consistent with previous work (Thompson et al., 2008). The HGP also resulted in a small increase in compression in the LLM in WA.

The magnitude of the combined effects of the tenderness markers on shear force suggests that these differences are detectable by consumers (Huffman et al., 1996; Perry et al., 2001b), and that the use of the markers will improve beef tenderness. The Meat Standards Australia grading system has been developed to use commercially measurable traits to predict palatability of individual beef cuts in the carcass (Polkinghorne et al., 2008). Meat samples from this experiment will be tested using the Meat Standards Australia consumer testing protocol to quantify the magnitude of effect of the tenderness markers on consumer palatability. This will be the first step toward incorporating gene markers as a new input into the Meat Standards Australia grading system.

In conclusion, the findings of the present study provide further evidence that selection based on the *CAST* and *CAPN3* gene markers improves meat tenderness in Brahman cattle by more than the minimum values necessary to be detectable by consumers. It also appears that selection for the favorable *CAST* and *CAPN3* alleles would have little if any detrimental effect on nontenderness objective meat quality traits. The present study also supports previous findings that the *CAPN1–4751* gene marker improves beef tenderness and shows a lack of effects of the *CAPN1–4751* marker on nontenderness meat quality characteristics, at least between heterozygotes and cattle homozygous for the unfavorable allele. Based on the findings for the cattle produced and processed within the systems in the present study, calpain-system gene markers appear suitable for use in marker-assisted selection to improve meat tenderness, with no serious adverse effects on other objective measurements of beef quality. Further research to confirm the value of these findings using consumer assessment of eating quality is warranted.

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