Molecular value predictions: Associations with beef quality, carcass, production, behavior, and efficiency phenotypes in Brahman cattle[1]

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ABSTRACT: Data from 2 previously published experiments, New South Wales (NSW; n = 161) and Western Australia (WA; n = 135), were used to test molecular value predictions (MVP), generated from commercially available gene markers, on economically important traits of *Bos indicus* (Brahman) cattle. Favorable tenderness MVP scores were associated with reduced shear force values of strip loin (LM) steaks aged 7 d from Achilles-hung carcasses ($P \leq 0.06$), as well as steaks aged 1 ($P \leq 0.08$) or 7 d ($P \leq 0.07$) from carcasses hung from the pelvis (tenderstretch). Favorable tenderness MVP scores were also associated with improved consumer tenderness ratings for strip loin steaks aged 7 d and either Achilles hung ($P \leq 0.006$) or tenderstretched ($P \leq 0.07$). Similar results were observed in NSW for rump (top butt; gluteus medius) steaks, with favorable tenderness MVP scores associated with more tender (P = 0.006) and acceptable (P = 0.008) beef. Favorable marbling MVP scores were associated with improved ($P \leq 0.021$) marbling scores and intramuscular fat (IMF) content in the NSW experiment, despite low variation in marbling in the Brahman cattle. For the WA experiment, however, there were no ($P \geq 0.71$) relationships between marbling MVP and marbling scores or IMF content. Although residual (net) feed intake (RFI) was not associated (P = 0.63) with the RFI (feed efficiency) MVP, the RFI MVP was adversely associated with LM tenderness and acceptability of 7-d-aged Achilles-hung carcasses in NSW ($P \leq 0.031$) and WA ($P \leq 0.037$). Some other relationships and trends were noted between the MVP and the other traits, but few reached statistical significance, and none were evident in both experiments. Results from this study provide evidence to support the use of the tenderness MVP. The value of the marbling MVP, which was associated with marbling in only 1 herd, warrants further evaluation; however, there appears to be no evidence to support use of the RFI MVP in Brahman cattle.

Key words: beef quality, *Bos indicus*, genetic markers, marbling, residual feed intake, SNP

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INTRODUCTION

Genomic technologies have the potential to improve livestock production [National Beef Cattle Evaluation Consortium (**NBCEC**), 2012]. Some gene markers, or SNP, are reported to be associated with enhanced performance for commercial traits, including meat tenderness and marbling (Barendse, 2009; Mullen et al., 2009) and feed efficiency (Barendse et al., 2007; Nkrumah et al., 2007; Sherman et al., 2008). Recently, panels of SNP have become commercially available (Van Eenennaam et al., 2007; DeVuyst et al., 2011), including a 56-SNP panel, which allows molecular value predictions (**MVP**) of breeding values to be calculated for tenderness, marbling, and residual (net) feed intake (**RFI;** Pfizer, 2009b).

There is a continuing need to evaluate associations between MVP and economically important traits in different commercial beef production and processing systems. There is also a need for evaluation of MVP against a broader range of production, carcass, and beef quality traits to quantify favorable or antagonistic relationships with other traits of interest. Improved tenderness is phenotypically associated with increased protein turnover (Koohmaraie et al., 2002), as well as with gene markers associated with protein turnover (Cafe et al., 2010b; Robinson et al., 2012), suggesting possible adverse associations of tenderness MVP with feed efficiency and marbling.

It was hypothesized that MVP generated from a commercially available SNP panel (Pfizer, 2009b) would have favorable associations with the traits (tenderness, marbling, and RFI) they are designed to predict but no unfavorable associations with other traits of economic importance. This hypothesis was tested using data from 2 previously published experiments (Cafe et al., 2010a, 2010b; Robinson et al., 2012) designed to examine tenderness gene markers and their interactions with production and processing factors in *Bos indicus* (Brahman) cattle.

Table 1. Frequency (% of cattle tested) of favorable alleles for the 4 calpain-system gene markers in Brahman cattle in New South Wales and Western Australia (Cafe et al., 2010a)

Herd and gene marker	Gene markers[1]		
	0	1	2
New South Wales (n = 1090)			
CAST	17.0	42.6	40.3
CAPN3	31.6	47.0	21.4
CAPN1–4751	69.6	25.9	4.6
CAPN1-316	93.2	6.8	0.0
Western Australia (n = 574)			
CAST	24.2	44.3	31.4
CAPN3	19.4	41.7	38.9
CAPN1-4751	49.3	40.4	10.3
CAPN1-316	85.5	14.0	0.6

[1]Gene markers for *CAST* = calpastatin; *CAPN3* = calpain 3; and *CAPN1-4571* and *CAPN1-316* = μ-calpain.

MATERIALS AND METHODS

Cattle care and use as well as all procedures performed in these studies were approved by the New South Wales Department of Primary Industries Orange Agricultural Institute Animal Ethics Committee (approval numbers ORA 06/001 and ORA 06/004), Commonwealth Scientific and Industrial Research Organisation (CSIRO) Rockhampton Animal Experimentation Ethics Committee (approval number RH216–06), and the Department of Agriculture and Food, Western Australia Animal Ethics Committee (approval number 2-06-11). These experiments were originally designed to assess the effects of calpain-system gene markers (calpastatin, ***CAST****; calpain 3*, ***CAPN3***; *μ-calpain*, ***CAPN1-4751*****,** *and* ***CAPN1-316***) on production and beef quality characteristics of *Bos indicus* (Brahman) cattle, as well as to identify interactions of the gene markers with production [sex and hormonal growth promotant (**HGP**) implantation] and processing (carcass suspension, muscle, and duration of the postmortem aging period) effects (Cafe et al., 2010a, 2010b; Robinson et al., 2012).

New South Wales Study

Brahman cattle were sourced at weaning (6 to 8 mo of age) from 4 commercial and 3 research herds (Springsure, Rockhampton, Marlborough, Julia Creek, and Millaroo regions of central and northern Queensland). All progeny were from natural matings. Pedigrees and birth dates were known for the 3 research herds, which supplied only heifers. The commercial herds supplied both steers and heifers, which were born during the same season as the research herds and weaned at 7 to 8 mo of age; however, the commercial herds used 20 to 30 sires and could not provide pedigree information or individual birth dates of calves.

Blood samples were collected for DNA analysis before weaning of calves from research herds and after weaning in commercial herds. A total of 1,090 weaned calves were DNA tested (gene marker frequencies are shown in Table 1), and the results were used to select 164 steers and heifers in groups that were homozygous for favorable and unfavorable *CAST* and *CAPN3* gene markers and as balanced as possible across groups for *CAPN1* gene marker allelic status. The number of Brahman cattle in the New South Wales (**NSW**) herd with MVP data, stratified by sex, implant status, and genotype (number of favorable alleles) for calpain-system gene markers, is shown in Table 2. The cattle were transported to the Queensland Department of Primary

Industries Brigalow Research Station (Theodore, Queensland, Australia), where they were held up to 4 wk while undergoing a cattle tick treatment program required for transport to Glen Innes, NSW, for backgrounding.

After 4 mo of grazing, calves were allocated to 4 backgrounding groups balanced for sex, gene marker status, origin, and previous management and were grazed an additional 2 mo. When necessary, calves were provided a pelleted energy supplement to maintain growth during the winter. At the end of the 6-mo backgrounding period, all calves were transported to the Australian Cooperative Research Centre for Beef Genetic Technologies "Tullimba" Research Feedlot near Kingstown, NSW. Upon arrival calves were segregated by sex, and the design algorithms of Robinson (2009) were used to allocate individual animals to treatment (implant/none) and management groups (8 large open bunk pens, then 20 automatic feeder pens), aiming for the greatest possible balance of genotypes, sex, BW, and treatments across property of origin and other management groups and to minimize the error variance of comparisons of marker and treatment effects. For more details, see Robinson et al. (2007) and Robinson (2009).

After 2 wk in the feed yard during a 4-wk adaption period to grain-based diets, half of the cattle were implanted with an HGP containing 200 mg trenbolone acetate and 20 mg estradiol-17β (Revalor-H; Virbac, Milperra, NSW, Australia). All cattle were fed a grain-based diet formulated to provide 12.0 MJ ME/kg, 16.0% CP, and 10.5% ADF (DM basis). Cattle were 17 to 19 mo of age at the end of the 117-d finishing period.

Feed Intake Measurement and Calculations. At the conclusion of the 4-wk adaption period, cattle were moved to the 20 intake pens (8 to 9 per pen), which contained an automated feed intake recorder that measured individual feed intake (Bindon, 2001) over a 70-d period. Cattle remained segregated by sex. During this test period, cattle were weighed weekly. It should be noted that 4 cattle did not eat from the automatic feeders, and 1 steer became ill during the final weeks, and at the end of the feed intake period, all cattle were returned to their original designated pens for 6 to 8 d before slaughter. The ADG was calculated by regressing individual BW over time for the 70-d intake test; the feed conversion ratio (**FCR**) for each animal was calculated by dividing DMI by ADG. Residual feed intake was calculated using a multiple linear regression of DMI on mean metabolic BW (**MMW** = mean $BW^{0.73}$) and ADG (Arthur et al., 2001) as the error term (**e**) in the equation for DMI: DMI = –3.18 + (0.129 × MMW) = (1.96 × ADG) + e (R^2 = 0.78).

Western Australia Study

Brahman cattle were sourced at weaning (6 to 8 mo of age) from 4 producers in the Northern Agricultural Region of Western Australia (**WA**); no records of birth dates or sire and dam pedigrees were available for these calves. A total of 574 calves were tested for calpain-system gene marker status (gene marker frequencies are presented in Table 1); 173 steers were then selected on the basis of their initial DNA tests for the calpain-system gene markers to create similarly sized groups of cattle that were homozygous or heterozygous for favorable and unfavorable *CAST* and *CAPN3* gene markers and as balanced as possible for *CAPN1* gene marker allelic status. The selected cattle were transported to Vasse Research Station for backgrounding and finishing.

Table 2. Number of Brahman cattle stratified by sex, implant status, and genotype (number of favorable alleles) for calpain-system gene markers for which molecular value predictions (MVP) were determined in New South Wales (NSW) and Western Australia (WA)[1]

Factor	NSW[1]	WA
Sex		
Heifer	79	—
Steer	82	135
Implant status[2]		
No HGP	80	68
HGP	81	67
CAST[3]		
0	65	39
1	—	48
2	76	48
CAPN3[3]		
0	87	31
1	5	58
2	69	46
CAPN1–4751[3]		
0	89	64
1	64	58
2	8	13
CAPN1-316[3]		
0	146	114
1	15	20
2	0	1

[1]Differences in total number of cattle within gene marker variables in the NSW herd from the experimental design criteria of Cafe et al. (2010a, 2010b) were due to reclassification of gene marker status of some cattle on validation testing and MVP not being able to be determined on a small number of cattle for which sensory data (DNA was extracted) were not collected.

[2]200 mg trenbolone acetate and 20 mg estradiol-17β (Revalor-H; Virbac, Milperra, NSW, Australia). HGP = hormonal growth promotant.

[3]Gene markers for *CAST* = calpastatin; *CAPN3* = calpain 3; and *CAPN1-4571* and *CAPN1-316* = μ-calpain.

Calves were grazed for 6 mo on pasture in groups based solely on BW before allocation using the algorithms of Robinson (2009) into replicates ($n = 4$), feedlot pens ($n = 12$), and HGP implant treatments, balanced for gene marker status, property of origin, and previous management groups. After an additional 2 mo grazing pasture, steers were transferred to the pens in the feedlot facility and, following a 2-wk adaption period, fed a high-grain diet containing 10.8 MJ ME/kg DM and 13.4% CP. As in the NSW experiment, half of the steers received a combination trenbolone acetate-estradiol-17β implant (Revalor-H; Virbac) 2 wk after arrival at the feed yard. At the end of the 80-d feedlot phase, steers were 21 to 24 mo of age. Table 2 shows numbers of cattle in the WA herd with MVP data, stratified by HGP implant status and genotype (number of favorable alleles) for calpain-system gene markers.

Data Collection

Cattle Temperament. Temperament was assessed at both locations during routine handling events throughout the experiment. Flight speed (m/s) was calculated from the electronically recorded time it took an animal to cover approximately 1.7 m on release from the squeeze chute (Burrow et al., 1988).

Slaughter. The NSW cattle were transported 270 km to John Dee Abattoir (Warwick, Queensland, Australia). The WA cattle were transported approximately 100 km to Harvey Beef plant (Harvey, Western Australia). After captive bolt stunning and exsanguination, standard AUS-MEAT carcasses (AUS-MEAT, 2007) were prepared and split into 2 sides. Rump (P8) fat depth was measured on each carcass, both sides weighed, and right sides were hung using a rope through the pelvic ligament (tenderstretch method of Thompson, 2002), whereas left sides were hung via the Achilles tendon. Both sides were subsequently placed in a chiller overnight; temperature and pH characteristics were described by Cafe et al. (2010b). No data were collected on 33 carcasses from the Harvey Beef plant because of a serious breakdown in the slaughter chain.

After an overnight chill, carcass sides were ribbed (quartered) between the 10th and 11th ribs and, within 20 min, graded according to Meat Standards Australia (2009). Data recorded included LM area (**LMA**), rib fat depth, meat color (1 = lightest to 9 = darkest; Meat Standards Australia, 2009), fat color (0 = whitest to 9 = darkest yellow; Meat Standards Australia, 2009), skeletal maturity (100 = A^{00} to 590 = E^{90}; USDA, 1997), and marbling score based on Australian (0 = Practically devoid to 6 = Abundant; Meat Standards Australia, 2009) and U.S. (100 = Practically $Devoid^{00}$ to 1100 = $Abundant^{00}$; USDA, 1997) scoring systems, as well as ultimate muscle pH. All carcass data were collected by the same AUS-MEAT trained personnel at both slaughter facilities.

Objective Beef Quality. At approximately 20 (WA) and 28 h (NSW) postmortem, the LM, semitendinosus (**ST**), gluteus medius (**GM**), and supraspinatus (**SS**) were removed from the Achilles-hung carcasses; the LM was the only muscle excised from tenderstretch carcasses. The LM (from both Achilles- and tenderstretch-hung carcasses) was cut into 3 equal portions, and the ST was cut into 2 equal portions, which were vacuum packaged. One portion from each muscle was immediately frozen at –20°C (1 d aged), and another was aged an additional 6 d at 1°C before freezing for storage at –20°C (7 d aged). Details of thawing, intramuscular fat (**IMF**) content, cooking, and instrumental shear force and compression are provided by Cafe et al. (2010b) in accordance with the protocols of Perry et al. (2001).

The third section of the LM from both carcass suspension treatments, as well as the GM and SS, were processed into 25-mm-thick steaks, individually wrapped, vacuum packaged in sets of 5 steaks/muscle, stored at 2°C, and at 7 d postmortem, packages of steaks were frozen at –20°C for consumer sensory testing according to the protocol described by Watson et al. (2008). Consumer recruitment, steak preparation, and sample service are provided in greater detail by Robinson et al. (2012). Consumers scored each sample for tenderness, juiciness, and liking the flavor on a 100-mm line, anchored at 0 (least favorable) and 100 (most favorable), and overall liking on a 100-mm line, anchored at 0 (least favorable) and 5 (most favorable). In addition, a meat quality score (**MQ4**) was calculated using the formula of Watson et al. (2008): MQ4 = (0.4 × tenderness score) + (0.1 × juiciness score) + (0.2 × flavor liking score) + (0.3 × overall liking score).

Molecular Value Predictions

The DNA, extracted from blood samples as described by Cafe et al. (2010a), was provided to Pfizer Animal Health Australia (Albion, Queensland, Australia). The MVP for tenderness (predicting Warner-Bratzler shear force at 14 d of postmortem aging), marbling (AUS-MEAT marble score), and RFI were calculated from results of a panel of 56 SNP, with the aim of predicting true breeding values and resulting phenotypes (Pfizer, 2009b).

Development and validation of the MVP used a 4-step process described in detail by Pfizer (2009b): 1) marker discovery, 2) incorporation of individual markers into panels for MVP and reliability predictions using "shrinkage" methodology, 3) internal assessment of associations between MVP and phenotypes by Pfizer Animal Genetics, and 4) independent validation of the MVP. The shrinkage methodology reduces the contribution of individual marker effects according to their estimated

standard errors so that the more reliable makers carry more weight in the MVP prediction.

Details of the cattle populations used for development, internal refinement, and external validation of MVP are provided in Pfizer (2009b). Briefly, 5 populations (n = 2,866 head) comprising 4 populations of *Bos taurus* cattle (n = 2,072 to 2,515 head) and 1 *Bos taurus* × *Bos indicus* composite population (n = 114 to 254 head) were used to develop the MVP.

Internal evaluation and refinement of calibrations and prediction equations were undertaken using a further 8 populations (total n = 4,455 head). Included were 6 *Bos taurus* populations, 1 Brangus population (n = 468 head) with RFI phenotypes, and 1 Santa Gertrudis population (n = 206 to 230 head) with marbling score, shear force, and RFI phenotypes. The overall correlations between MVP and the phenotypes were 0.30 for tenderness, 0.12 for marbling, and 0.13 for RFI; reliabilities of the MVP for these traits were 49.1%, 25.5%, and 29.8%, respectively.

Independent validation was undertaken using 4 National Beef Cattle Evaluation Consortium populations (NBCEC, 2011): A) European Maternal Line Composite bulls (n = 462 to 671 head), B) European Maternal Line Composite steers (n = 723 to 785 head), C) a *Bos indicus*–influenced composite (n = 390 to 394 head), and D) the Australian Beef Cooperative Research Centre multibreed population that included Angus, Brahman, Belmont Red, Hereford, Murray Grey, Santa Gertrudis, and Shorthorn cattle (n = 1,244 to 1,345 head).

In the external validation populations (Pfizer, 2009b), tenderness MVP was associated with shear force at 1-d aging ($P \leq 0.021$) in all 3 populations (A, C, and D) where shear force was measured. Marbling was not measured in population A. Marbling MVP was or tended to be associated with marbling score and IMF content in populations B ($P \leq 0.146$) and C ($P \leq 0.096$) but not D ($P \geq 0.43$). The RFI MVP was associated with RFI in populations A ($P = 0.020$) and D ($P = 0.001$) but not C ($P > 0.50$).

Statistical Analyses of NSW and WA Experiments

Statistical analyses were conducted by fitting linear mixed models with the REML methodology of Robinson (1987) in Genstat (version 10, VSN International Ltd., Hemel Hempstead, UK). Because of subtle differences in experimental designs, experimental sites (NSW and WA) were analyzed separately. For each trait, individual animals were the experimental unit; the effect of each MVP was determined separately by including the MVP as a single covariate in the model fitted to each trait:

$$y = (\text{other terms}) + S \times MVP + \text{error}, \quad [1]$$

where S is the slope of the relationship between the trait of interest and the MVP.

Other fixed effects in the model were implant status and (NSW data only) sex. Random effects included property of origin, backgrounding replicate, feedlot replicate, and sex × HGP implant status (NSW). Slaughter date and slaughter group were also included as random effects in the analyses of carcass and beef palatability traits. Additionally, the estimated percentage of *Bos indicus* inheritance was included as a covariate in the analyses of the WA data (Cafe et al., 2010a, 2010b); however, there were only a small number of cattle with some *Bos taurus* influence, and this did not affect the results. Associations between MVP and each trait were deemed significant at $P < 0.05$, with a P-value between 0.05 and 0.10 considered a tendency.

When a relationship was identified between an MVP and a trait that it was designated to predict (i.e., tenderness traits for the tenderness MVP, marbling scores or IMF content for the marbling MVP, and RFI for the RFI MVP), the percentage of phenotypic variation (**%PV**) explained by the MVP was calculated according to the equation of Thallman et al. (2009): $\%PV = S^2PV(MVP)/PV(trait)$, where S = slope of the regression coefficient of the MVP from Eq. [1], PV(trait) = phenotypic variation of the trait, and PV(MVP) = phenotypic variation of the MVP, which was assumed to be equal to the observed variance of the MVP.

The phenotypic variance of the trait (y) was calculated as $S^2Var(MVP) + RV$, where **RV** was the residual variance from Eq. [1]. To enable comparisons with the results of Johnston and Graser (2009), approximate percentages of genetic variation were derived as $\%PV/h^2$, using weighed heritability estimates of 20.7%, 33.0%, and 36.4% for shear force/sensory tenderness, marbling scores, and IMF content, respectively.

Table 3. Molecular value predictions (MVP) for tenderness (shear force), marbling (AUS-MEAT marble scores), and residual feed intake (RFI) of Brahman cattle in New South Wales (NSW; n = 161) and Western Australia (WA; n = 135)

MVP	NSW				WA			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Tenderness, kg	0.49	0.15	0.14	0.81	0.43	0.16	0.08	0.84
Marbling[1]	–0.30	0.11	–0.71	–0.003	–0.29	0.12	–0.59	0.10
RFI, kg DM/d	–0.04	0.20	–0.52	0.58	–0.07	0.19	–0.51	0.38

[1]0 = Practically devoid to 6 = Abundant (Meat Standards Australia, 2009).

RESULTS AND DISCUSSION

Distributions of MVP

Distributions for each MVP at each experimental site were examined and found to be unimodal with only a small amount of skewness (Table 3). The tenderness MVP predicts shear force, so lower values represent more tender beef. The marbling MVP predicts the AUS-MEAT marble score. The RFI MVP predicts RFI (difference between an animal's expected ADFI based on BW and ADG), so a negative RFI MVP is indicative of a more efficient animal.

Relative to the full published range for the MVP, the range in the present study represented 50% and 57% (NSW and WA, respectively) of the full published range of tenderness MVP, which was –0.47 to 0.96 kg shear force (Pfizer, 2009a). For the marbling MVP, the range in the present study was 34% and 33% (NSW and WA, respectively) of the full range (–1.00 to 1.11; AUS-MEAT marbling score; Pfizer, 2009a), whereas the range in RFI MVP was 44% and 35% (NSW and WA, respectively) of the full range from –1.44 to 1.08 kg/d (Pfizer, 2009a). The observed ranges of MVP relative to the full published ranges probably reflect the assessment of Brahman cattle in the present study compared with Wagyu, Angus, Composite, and Shorthorn cattle used for development and refinement of the MVP (Pfizer, 2009b). Current MVP percentiles vary according to breed and breed type. For Australian *Bos indicus* breeds, the 90th to 1st percentile range for tenderness is from 0.57 to –0.17, compared with 0.17 to –0.33 for *Bos taurus* breeds (Pfizer, 2011).

It is important to recognize that the relationship between the 2 populations from which the experimental cattle were sourced is unknown, with no common sires. The present study was designed 1) to create 2 independent populations of *Bos indicus* cattle sourced from geographically distinct locations in distinctly different environments on opposite sides of Australia to test the robustness of the results for effects of the calpain-system gene markers and MVP and 2) to make a detailed assessment of traits other than those for which the markers and MVP were developed within populations of cattle run under commercial conditions.

Correlations Among MVP

There were no significant correlations among MVP at either site ($P \geq 0.10$) except for a tendency toward a negative correlation ($P = 0.06$) between the tenderness and RFI MVP in the NSW herd (Table 4). Even though the latter could be a chance effect, it may relate to weightings on the calpain-system gene markers that form part of the 56-SNP marker panel. Calpain activity and protein degradation affect tenderness, and lines of cattle divergently selected for RFI were noted to differ in postslaughter calpastatin levels (McDonagh et al., 2001).

Table 4. Correlations among molecular value predictions (MVP) for tenderness, marbling, and residual feed intake (RFI) in the New South Wales (NSW, $n = 161$; above diagonal) and Western Australian (WA, $n = 135$; below diagonal) herds

WA herd MVP correlations	NSW herd MVP correlations		
	Tenderness	Marbling	RFI
Tenderness		0.127	–0.148*
Marbling	–0.007		0.034
RFI, kg DM/d	0.005	0.137	

*$P < 0.10$.

MVP and Corresponding Phenotypic Traits

Beef Quality Phenotypes. Cafe et al. (2010b) noted that average shear forces for 1- and 7-d-aged LM steaks from Achilles-hung carcasses from WA cattle were less than those from NSW cattle (Table 5). However, differences in sensory and MQ4 scores between NSW and WA cattle were less pronounced (Table 5). Comparison between the range for phenotypic values obtained in the present study and those of Johnston and Graser (2009) and NBCEC (2011) is of limited value because of processing differences, as well as other factors that varied across this and past experiments.

Marbling Phenotypes. The AUS-MEAT marbling scores ranged from 0 to 1, with means of 0.16 ± 0.37 and 0.26 ± 0.44 in NSW and WA, respectively (Table 6). Descriptive statistics for other marbling and carcass traits are also presented in Table 6. The range of values for the marbling phenotypes in the present study was less than in the Johnston and Graser (2009) study, which included a purebred *Bos indicus* validation population.

Feed Efficiency Phenotypes. The range of RFI values in the NSW herd was –3.69 to 3.09, with a mean of –0.07 ± 0.83 (Table 6); RFI was not measured in WA. Descriptive statistics for growth, flight speed, and intake traits are also presented in Table 6. The range of RFI values in the NSW herd was similar to the range for the purebred *Bos indicus* validation population in the study of Johnston and Graser (2009).

Association among MVP and All Phenotypic Traits

Tenderness MVP. In both NSW and WA, the tenderness MVP was, or tended to be, associated with reduced shear force (more tender beef) of 1- and 7-d-aged LM from tenderstretched sides and 7-d-aged LM from Achilles-hung sides (Table 7). In addition, tenderness MVP tended to be associated with lower shear force values in 1-d-aged ST from Achilles-hung carcasses of

Table 5. Phenotypic statistics for beef quality traits in the New South Wales (NSW, $n = 161$) and Western Australian (WA, $n = 135$) herds

	NSW				WA			
Trait[1]	Mean	SD	Minimum	Maximum	Mean	SD	Minimum	Maximum
Shear force, N								
LM								
1 d aged, Achilles hung	78.2	18.53	47.0	142.3	52.2	11.45	31.3	83.1
7 d aged, Achilles hung	68.1	17.63	32.7	126.0	49.5	10.25	28.4	84.5
1 d aged, tenderstretched	47.2	5.61	30.7	72.8	51.6	11.81	31.5	106.8
7 d aged, tenderstretched	45.6	5.56	32.6	66.9	46.0	9.63	28.7	90.3
Semitendinosus								
1 d aged, Achilles hung	56.3	6.54	40.7	72.9	54.0	8.05	38.2	78.2
7 d aged, Achilles hung	55.7	6.21	41.8	73.5	50.5	6.25	37.4	69.3
Sensory beef quality scores								
LM (Achilles hung)								
Tenderness[1]	38.9	11.89	12	75	40.3	12.51	14	69
Juiciness[1]	46.6	10.75	16	70	47.4	10.99	24	75
Flavor[1]	48.6	9.81	23	70	49.8	9.90	26	72
Overall liking[2]	2.83	0.345	2.2	3.9	2.88	0.404	2.1	3.9
MQ4[1,3]	43.1	10.45	18	72	44.6	11.10	20	72
LM (Tenderstretched)								
Tenderness[1]	51.8	10.80	25	77	51.4	11.11	20	85
Juiciness[1]	50.3	10.82	26	75	52.8	10.34	24	78
Flavor[1]	55.0	9.58	30	77	56.6	9.32	33	77
Overall liking[2]	3.17	0.359	2.4	2.9	3.19	0.362	2.3	42
MQ4[1,3]	52.8	9.85	28	75	53.6	9.74	26	78
Gluteus medius								
Tenderness[1]	47.7	11.73	15	77	46.8	11.09	21	79
Juiciness[1]	51.5	9.87	31	74	50.6	10.27	30	76
Flavor[1]	54.1	9.12	27	73	53.7	9.91	33	81
Overall liking[2]	3.07	0.333	2.3	3.8	3.06	0.337	2.4	4.0
MQ4[1,3]	50.5	10.11	24	76	49.6	10.0	30	77
Supraspinatus								
Tenderness[1]	70.0	9.60	46	90	69.0	9.42	45	92
Juiciness[1]	71.3	8.33	51	88	70.2	7.69	50	89
Flavor[1]	67.1	9.10	43	87	66.6	8.36	36	89
Overall liking[2]	3.69	0.373	2.6	4.5	3.64	0.372	2.7	4.6
MQ4[1,3]	68.9	8.81	43	86	68.0	8.22	42	88

[1]0 = least desirable to 100 = most desirable.

[2]0 = least liked to 5 = most liked.

[3]Meat quality score (MQ4) = (0.4 × tenderness score) + (0.1 × juiciness score) + (0.2 × flavor score) + (0.3 × overall liking score).

cattle from NSW; however, there were no associations of tenderness MVP with either compression force or drip loss (results not shown). There were favorable associations, or tendencies toward favorable associations, between tenderness MVP and tenderness, flavor, and MQ4 scores among cattle from both NSW and WA, but favorable associations between tenderness MVP and juiciness and overall liking were only observed in the NSW herd (Table 8). In the LM from tenderstretched sides, tenderness MVP was associated favorably with tenderness and overall liking ratings in the NSW herd and tended to be associated favorably with tenderness and MQ4 scores in the WA herd. Additionally, tenderness MVP was associated favorably with tenderness, juiciness, flavor, overall liking, and MQ4 scores for the GM in the NSW herd, but there were no associations with consumer sensory ratings for the GM from the WA herd (Table 9). There were no associations of tenderness MVP with any sensory assessment of the SS in either herd.

An important issue in comparing results of associations between MVP and beef quality phenotypes is the lack of standardization of objectively measured tenderness phenotypes and a scarcity of phenotypes for consumer-assessed eating quality and other measures of palatability. For example, other studies have assessed the palatability of 1- and 14-d-aged (NBCEC, 2011) or 2-d-aged (Johnston and Graser, 2009) LM from Achilles-hung carcasses but did not report any other

Table 6. Phenotypic statistics for performance, behavior, and carcass traits in the New South Wales (NSW, $n = 161$) and Western Australian (WA, $n = 135$) herds

	NSW				WA			
Trait	Mean	SD	Minimum	Maximum	Mean	SD	Minimum	Maximum
Performance traits								
Start background BW, kg	218	36.0	152	354	208	59.2	105	396
Background ADG, g	717	118.6	394	1013	640	169.2	91	945
End background BW, kg	321	38.1	238	421	342	35.6	240	468
Feedlot ADG, kg	1.13	0.314	0.22	2.28	1.28	0.345	0.35	2.36
Feedlot ending BW, kg	435	55.8	286	602	449	51.1	269	600
Feedlot DMI, kg/d	8.0	1.36	4.5	12.5	—	—	—	—
Feedlot FCR[1]	7.5	2.39	3.9	27.3	—	—	—	—
Feedlot RFI[2]	–0.07	0.83	–3.69	3.09	—	—	—	—
Behavior traits								
Background flight speed, m/s	1.82	0.669	0.73	3.99	1.56	0.419	0.61	3.02
Feedlot flight speed, m/s	2.07	0.694	0.74	4.56	1.50	0.454	0.61	2.75
DMI/feeding session, kg	1.02	0.886	0.28	5.12	—	—	—	—
Feeding time, s/d	4,403	1,232	1,050	7,950	—	—	—	—
Feed sessions, no./d	11.7	6.14	1.4	30.5	—	—	—	—
Carcass traits								
HCW, kg	243	32.3	157	338	242	25.7	151	315
LM area, cm^2	60	8.6	41	82	64	6.3	46	77
Skeletal maturity[3]	152	20.9	120	280	138	16.1	100	190
Rump (P8) fat, mm	12.0	2.61	8	25	8.0	2.56	3	18
10th rib fat, mm	6.2	2.08	2	17	5.3	2.38	0	14
AUS-MEAT marbling score[4]	0.16	0.366	0	1	0.26	0.440	0	1
USDA marbling score[5]	261	66.2	130	440	293	61.9	130	410
Intramuscular fat %	1.90	0.750	0.15	4.04	2.14	0.946	0.56	5.43
Fat color score[6]	0.43	0.588	0	2	0.70	0.641	0	3
Lean color score[7]	2.84	1.070	2	6	2.72	1.051	2	8
Ultimate pH	5.49	0.051	5.36	5.80	5.57	0.085	5.41	6.25

[1]Feed conversion ratio, kg DM/kg gain.

[2]Residual (net) feed intake, kg DM/d.

[3]100 = A^{00} to 590 = E^{90} (USDA, 1997).

[4]0 = Practically devoid to 6 = Abundant (Meat Standards Australia, 2009).

[5]100 = Practically $Devoid^{00}$ to 1100 = $Abundant^{00}$ (USDA, 1997).

[6]0 = whitest to 9 = darkest yellow (Meat Standards Australia, 2009).

[7]1 = lightest to 9 = darkest (Meat Standards Australia, 2009).

objective or consumer assessments of beef palatability or results for other abattoir processing methods. This is in stark contrast to the present study, which measured phenotypes for a broad range of commercially important palatability characteristics under various processing conditions, both within and between experiments and between cuts of beef (Cafe et al., 2010b; Robinson et al., 2012). These issues are particularly important in identifying ways to improve eating quality in beef from *Bos indicus* cattle, which can have substantially inferior eating quality than beef from *Bos taurus* cattle (Robinson et al., 2012).

There were no associations between tenderness MVP and marbling or carcass traits (Table 10). There was, however, a tendency for tenderness MVP to have an unfavorable association with BW at the start of backgrounding in the NSW herd, but this apparent effect did not persist (Table 11). Tenderness MVP also tended to have an unfavorable association with feedlot flight speed in both NSW and WA cattle, and this is consistent with the results of Cafe et al. (2010a) in the WA experiment, which revealed that cattle with 2 favorable alleles for 2 of the tenderness markers (*CAPN14751* and *CAPN3*) had, or tended to have, greater flight speeds. However, phenotypic correlations for the directly measured traits were positive (Cafe et al., 2011), implying that cattle with greater flight speed measurements produced less tender beef.

Ideally, a 1-kg difference in tenderness MVP should produce a 1-kg (9.8 N) difference in shear force for the cut of meat, ageing period, and processing conditions used in the original calibration. The average slope (9.3 N) for 1- and 7-d-aged LM suggests that the calibration is both useful and reasonable.

Table 7. Estimates (slope) of the relationship of a 1.0-unit change in molecular value predictions (MVP) with shear force values of the LM and semitendinosus (ST) from Brahman cattle from New South Wales (NSW; *n* = 161) and Western Australia (WA; *n* = 135)

		Tenderness MVP				Marbling MVP			RFI MVP[2]		
Trait	Site	Estimate	SE	*P*-value	%Var[1]	Estimate	SE	*P*-value	Estimate	SE	*P*-value
LM shear force, N											
1 d aged, Achilles hung	NSW	6.2	8.33	0.46		14.2	11.28	0.21	3.3	6.64	0.62
	WA	1.0	6.11	0.87		6.0	8.04	0.46	8.2	5.16	0.12
7 d aged, Achilles hung	NSW	15.5	7.99	0.06	2.6 (12.4)	6.9	10.60	0.51	–11.2	6.19	0.07
	WA	17.8	5.14	0.001	9.1 (44.2)	7.8	7.12	0.27	–2.1	4.78	0.66
1 d aged, Tenderstretched	NSW	7.2	2.48	0.004	5.5 (26.6)	–2.9	3.39	0.39	–1.6	1.98	0.43
	WA	11.0	6.15	0.08	2.6 (12.5)	–0.81	8.099	0.92	0.41	5.302	0.94
7 d aged, Tenderstretched	NSW	4.9	2.61	0.07	2.3 (11.1)	1.7	3.49	0.62	–2.9	2.03	0.15
	WA	11.0	4.97	0.029	4.0 (19.3)	–10.4	6.96	0.14	–0.35	4.486	0.94
ST shear force, N											
1 d aged, Achilles hung	NSW	6.0	3.13	0.06	2.4 (11.6)	–2.0	4.21	0.64	2.0	2.43	0.41
	WA	5.4	4.47	0.23		3.0	5.91	0.61	–3.7	3.83	0.34
7 d aged, Achilles hung	NSW	4.5	3.04	0.14		–5.7	4.12	0.17	–1.0	2.37	0.68
	WA	3.9	3.39	0.25		–0.28	4.479	0.95	0.65	2.915	0.82

[1]Percentage of phenotypic variation explained by tenderness MVP, if *P*-value for slope < 0.1. Values in parentheses are percentage of genetic variation explained, assuming h^2 = 20.7%.

[2]Residual (net) feed intake.

Table 8. Estimates (slope) of the relationship of a 1.0-unit change in molecular value predictions (MVP) with consumer sensory scores for 7-d-aged LM steaks from Brahman cattle from New South Wales (NSW; *n* = 161) and Western Australia (WA; *n* = 135)

		Tenderness MVP				Marbling MVP			RFI MVP[2]		
Trait	Site	Estimate	SE	*P*-value	%Var[1]	Estimate	SE	*P*-value	Estimate	SE	*P*-value
LM, Achilles hung											
Tenderness[3]	NSW	–19.11	5.879	0.001	6.9 (33.3)	–4.85	8.051	0.55	12.14	4.621	0.010
	WA	–17.30	6.178	0.006	6.0 (29.2)	–0.29	8.354	0.97	11.73	5.364	0.031
Juiciness[3]	NSW	–11.92	5.798	0.042	2.9 (13.8)	7.51	7.669	0.33	11.46	4.458	0.011
	WA	–7.73	5.662	0.17		0.58	7.556	0.94	8.25	4.848	0.091
Flavor[3]	NSW	–12.39	5.198	0.018	3.8 (18.4)	–7.86	6.908	0.26	6.08	4.049	0.14
	WA	–8.15	4.678	0.084	2.4 (11.7)	1.01	6.241	0.87	4.27	3.987	0.29
Overall liking[4]	NSW	–0.44	0.177	0.015	4.0 (19.5)	–0.16	0.237	0.51	0.297	0.138	0.033
	WA	–0.28	0.197	0.163		0.03	0.262	0.93	0.18	0.170	0.30
MQ4[3,5]	NSW	–16.17	5.342	0.003	6.0 (28.9)	–5.16	7.206	0.48	9.11	4.192	0.031
	WA	–12.49	5.340	0.021	4.2 (20.3)	0.12	7.215	0.99	9.75	4.617	0.037
LM, tenderstretched											
Tenderness[3]	NSW	–12.44	5.647	0.029	3.2 (15.7)	1.88	7.491	0.80	–2.57	4.328	0.55
	WA	–10.88	5.926	0.07	2.7 (13.0)	1.08	7.870	0.89	8.35	5.035	0.10
Juiciness[3]	NSW	–1.09	5.823	0.85		0.15	7.609	0.98	0.62	4.398	0.89
	WA	–7.22	5.554	0.20		–0.9	7.340	0.90	3.91	4.673	0.40
Flavor[3]	NSW	–2.77	5.197	0.60		–3.30	6.804	0.63	–1.74	3.926	0.66
	WA	–7.26	5.215	0.17		2.68	6.850	0.70	3.63	4.387	0.41
Overall liking[4]	NSW	–0.39	0.187	0.042	2.9 (13.8)	0.02	0.249	0.92	0.03	0.145	0.85
	WA	–0.24	0.198	0.23		0.09	0.261	0.72	0.24	0.165	0.16
MQ4[3,5]	NSW	–8.01	5.231	0.13		–0.17	6.882	0.98	–2.56	3.981	0.52
	WA	–9.58	5.221	0.07	2.7 (13.0)	0.83	6.942	0.91	5.70	4.428	0.20

[1]Percentage of phenotypic variation explained by tenderness MVP, if *P*-value for slope < 0.1. Values in parentheses are percentage of genetic variation explained, assuming h^2 = 20.7%.

[2]Residual (net) feed intake.

[3]0 = least desirable to 100 = most desirable.

[4]0 = least liked to 5 = most liked.

[5]Meat quality score (MQ4) = (0.4 × tenderness score) + (0.1 × juiciness score) + (0.2 × flavor score) + (0.3 × overall liking score).

Table 9. Estimates (slope) of the relationship of a 1.0-unit change in molecular value predictions (MVP) with consumer sensory scores for steaks from the gluteus medius (GM) and supraspinatus (SS) of Brahman cattle from New South Wales (NSW; n = 161) and Western Australia (WA; n = 135)

		Tenderness MVP				Marbling MVP			RFI MVP[2]		
Trait	Site	Estimate	SE	P-value	%Var[1]	Estimate	SE	P-value	Estimate	SE	P-value
GM sensory score											
Tenderness[3]	NSW	–16.59	6.000	0.006	4.8 (23.2)	2.65	8.192	0.75	3.08	4.732	0.52
	WA	–4.40	5.756	0.45		5.80	7.454	0.44	5.27	4.911	0.29
Juiciness[3]	NSW	–11.54	5.183	0.028	3.2 (15.2)	–3.08	7.031	0.66	4.68	4.040	0.25
	WA	–4.26	5.491	0.44		2.29	7.157	0.75	3.95	4.685	0.40
Flavor[3]	NSW	–10.17	4.721	0.034	2.9 (14.2)	–5.10	6.371	0.43	–0.98	3.69	0.79
	WA	–3.29	5.395	0.54		12.22	6.925	0.08	5.14	4.612	0.27
Overall liking[4]	NSW	–0.50	0.170	0.004	5.4 (26.2)	–0.05	0.234	0.85	0.046	0.135	0.73
	WA	–0.14	0.181	0.45		0.49	0.232	0.037	0.05	0.156	0.75
MQ4[3,5]	NSW	–13.87	5.174	0.008	4.5 (21.8)	0.57	7.075	0.94	1.62	4.086	0.69
	WA	–4.88	5.270	0.36		8.55	6.802	0.21	4.48	4.513	0.32
SS sensory score											
Tenderness[3]	NSW	–1.25	5.215	0.81		3.30	7.184	0.65	3.50	4.029	0.39
	WA	–6.67	5.130	0.20		–2.94	6.630	0.66	7.77	4.340	0.08
Juiciness[3]	NSW	–2.15	4.462	0.63		0.37	6.16	0.95	3.40	3.451	0.33
	WA	–0.87	4.329	0.84		–1.19	5.606	0.83	7.87	3.606	0.031
Flavor[3]	NSW	–3.66	4.728	0.44		–3.05	6.543	0.64	2.57	3.696	0.49
	WA	–4.33	4.651	0.35		–6.79	5.969	0.26	5.26	3.949	0.19
Overall liking[4]	NSW	–0.14	0.199	0.47		–0.02	0.276	0.94	0.10	0.156	0.51
	WA	–0.16	0.212	0.45		–0.34	0.273	0.21	–0.01	0.181	0.95
MQ4[3,5]	NSW	–3.17	4.684	0.50		0.42	6.483	0.95	3.33	3.648	0.36
	WA	–5.70	4.525	0.21		–5.69	5.827	0.33	5.68	3.843	0.14

[1]Percentage of phenotypic variation explained by tenderness MVP, if P-value for slope < 0.1. Values in parentheses are percentage of genetic variation explained, assuming h^2 = 20.7%.

[2]Residual (net) feed intake.

[3]0 = least desirable to 100 = most desirable.

[4]0 = least liked to 5 = most liked.

[5]Meat quality score (MQ4) = (0.4 × tenderness score) + (0.1 × juiciness score) + (0.2 × flavor score) + (0.3 × overall liking score).

Tenderness MVP explained 2.4% to 9.1% of the phenotypic variation in shear force traits, virtually identical to the phenotypic variation reported by Johnston and Graser (2009) in 2 unrelated data sets of *Bos indicus* cattle. Using the weighted mean estimate of 20.7% for shear force heritability from Johnston and Graser (2009), the tenderness MVP explained 11% to 44% of the genetic variation in shear force, implying that the inclusion of the tenderness MVP in a selection index could be a useful strategy.

Ultimately, consumer satisfaction depends on cooked beef palatability. The tenderness MVP was consistently associated with improved consumer-assessed palatability of the LM from Achilles-hung carcasses but less consistently for LM from tenderstretched carcasses. Consumer palatability ratings for the GM were also correlated with tenderness MVP in the NSW herd. This demonstrates the potential of tenderness MVP for improving the palatability attributes of muscles with the capacity to age, such as the LM and GM. These findings are consistent with the effects of calpain-system tenderness gene markers on tenderness (Cafe et al., 2010b; Johnston and Graser, 2010; Robinson et al., 2012), particularly in muscles with the capacity to age (Cafe et al., 2010b; Robinson et al., 2012) but not other traits (Cafe et al., 2010a, 2011), apart from minor effects on fatness (Wolcott and Johnston, 2009).

The contribution of the calpain-system gene markers to the tenderness MVP is not publicly known; however, inclusion of the gene marker status for the calpain-system markers in the statistical models of the present study resulted in the disappearance of statistical significance of the tenderness MVP in relation to shear forces and eating quality (L. M. Cafe, D. L. Robinson, and P. L. Greenwood, unpublished data). This suggests that despite it not being known whether any of the calpain-system gene markers are causal, they were major contributors to the improvement in tenderness from tenderness MVP. In the current data set, 3 of the 4 calpain-system markers explained 44% and 43% of the variation in tenderness MVP in the NSW and WA herds, whereas adding the *CAPN3* marker produced only a marginal change in R^2. If tenderness is to

Table 10. Estimates (slope) of the relationship of a 1.0-unit change in molecular value predictions (MVP) with carcass characteristics of Brahman cattle from New South Wales (NSW: $n = 161$) and Western Australia (WA; $n = 135$)

Trait	Site	Tenderness MVP			Marbling MVP				RFI MVP[2]		
		Estimate	SE	*P*-value	Estimate	SE	*P*-value	%Var[1]	Estimate	SE	*P*-value
HCW, kg	NSW	–8.2	12.68	0.52	–20.5	17.29	0.24		–3.4	10.25	0.74
	WA	1.7	11.10	0.88	–17.1	14.27	0.23		–9.6	9.28	0.30
LM area, cm^2	NSW	–3.7	3.53	0.29	–5.2	4.80	0.28		–0.10	2.821	0.97
	WA	–2.4	3.36	0.47	3.2	4.37	0.45		3.8	2.82	0.18
Skeletal maturity[3]	NSW	4.7	8.21	0.57	–8.3	11.02	0.45		–0.69	6.628	0.92
	WA	–0.43	7.64	0.96	1.3	10.05	0.90		–1.9	6.41	0.77
Rump (P8) fat, mm	NSW	–0.9	1.41	0.50	–0.48	1.87	0.80		–0.74	1.079	0.49
	WA	0.73	1.381	0.60	0.44	1.83	0.81		0.63	1.165	0.59
10th rib fat, mm	NSW	–0.6	1.06	0.59	2.3	1.41	0.10		0.06	0.814	0.95
	WA	–1.5	1.31	0.25	–0.58	1.749	0.74		–0.50	1.112	0.66
AUS-MEAT marbling score[4]	NSW	0.2	0.22	0.32	1.0	0.29	0.001	6.5 (19.6)	–0.22	0.172	0.20
	WA	–0.05	0.242	0.85	0.12	0.315	0.71		0.37	0.201	0.07
USDA marbling score[5]	NSW	1.9	34.20	0.96	107.3	45.83	0.021	3.4 (10.3)	–66.5	26.35	0.013
	WA	–3.4	32.95	0.92	15.1	42.83	0.73		4.3	27.69	0.88
Intramuscular fat, %	NSW	0.03	0.367	0.95	1.6	0.49	0.002	6.4 (17.6)	–1.08	0.279	<0.001
	WA	–0.12	0.456	0.79	–0.03	0.600	0.96		0.24	0.384	0.54
Fat color score[6]	NSW	–0.01	0.188	0.95	0.12	0.250	0.63		–0.02	0.144	0.87
	WA	–0.05	0.373	0.91	–0.24	0.482	0.62		0.13	0.303	0.67
Lean color score[7]	NSW	0.64	0.498	0.20	–0.13	0.671	0.85		–0.11	0.386	0.78
	WA	0.25	0.486	0.61	–0.60	0.641	0.35		–0.47	0.409	0.25
Ultimate pH	NSW	0.03	0.023	0.19	0.07	0.032	0.025		–0.01	0.019	0.75
	WA	–0.04	0.029	0.15	0.03	0.039	0.39		–0.05	0.024	0.031

[1]Percentage of phenotypic variation explained by marbling MVP for marble score and intramuscular fat for traits where $P \leq 0.10$ for the slope. Values in parentheses are percentage of genetic variation explained, assuming $h^2 = 33.0\%$ for marbling scores and 36.4% for intramuscular fat percentage.

[2]Residual (net) feed intake.

[3]100 = A^{00} to 590 = E^{90} (USDA, 1997).

[4]0 = Practically devoid to 6 = Abundant (Meat Standards Australia, 2009).

[5]100 = Practically $Devoid^{00}$ to 1,100 = $Abundant^{00}$ (USDA, 1997).

[6]0 = whitest to 9 = darkest yellow (Meat Standards Australia, 2009).

[7]1 = lightest to 9 = darkest (Meat Standards Australia, 2009).

be incorporated into a selection index for breeding herds, a selection function is required that clearly and validly predicts tenderness for the range of breeding herds that will use it. Results of this study confirm the potential of the current tenderness MVP, which is readily available to cattle breeders, to serve this purpose.

There were large differences between NSW and WA in the rate of pH and temperature decline of the carcasses during processing (Cafe et al., 2010b), which resulted in differences between sites in the postmortem tenderization process. Despite this, the overall consistency of the effects of the tenderness MVP on cooked beef palatability, including tenderness and overall liking, by consumers in the 2 experiments suggested robustness in the associations between tenderness MVP and palatability traits in Brahman carcasses processed under widely different conditions.

Marbling MVP. A favorable marbling MVP was associated with more marbling in the NSW but not the WA herd (Table 10) for the very limited range of marbling MVP and marbling scores and IMF in Brahman cattle (Table 6). The marbling MVP explained approximately 3.4% to 6.5% of the phenotypic variation in marbling assessments (Table 10). In this regard, the reliability of individual gene markers for marbling has been shown to be poor (Hocquette et al., 2010; Johnston and Graser, 2010), suggesting the value of using the marbling MVP for selection may be limited in Brahman cattle. In fact, Johnston and Graser (2009) reported that the marbling MVP explained only 0.1% of the phenotypic variation and 0.4% of the genetic variation in IMF content in purebred *Bos indicus* breeds. Yet Igenity (Lincoln, NE) panel scores for marbling had a genotypic correlation of 0.63 with USDA quality grades (DeVuyst et al., 2011), and there were significant associations between marbling MVP and marbling phenotypes in a North American *Bos indicus*–influenced validation population (NBCEC, 2011). Further elucidation of the biology of intramuscular adipocyte development and accumulation of IMF using genomic, transcriptomic, and proteomic techniques should enhance the capacity to identify useful markers for marbling in beef cattle (Hocquette et al., 2010).

Table 11. Estimates (slope) of the relationship of a 1.0-unit change in molecular value predictions (MVP) with growth performance and behavior traits of Brahman cattle from New South Wales (NSW; n = 161) and Western Australia (WA; n = 135)

		Tenderness MVP			Marbling MVP			RFI MVP		
Trait	Site	Estimate	SE	*P*-value	Estimate	SE	*P*-value	Estimate	SE	*P*-value
Performance traits										
Start background BW, kg	NSW	29.1	15.05	0.06	–23.8	21.14	0.26	–1.4	12.23	0.91
	WA	2.9	18.00	0.87	–25.5	23.23	0.28	–13.7	14.95	0.36
Background ADG, g/d	NSW	–0.03	0.047	0.49	–0.07	0.067	0.27	–0.05	0.038	0.23
	WA	–14.7	58.23	0.80	20.0	75.58	0.79	–39.8	48.43	0.41
End background BW, kg	NSW	19.9	16.14	0.22	–20.6	22.62	0.36	–9.3	13.00	0.48
	WA	0.79	15.33	0.96	–21.2	19.84	0.29	–22.1	12.64	0.08
Feedlot ADG, kg/d	NSW	–0.04	0.123	0.76	–0.05	0.171	0.76	–0.10	0.097	0.33
	WA	0.03	0.149	0.87	–0.22	0.196	0.27	–0.08	0.126	0.53
Feedlot ending BW, kg	NSW	9.3	22.53	0.68	–36.7	31.28	0.24	–17.7	18.01	0.33
	WA	2.6	22.29	0.91	–41.4	28.81	0.15	–19.2	18.56	0.30
Feedlot DMI, kg/d	NSW	0.30	0.617	0.63	–0.45	0.855	0.60	–0.19	0.489	0.70
Feedlot FCR[1]	NSW	0.51	1.098	0.65	–0.72	1.510	0.64	0.62	0.859	0.47
Feedlot RFI[2]	NSW	0.08	0.412	0.85	0.43	0.563	0.44	0.15	0.324	0.63
Behavior traits										
Background flight speed, m/s	NSW	–0.16	0.332	0.64	–0.68	0.460	0.14	0.24	0.266	0.37
	WA	–0.24	0.230	0.29	–0.21	0.307	0.50	–0.34	0.193	0.08
Feedlot flight speed, m/s	NSW	–0.58	0.342	0.09	–0.37	0.472	0.44	0.22	0.273	0.43
	WA	–0.47	0.245	0.06	0.42	0.327	0.21	–0.40	0.207	0.06
DMI/feeding session, kg	NSW	–0.04	0.174	0.81	0.02	0.244	0.93	0.34	0.136	0.015
Feeding time, s/d	NSW	413	550.4	0.45	474	766.8	0.54	–782	432.2	0.07
Feed sessions, no./d	NSW	–3.10	1.99	0.12	–2.73	2.804	0.33	–1.45	1.605	0.37

[1]Feed conversion ratio, kg DM/kg gain.

[2]Residual (net) feed intake, kg DM/d.

Marbling MVP was associated with overall liking scores for the GM and tended to be associated positively with flavor of the GM in the WA herd (Table 9). This finding is consistent with the generally accepted notion that IMF has a positive influence on eating quality characteristics of beef (Hocquette et al., 2010), although there were no associations between marbling MVP and other objective and sensory meat quality traits (Tables 7 to 9). In the NSW herd, marbling MVP was also associated with greater ultimate pH and tended to be associated with greater 10th-rib fat depth (Table 10), consistent with previous research on genetic and phenotypic relationships between IMF and subcutaneous fat depths (Robinson and Oddy, 2004).

Residual Feed Intake MVP. The MVP for RFI was not related to RFI or FCR in the Brahman cattle in this experiment (Table 11). This is consistent with failure of feed efficiency markers to validate across different cattle breeds (Johnston and Graser, 2010; Bolormaa et al., 2011a; Littlejohn et al., 2012), with the RFI MVP explaining only 1% of phenotypic variation in RFI in purebred *Bos indicus* cattle and less than 1% of phenotypic variation in *Bos taurus* and *Bos indicus* × *Bos taurus* crossbred cattle (Johnston and Graser, 2009). This is despite reports of multiple markers explaining a large proportion of genetic variation in several other studies (Moore et al., 2009).

Even though there were no associations of RFI MVP with palatability traits for the LM from tenderstretched carcasses (Table 8) or the GM from Achilles-hung carcasses (Table 9), RFI MVP had unfavorable associations with tenderness, juiciness, overall liking, and MQ4 scores of LM steaks from Achilles-hung carcass from NSW cattle and tenderness and MQ4 scores of steaks from WA cattle (Table 8). Furthermore, there were negative associations of RFI MVP with shear force values of 7-d-aged LM steaks from Achilles-hung carcasses of NSW cattle (Table 7), as well as juiciness of LM steaks and juiciness and tenderness of SS steaks from WA cattle (Table 9).

The RFI and tenderness MVP tended to be correlated in the NSW herd but not the WA herd (Table 4). The correlation may relate to the inclusion of the calpain-system gene markers in the 56-SNP marker panel and, presumably, their contribution to both the tenderness and RFI MVP and to calpain activity and protein degradation, which were found to differ in lines divergently selected

for RFI (McDonagh et al., 2001). However, the lack of association between RFI measurements in the NSW herd and the RFI MVP suggests that protein turnover represents only a small proportion of the complex trait representing feed efficiency and that the RFI MVP will need to be recalibrated, possibly using a wider set of SNP, before it could be recommended for use in Brahman cattle.

The RFI MVP had favorable associations with USDA marbling scores and IMF content in the NSW herd but an unfavorable association with ultimate pH in the WA herd. In WA, there was a tendency for the RFI MVP to be associated unfavorably with AUS-MEAT marbling scores. In the NSW herd, where feed intake and efficiency were measured, RFI MVP was associated with intake per session and tended to be associated with feeding time (Table 11). In the WA herd, there were tendencies for the RFI MVP to be associated favorably with the end of backgrounding BW and unfavorably with backgrounding and feedlot flight speeds (Table 11).

These findings do not support the use of the current RFI MVP in Brahman cattle. Indeed, because numerous factors, including growth and maintenance of body components, are known to contribute to feed conversion efficiency of beef cattle (Robinson and Oddy, 2004) and because RFI is a complex, index-based trait, the capacity to develop markers for this and other traits would be enhanced by genome-wide association studies on the component traits that contribute to RFI, including a wider range of biological phenotypes (Hocquette et al., 2012; Pollak et al., 2012).

CONCLUSIONS

The findings of the present study demonstrated good consistency between experiments in effects of the MVP across Brahman cattle, and they confirm that tenderness MVP were favorably associated with objective and consumer assessments of beef quality, with little or no adverse effects on the other traits assessed. Therefore, tenderness MVP may be potentially useful in genetic improvement programs and prediction of genotypes for Brahman cattle, although it might not explain much additional variation in tenderness beyond that explained by the calpastatin and calpain gene markers. The results for marbling MVP were inconsistent between the NSW and WA herds across the limited ranges of marbling scores and IMF content, although there were few adverse effects of marbling MVP on other traits. Consequently, further evaluation in Brahman cattle is warranted before use of the marbling MVP could be recommended for genetic selection or prediction of phenotypes for Brahmans. The utility of the marbling MVP will depend on the cost of the test relative to a seemingly inconsistent benefit. By contrast, the RFI MVP was not associated with feed efficiency and had adverse effects on beef eating quality traits; thus, results of this study do not support the use of the RFI MVP in Brahman cattle. On the basis of the evidence presented in this paper, there is little reason to believe that the markers on the 56-SNP panel are causal for marbling or feed efficiency.

The development of improved MVP for feed efficiency and other traits will require large-scale discovery and validation of SNP from genome-wide association studies (Bolormaa et al., 2011a, 2011b, 2013; Eggen, 2012) and SNP panels, which are becoming increasingly available commercially, with more gene markers contributing to genotypic and phenotypic variation. Their utility would be enhanced by the development of phenotyping systems with more efficient, higher throughput and standardized phenotyping, particularly for difficult to measure traits, such as cooked beef palatability and FCR, that allow for deeper biological phenotyping, enabling meaningful biological phenotypes to contribute to commercial traits (Hocquette et al., 2012; Pollak et al., 2012). This is likely to be particularly important for complex, index-based traits, such as FCR and RFI, so that variation in the component traits and their biology can be determined and would enhance the capacity to identify causal mutations.

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