Estimated gene frequencies of GeneSTAR markers and their size of effects on meat tenderness, marbling, and feed efficiency in temperate and tropical beef cattle breeds across a range of production systems

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ABSTRACT: The objectives of this study were to use genotypes for 12 commercially available GeneSTAR gene markers on 12,330 animals to estimate gene frequencies of the markers across a range of beef cattle breeds and to determine the effects of these markers on target traits using a subset of animals with both genotypic and phenotypic data (n = 9,414) for at least one trait. Tenderness markers (T1, T2, T3, T4) were assessed against shear force of 2 muscles, marbling markers (M1, M2, M3, M4) were assessed against intramuscular fat percent and marbling score, and the feed-efficiency markers (N1, N2, N3, N4) were assessed on daily feed intake and residual feed intake. Animals used were from 5 beef cattle research populations: Beef Cooperative Research Centre 1 (CRC1) temperate breeds (Angus, Hereford, Murray Grey, Shorthorn; n = 3,721), Beef CRC1 tropical breeds (Brahman, Santa Gertrudis, Belmont Red; n = 3,899), Beef CRC2 tropically adapted genotypes (Brahman and Tropical Composite; n = 4,446), and progeny test programs in Angus (n = 742) and Shorthorn (n = 347). Gene frequencies varied significantly across breeds and markers, with 86% of the markers estimated to be in Hardy-Weinberg equilibrium. Tenderness markers T1 and T2 had significant effects (P < 0.0001) on shear force, with the size and direction of effects consistent across the range of breeds for the 3 populations with phenotypes. However, sizes of marker effects differed across muscles and reduced upon tenderstretch hanging. Marker T3 was not significant (P > 0.05) in CRC1 temperate breeds but was significant (P < 0.0001) in tropically adapted breeds, with a large effect in Brahman. Marker T4 was significant for shear force in 2 CRC1 tropical breeds but with a different favorable allele. The 4 marbling markers were generally not significantly associated with intramuscular fat percent or marbling score across the 5 populations studied. Feed-efficiency markers N3 and N4 were significantly associated with residual feed intake and daily feed intake in the CRC1 temperate data set, in which a subset of the CRC1 data was used in their discovery, but were not significant in the other 4 populations. Markers N1 and N2 were generally not significant, but when they were significant, their direction of effects differed. The 12 GeneSTAR markers were studied in populations consisting of different breeds and genetic variability and showed gene frequencies and estimated effects that varied greatly across traits, suggesting large differences between the markers for their utility as selection tools in these populations.

Key words: beef, estimation, gene marker, marbling, residual feed intake, tenderness

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INTRODUCTION

New DNA-based tests are providing the livestock industries with the opportunity to increase the rate of genetic gain (Meuwissen and Goddard, 1996; Dekkers, 2004) through the discovery of gene markers that explain significant amounts of the additive variance of traits. However, to ensure their correct use in selection, it is important that the gene-marker effects are evaluated in the populations in which they are intended to be used and the size of effects, gene frequencies, and variance explained by the markers are accurately estimated for each population. This will enable genotypic information to be combined with the traditional systems of genetic evaluation (e.g., using animal model BLUP) to compute marker-assisted EBV (EBV\textsuperscript{M}). Heritability estimates are commonly plentiful in the literature, including many Australian studies, whereas information on gene-marker effects and gene frequencies are not yet plentiful, particularly from independent studies (see review by Van Eenennaam et al., 2007). Therefore, to allow the development of EBV\textsuperscript{M}, through the national genetic beef cattle evaluation scheme in Australia, BREEDPLAN, the study aimed to establish the gene frequencies, size of effects, and contribution to genetic variation of the 12 commercially available GeneSTAR markers (Catapult Genetics, Albion, Queensland, Australia; see complete detail in Catapult Genetics, 2006) for several economically important traits in a range of breeds and production systems from several well-recorded Australian beef cattle populations.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not required for this study because the data were obtained from existing phenotypic databases and DNA storage banks as described in the following.

Phenotypic Data Sets

The animals used in this study were genotyped as part of the SmartGene for Beef Project (Johnston and Graser, 2008) and were from 5 populations representing previous research experiments and industry progeny testing programs conducted over the past 2 decades. Mean unadjusted phenotypic performance and SD for the target traits (i.e., tenderness, marbling, and feed efficiency) are presented in Table 1 for each experiment. The number of records and available GeneSTAR genotypes were dependent on specific experiments and, therefore, theoretical statistical power to detect significant effects varied, but in general, the number of records was expected to be large enough to detect the effects of the markers as reported by the commercializing company (Catapult Genetics, 2006). The experiments are described in brief, with reference to the full experimental design and results. Particular emphasis is given on aspects of the experimental design pertaining to the collection of tenderness, marbling, and feed-intake phenotypes.

**Beef CRC1.** The data from Beef Cooperative Research Centre 1 database (CRC1) consisted of a straightbred temperate (TEMP) breed data set (i.e., Angus, Hereford, Murray Grey, and Shorthorn; n = 3,958) and a straightbred tropically adapted (TROP) breed data set (i.e., Brahman, Santa Gertrudis, and Belmont Red; n = 3,823). The basic design of the project and phenotypic and genetic parameters for these data have been described by Upton et al. (2001), Johnston et al. (2003), and Reverter et al. (2003). In brief, the progeny generated were born between 1993 and 1998 in 36 cooperator herds throughout eastern Australia. However, each herd only had one breed, so herd and breed were confounded. Genetic linkage across herd and years within a breed were generated through the use of common link sires. The total numbers of sires used were 232 and 163 for TEMP and TROP, respectively. Progeny (both steers and heifers) were purchased by the Cooperative Research Centre (CRC) at weaning and then backgrounded as cohorts in mixed-breed groups, finished (either feedlot or pasture), and slaughtered together at 1 of 3 target market carcass-weight endpoints [i.e., domestic (DOM) 220 kg, Korean (KOR) 280 kg, and Japanese (JAP) 340 kg].

Individual feed intake was recorded using automatic feeders on a subset of the feedlot-finished groups comprising 785 TEMP animals (steers only) and 687 TROP animals (steers and heifers). These animals were from all 3 markets, and the mean age and BW at the start of the feed test were 477 d and 377 kg for DOM, 612 d and 490 kg for KOR, and 636 d and 548 kg for JAP markets. The average number of days of recorded feed intake for DOM, KOR, and JAP market animals was 53, 57, and 74 d, respectively. For a full description of the feed intake data, see Robinson and Oddy (2004).

Slaughter occurred when the average of the cohort group reached the target BW (Reverter et al., 2003). All steers were handled preslaughter using industry best practice including controls on the slaughter procedures to minimize extraneous variation, particularly for tenderness traits. All carcasses were electrically stimulated and dressed in accordance with AUSMEAT standard specifications (AUSMEAT, 1998). Carcasses were placed in chillers within 1 h of stunning and were Achilles hung. The left side of each carcass was quartered at either the 12/13th or 10/11th rib, and chiller assessment was performed by trained CRC technicians and marbling score by certified Meat Standards Australia graders. At 24 h postmortem, a sample of the M. longissimus thoracis et lumborum (LTL) and M. semitendinosus (STN) muscles were taken and frozen for later meat-quality assessments (see Perry et al., 2001, for full details) including shear force measure on cooked samples (equating to approximately 2 d aging) on both muscles using Lloyd Instruments LRX Materials Testing Machine fitted with a 500-N load cell (Lloyd Instruments Ltd., Hampshire, UK). Intramuscular fat
percentage (IMF) was determined on a sample of the LTL using near-infrared spectroscopy technology (Technicon Infralyers 450, Bran and Luebbe, Homebush Bay, NSW, Australia) or Soxhlet extraction of fat in boiling chloroform for 24 h.

**Beef CRC2.** The data were from the Beef CRC2 (CRC2) northern breeding project (Burrow et al., 2003) using tropically adapted genotypes of straightbred Brahman (n = 2,047) and Tropical Composite (n = 2,399). The Tropical Composite cattle were from 3 large northern Australia breeding programs and were developed using approximately 50% tropically adapted breeds and 50% non-tropically adapted *Bos taurus* breeds. The complete experimental design is described in Barwick et al. (2009). In brief, calves were born over 4 yr from a total of 8 cooperators, and AI was used to generate linkage across properties of origin and year within a genotype. The total numbers of Brahman and Tropical Composite sires used in the experiment were 53 and 50, respectively. Each year, steers were assembled at weaning and allocated to a grow-out cohort group (n = 12) that was backgrounded at various locations throughout Queensland and northern New South Wales. At approximately 400 kg of BW, the cohort entered the feedlot. On average, the cohort groups were fed for 120 d and slaughtered as a single group when the average carcass weight of the cohort was predicted to be 320 kg. All steers were treated with the hormone growth promotant Compudose 200 (Elanco, West Ryde, Australia; active ingredient estradiol 17β) from weaning onward through to finishing. At feedlot entry, the steers were implanted with Compudose 100. Individual daily feed intake (DFI) was recorded on about two-thirds of the steers for an average of 71 d, and the average age at the start of test was 700 d (Barwick et al., 2009).

At slaughter, carcasses were dressed in accordance with AUSMEAT specifications, and because all steers were 120-d feedlot finished, the carcasses were not electrically stimulated, although a low-voltage rigidity probe was applied during hide pulling. Postslaughter, the carcasses were handled under the same protocols as Beef CRC1, with the exception that the right side of each carcass was normally hung from the Achilles tendon and the left side was transferred to tenderstretch hooks, which secured the side by the aitchbone. The tenderstretch process changes the tension on the muscles during cooling and affects meat tenderness, particularly of the greater value loin muscles (Hostetler et al., 2009).

### Table 1. Raw statistics for each trait and data set

| Data set and breed group | Trait | n  | Mean | SD  | Minimum | Maximum |
|--------------------------|-------|----|------|-----|---------|---------|
| **CRC1 TEMP**            | IMF   | 3,594 | 4.64 | 2.23 | 1.23    | 18.94   |
|                          | MARB  | 1,454 | 1.17 | 0.75 | 0.00    | 4.30    |
|                          | LTL_SF| 3,322 | 4.12 | 0.82 | 2.01    | 8.75    |
|                          | STN_SF| 3,357 | 4.78 | 0.72 | 2.80    | 7.56    |
|                          | DFI   | 785   | 12.84| 1.98 | 5.53    | 18.35   |
|                          | RFI   | 785   | 0.01 | 1.19 | 4.03    | 4.52    |
| **CRC1 TROP**            | IMF   | 3,524 | 2.88 | 1.41 | 0.08    | 13.19   |
|                          | MARB  | 1,808 | 0.76 | 0.62 | 0.00    | 3.80    |
|                          | LTL_SF| 3,254 | 4.55 | 0.94 | 2.34    | 8.92    |
|                          | STN_SF| 3,313 | 4.73 | 0.63 | 2.78    | 7.24    |
|                          | DFI   | 687   | 11.82| 1.99 | 6.51    | 18.67   |
|                          | RFI   | 687   | 0.00 | 1.01 | −3.92   | 3.10    |
| **CRC2 Brahman**         | IMF   | 972   | 2.37 | 0.87 | 0.31    | 6.72    |
|                          | MARB  | 983   | 0.61 | 0.40 | 0.10    | 2.40    |
|                          | LTL_SF| 957   | 5.38 | 1.16 | 2.55    | 9.00    |
|                          | TS_SF | 857   | 4.42 | 0.57 | 2.89    | 6.49    |
|                          | DFI   | 700   | 11.24| 1.94 | 5.97    | 17.88   |
|                          | RFI   | 680   | −0.18| 1.06 | −3.33   | 3.02    |
| **CRC2 Tropical Composite** | IMF   | 1,197 | 2.91 | 1.11 | 1.04    | 14.66   |
|                          | MARB  | 1,194 | 0.83 | 0.55 | 0.10    | 3.40    |
|                          | LTL_SF| 1,187 | 4.74 | 1.22 | 1.57    | 8.85    |
|                          | TS_SF | 1,040 | 3.91 | 0.53 | 2.41    | 6.00    |
|                          | DFI   | 787   | 13.10| 1.95 | 6.02    | 20.46   |
|                          | RFI   | 783   | 0.15 | 1.17 | −4.04   | 3.81    |
| **Progeny test Angus**   | MARB  | 415   | 1.92 | 0.74 | 0.60    | 4.60    |
|                          | DFI   | 387   | 14.57| 1.57 | 10.19   | 19.50   |
|                          | RFI   | 387   | −1.62| 1.38 | −5.35   | 3.12    |
| **Progeny test Shorthorn** | IMF   | 342   | 5.22 | 2.01 | 0.80    | 13.10   |
|                          | MARB  | 342   | 2.55 | 1.17 | 0.00    | 6.00    |
|                          | DFI   | 165   | 12.74| 1.42 | 7.84    | 15.70   |
|                          | RFI   | 165   | −1.142| 1.05 | −4.09   | 1.70    |

1CRC = Cooperative Research Centre database; TEMP = pooled temperate breeds (Angus, Hereford, Murray Grey, and Shorthorn); TROP = pooled tropically adapted breeds (Brahman, Santa Gertrudis, and Belmont Red).

2IMF = intramuscular fat (%); MARB = Meat Standards Australia marbling score measured on a 0 to 9 scale; LTL_SF = M. longissimus thoracis et lumborum (LTL) shear force (kg); STN_SF = M. semitendinosus shear force (kg); TS_SF = tenderstretch-hung LTL shear force (kg); DFI = daily feed intake (kg/d); RFI = residual feed intake (kg/d).
al., 1970). After 24 h postmortem, a sample of the LTL muscle from both sides was taken and frozen for later meat-quality assessments (as per Beef CRC1 protocols; Perry et al., 2001). The average carcass weights were 300 and 325 kg for Brahman and Tropical Composite, respectively. For a complete description of the design, methods, and analyses of carcass and meat-quality assessments, see Wolcott et al. (2009).

**Angus Australia Progeny Test.** These data were from the Angus Australia progeny test (PT) program conducted using the New South Wales Department of Primary Industry’s “Trangie” Angus herd (http://www.angusaustralia.com.au/BA_Trangie.htm). Three calf crops were generated during 2002 to 2004 using 13, 13, and 12 sires, respectively. All male calves were castrated, and carcass data of 415 progeny were available. After weaning, the steers were backgrounded at pasture, entered the feedlot at an average of 420 kg, and were fed for approximately 150 d to an average carcass weight of 370 kg. Residual feed intake (RFI) records were available on a total of 387 steers on which individual feed intake was recorded for an average of 70 d, with an average age at the start of test of 535 d. All steers within a cohort (i.e., year and location) were slaughtered at the same time, and carcass and chillier assessment traits were recorded. The phenotypic data were recorded in the National Beef Recording Scheme database, and an extract was obtained for this study. Genotypic data on the 12 GeneSTAR markers were provided by Angus Australia.

**Shorthorn Beef Progeny Test.** Data were available from the PT program conducted by the Durham Research and Development Project of Shorthorn Beef (for complete details, see http://www.durhamresearch.com.au/). Straightbred Shorthorn steers (n = 342) were used in this study and were from the first 3 yr of the project that had complete carcass records, including marbling phenotypes. Individual feed intake was recorded on a subset of these steers (n = 165) at the Beef CRC Tullimba research feedlot, and this subset represented the domestic market finished steers from that project. Mean age and BW of the steers at the start of the feed intake test were 392 d and 398 kg, respectively. Feed intake was recorded for a standard 70 d. All steers were slaughtered, and abattoir chiller traits were recorded. All data were available through the Durham Project and the Shorthorn National Beef Recording Scheme database.

**Trait Definitions**

**Meat Tenderness.** Three traits were examined as dependent variables of tenderness: shear force of LTL muscle that was normal hung (LTL_SF), shear force of LTL that was tenderstretch hung (TS_SF), and shear force of STN muscle (STN_SF). Phenotypic records of LTL_SF and STN_SF were available for CRC1 on both steers and heifers. For CRC2, the traits LTL_SF and TS_SF were recorded on steers only. For CRC1, the data edits and models were as described by Johnston et al. (2003) and included fixed effects for herd of origin, sex, kill group, and carcass weight as a linear covariate. Herd of origin accounted for the effect of breed, and kill group accounted for market and finishing regimen. For CRC2, models were described by Wolcott et al. (2009) and included main effects and interactions of property of origin, month of birth, age of dam, feedlot cohort, and kill date. For Tropical Composite, additional fixed-effects terms were included for sire and dam breed groups and their interaction to account for the average additive difference between the composite groups and possible differences in the heterosis in combinations of sire and dam groups. It is important to note that hormone growth promotant implants were used on all CRC2 steers, and no electrical stimulation was applied.

**Marbling Traits.** Two traits were examined as dependent variables of marbling: IMF, determined by near-infrared spectroscopy or ether extract, and Meat Standards Australia marbling score (MARB) measured on a 0 to 9 scale with 0.1 gradations. Phenotypic records were available from CRC1, CRC2, Shorthorn PT for both traits, and only MARB for Angus PT (Table 1). Records were on steer carcasses with the exception of CRC1, which also included heifers. The CRC1 data were recorded on a combination of animals slaughtered for DOM, KOR, and JAP markets in which age, carcass weight, IMF, and MARB were reported to increase over market endpoints from DOM to JAP (Reverter et al., 2003). Models for analyzing CRC1 MARB and IMF were described by Johnston (2001) and Reverter et al. (2003) and included fixed effects for herd of origin, sex, kill group, and carcass weight as a linear covariate.

For CRC2 data, the models were described by Wolcott et al. (2009) and included the same set of fixed effects described earlier for LTL_SF. All animals were feedlot finished (120 d on feed) to a single market endpoint (approximately 320-kg carcass weight).

Analyses of PT data were done separately for each breed. The fixed-effect models included a single contemporary group effect as defined by BREEDPLAN for abattoir carcass traits (Graser et al., 2005), and slaughter age or carcass weight was included as a linear covariate.

**Feed-Intake Traits.** Two traits were examined as dependent variables of feed efficiency (i.e., RFI and DFI). Phenotypic records were available for all 5 data sets (Table 1) and were recorded on steers, except for CRC1, which also included TROP heifers. For CRC1 data, the derivation of RFI and models for analysis were described by Robinson and Oddy (2004). For CRC2, RFI was derived using methods described by Barwick et al. (2009), and models for analyzing RFI and DFI included fixed effects and interactions of property of origin, month of birth, age of dam, feedlot cohort, and for Tropical Composite, terms for sire and dam breed groups (as described previously). Angus and Shorthorn PT data were initially processed through the
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New South Wales Department of Primary Industries Trangie Research station service before being forwarded to the National Beef Recording Scheme databases. The derivation and models for analysis of RFI and DFI were as defined for BREEDPLAN and included a single fixed effect for contemporary group, and age at the start of test was included as a linear covariate. The contemporary group for both traits included test station, sex, feed-test start date, feed-test management group, prefeedlot management group, and 60 d age slicing interval.

**Trait Genetic Variation.** A description of the additive genetic variances and heritabilities for each trait and data set is presented in Table 2 and shows a range in the estimates across the traits and data sets. In general, the marbling traits were moderate to highly heritable; the feed-intake traits were also moderate, with reduced estimates in the CRC1 data sets. For tenderness, the estimates were moderate in CRC2 and CRC1 TROP but considerably less in CRC1 TEMP.

**Genotypic Data**

Genotypic data on each animal was supplied by Catapult Genetics for the 12 commercially available markers using stored DNA samples from the 5 populations. Four GeneSTAR markers were tested for each of tenderness, marbling, and feed efficiency. Genotypic results for each animal were received for each marker as 0, 1, or 2 copies of the marker allele; this was predetermined by the company. Any genotype that failed to be called was coded as NR (i.e., no result). Descriptions of each of the tenderness markers (T1, T2, T3, T4), the marbling markers (M1, M2, M3, M4), and the feed-efficiency markers (N1, N2, N3, N4) are presented in Table 3. Comparing results across published studies is difficult due to different nomenclature when referring to these gene markers. Also, differences can occur in the genotype reported depending on whether the reverse strand has been used, and in some cases, the alleles are reported only as number of stars. Table 3 provides a summary of the existing nomenclature to allow comparison and discussion of our results with other studies.

**Statistical Analysis**

Gene-marker frequencies for each breed and gene marker were estimated using the genotype data, and test of deviation from Hardy-Weinberg equilibrium (HWE) was performed and tested against their expectations using the chi-squared test statistic on 1 df. The additive effects of the gene markers were estimated by fitting the 4 markers as linear covariates (i.e., 0, 1, or 2 copies of the marker allele) using the Proc Mixed procedure (SAS Inst. Inc., Cary, NC). The 4 markers were fitted jointly along with the fixed effects and covariates described previously for each experiment and trait. Sire was included as a random effect with no relationships. For all analyses, all available phenotypes were used, including those from animals with missing genotypes (i.e., not genotyped or failed genotyping). These records were included by adding a term to the model describing, for each individual, if it had a genotype known for a given marker (i.e.,

Table 2. Summary of additive variances (Va) and heritabilities (h²) and approximate SE (in parentheses) for traits across data sets with reference to available publications1,2

| Trait            | Effect | TEMP         | TROP          | CRC2 | Prolificity test |
|------------------|--------|--------------|---------------|------|------------------|
|                  |        | Brahman      | Tropical      | Angus| Shorthorn        |
|                  |        |              | Composite     |      |                  |
| LTL_SF           |        | 0.04B        | 0.19B         | 0.37B| 0.35B            | —                |
|                  |        | 0.09 (0.02)  | 0.30 (0.04)   | 0.33 (0.10) | 0.32 (0.10)   | —                |
| STN_SF           |        | 0.03B        | 0.13B         | —    | —                | —                |
|                  |        | 0.11 (0.02)  | 0.42 (0.04)   | —    | —                | —                |
| IMF              |        | 0.80B        | 0.37B         | 0.13B| 0.62B            | —                |
|                  |        | 0.38         | 0.39          | 0.26 (0.10) | 0.64 (0.18)   | 0.19 (0.13)     |
| MARB             |        | 0.09         | 0.10          | 0.02B| 0.09B            | —                |
|                  |        | 0.36 (0.08)  | 0.36 (0.09)   | 0.17 (0.08) | 0.35 (0.10)   | 0.24 (0.16)     |
| RFI              |        | 0.14         | 0.12          | 0.19B| 0.41B            | 0.49 (0.16)     |
|                  |        | 0.16 (0.11)  | 0.18 (0.12)   | 0.24 (0.11) | 0.38 (0.12)   | 0.49 (0.22)     |
| DFI              |        | 0.92         | 0.23          | 1.39B| 1.72B            | 0.37 (0.16)     |
|                  |        | 0.39 (0.14)  | 0.10 (0.12)   | 0.49 (0.15) | 0.51 (0.14)   | 1.26             |
|                  |        | 0.56 (0.16)  | 0.40 (0.24)   |      |                  |                  |

1A = Johnston et al., 2003; B = Wolcott et al., 2009; C = Reverter et al., 2003; D = Barwick et al., 2009.

2CRC = Cooperative Research Centre database; TEMP = pooled temperate breeds (Angus, Hereford, Murray Grey, and Shorthorn); TROP = pooled tropically adapted breeds (Brahman, Santa Gertrudis, and Belmont Red).

3LTL_SF = M. longissimus thoracis et lumborum shear force; STN_SF = M. semitendinosus shear force; IMF = intramuscular fat (%); MARB = Meat Standards Australia marbling score; RFI = residual feed intake; DFI = daily feed intake.
yes or no), and then the marker genotype was fitted nested within “yes.” For “no,” this included all animals with missing genotypes and where fitted, were nested within breed. Missing marker genotypes were included to avoid significant loss of data, particularly for models in which all 4 markers were included. Animals with a phenotype, but a missing genotype, were included and nested within breed due to the large differences in gene frequencies commonly observed across the breeds.

The tenderness markers (T1 to T4) were tested against the dependent variables of LTL_SF, STN_SF, and TS_SF. The marbling markers (M1 to M4) were tested on IMF and MARB, and finally, the 4 feed-efficiency markers (N1 to N4) were tested for their effects on RFI and DFI.

For the CRC1 experiment, each of the breeds was analyzed separately and also pooled within line (i.e., TEMP and TROP). For all analyses, the significance of each marker was determined by an \( F \)-test statistic on 1 df \( (P < 0.05) \), and estimated partial regression coefficients and their SE were obtained for each marker. Markers that were estimated to have significant effects were further analyzed to quantify the amount of variance explained when fitting the markers. Analyses were performed with ASReml (Gilmour et al., 2004) using a single-trait animal model to estimate the additive genetic and phenotypic variances for each trait, with and without inclusion of the markers. The fixed-effect models were as described previously, and a relationship matrix was constructed using up to 3 generations of pedigree when available. Estimates of the additive variance and residual variance were summed to obtain an estimate of the phenotypic variance and the heritability. The difference in the variances from models with and without markers fitted was computed to give the percentage of additive variance explained by the markers (i.e., \( R^2 \)), and its square root provided estimates of the genetic correlation of the combined effects of the markers and the trait.

**RESULTS**

Call rates of the 12 markers were summarized to assess differences between markers and data sets. For CRC1, 63.7% of the 6,824 animals had all 12 markers scored, whereas 3.2% had 5 or more markers with noncalled genotypes. Of the 12 markers, most had a call rate of around 95%; however, there were 2 exceptions: T2 at 85% (i.e., NR = 15%) and M2 at 82%. In CRC2, only 56.2% of animals had all 12 markers scored, whereas 7.2% had 5 or more missing markers. Across the 12 markers, most had a call rate of around 95%; however, there were 2 exceptions: T2 at 75% and M2 at 81%. In the Angus PT data, 76% of animals had all 12 markers scored, and only 1% had 5 or more markers missing. Of the 12 markers, most had a call rate of around 98%; however, there were 2 exceptions: T3 at 84% and M2 at 92%. For Shorthorn PT data, the markers had call rates greater than 96%, except for N1, which had a 71% call rate with only one animal scored with a 0-star genotype and 129 animals with the 1-star genotype.

**Table 3.** Description of the 12 GeneSTAR markers,\(^1\) including variations in SNP names

| GeneSTAR marker | SNP name(s) | Gene containing SNP | Star assignment | Key reference |
|-----------------|-------------|---------------------|----------------|--------------|
| T1              | CAST:c2832A>G | Calpastatin (CAST) | 0 = GG, 1 = AG, 2 = AA | Barendse, 2002 |
| T2              | CAPN1–316      | Micromolar calcium activated neutral protease (CAPN1) | 0 = GG, 1 = CG, 2 = CC | Page et al., 2002 |
| T3              | CAPN1–4751   | CAPN1 | 0 = TT, 1 = CT, 2 = CC | White et al., 2005 |
| T4              | CALN3:c.1538+225G>T | CAPN3 | 0 = TT, 1 = GT, 2 = GG | Barendse et al., 2008 |
| M1              | TG5 | Thyroglobulin | 0 = CC, 1 = CT, 2 = TT | Barendse et al., 1999 |
| M2, M3, M4      | Anonymous SNP | Unknown | Unknown | None |
| N1, N2, N3, N4  | Anonymous SNP | Unknown | Unknown | Barendse et al., 2007b |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. T1 to T4 = tenderness markers; M1 to M4 = marbling markers; N1 to N4 = feed-efficiency markers.
Table 4. Number of animals with GeneSTAR genotypes and phenotypes for the 12 GeneSTAR markers\(^1\) by data set and breed\(^2\)

| Data set and breed\(^3\) | LTL_SF | IMF | RFI |
|--------------------------|--------|-----|-----|
|                          | T1     | T2  | T3  | T4  | M1  | M2  | M3  | M4  | N1  | N2  | N3  | N4  |
| CRC1                     |        |     |     |     |     |     |     |     |     |     |     |     |
| Angus                    | 1,111  | 931 | 1,106| 1,103| 1,167| 1,033| 1,212| 1,205| 318 | 303 | 305 | 311 |
| Hereford                 | 793    | 718 | 782  | 801  | 869 | 810 | 904 | 901  | 225 | 225 | 221 | 224 |
| Murray Grey              | 338    | 314 | 332  | 340  | 374 | 322 | 394 | 391  | 82  | 81  | 80  | 82  |
| Shorthorn                | 357    | 316 | 347  | 355  | 396 | 353 | 367 | 385  | 108 | 99  | 100 | 100 |
| TEMP                     | 2,599  | 2,279| 2,567| 2,590| 2,779| 2,518| 2,877| 2,882| 733 | 708 | 706 | 717 |
| Progeny test             |        |     |     |     |     |     |     |     |     |     |     |     |
| Angus                    | —      | —   | —    | —    | 382 | 355 | 399 | 397  | 370 | 370 | 369 | 368 |
| Shorthorn                | —      | —   | —    | —    | 328 | 342 | 340 | 333  | 112 | 161 | 160 | 160 |
| CRC1                     |        |     |     |     |     |     |     |     |     |     |     |     |
| Brahman                  | 759    | 583 | 749  | 759  | 806 | 616 | 807 | 811  | 132 | 133 | 133 | 133 |
| Belmont Red              | 1,243  | 1,100| 1,232| 1,239| 1,306| 1,169| 1,347| 1,341| 294 | 282 | 282 | 290 |
| Santa Gertrudis          | 1,023  | 931 | 1,026| 1,023| 1,104| 938 | 1,131| 1,128| 238 | 236 | 231 | 236 |
| TROP                     | 3,025  | 2,614| 3,007| 3,021| 3,216| 2,723| 3,285| 3,280| 664 | 651 | 646 | 659 |
| CRC2                     |        |     |     |     |     |     |     |     |     |     |     |     |
| Tropical Composite       | 1,103  | 848 | 1,072| 1,097| 1,108| 990 | 1,122| 1,111| 714 | 739 | 739 | 739 |
| Brahman                  | 888    | 742 | 876  | 886  | 905 | 716 | 922 | 901  | 631 | 641 | 640 | 639 |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. T1 to T4 = tenderness markers; M1 to M4 = marbling markers; N1 to N4 = feed-efficiency markers.

\(^2\)LTL_SF = M. longissimus thoracis et lumborum shear force; IMF = intramuscular fat (%); RFI = residual feed intake.

\(^3\)CRC = Cooperative Research Centre database; TEMP = pooled temperate breeds (Angus, Hereford, Murray Grey, and Shorthorn); TROP = pooled tropically adapted breeds (Brahman, Belmont Red, and Santa Gertrudis).
**Tenderness Markers**

Gene frequencies of the tenderness markers and HWE tests are presented in Tables 5 and 6. Temperate breeds had gene frequencies that were intermediate (0.30 to 0.70) to high (>0.70) for favorable alleles, except for Shorthorns (both CRC1 and PT data sets), for which extreme frequencies (>0.95 or <0.05) were estimated for all 4 markers. Gene frequencies were similar across breed samples from different data sets (i.e., Brahman CRC1 and CRC2, Angus CRC1 and PT, Shorthorn CRC1 and PT, CRC1 Belmont Red and CRC2 Tropical Composite). There were, however, some differences between Angus data sets for T2 and T3 and between Belmont Red data sets for T2 and T4. Estimates of HWE for the tenderness markers showed most gene frequencies within a breed were not significantly different from expectations, but this was not always the case when pooled across breeds (e.g., tenderness markers for CRC1 TROP).

Estimated size of effects of the 4 tenderness markers on LTL_SF is presented in Table 7. The expectation of each of the tenderness markers was that they would have a negative direction of effect on LTL_SF (i.e., increasing number of stars; 0 to 1 to 2 copies) associated with decreasing LTL_SF (i.e., improved meat tenderness). The effects of the T1 marker on LTL_SF were significant in all data sets and had consistently negative estimates (range −0.13 to −0.19 kg/w), with the exception of the nonsignificant Shorthorn CRC1 result. The effects of the T2 were significant in CRC2 Tropical Composite (−0.22 kg) and the CRC1 TEMP (−0.09 kg) and TROP (−0.17 kg) data sets, with estimates within CRC1 breeds ranging between −0.15 and −0.20 kg. The T2 marker was not significant in Hereford (P = 0.42) and CRC2 Brahman (P = 0.87), in which this marker was also estimated not to be in HWE in these breeds. Marker T3 did not have a significant effect (P < 0.05) in any of the CRC1 temperate breeds. However, in the tropical breed data sets, estimated effects of T3 were significant in CRC1 TROP (−0.12 kg), and sizes of effects within breed for CRC1 Belmont Red (−0.10 kg) and Santa Gertrudis (−0.11 kg) were smaller in magnitude compared with the effects for Brahman in CRC1 (−0.18 kg) and CRC2 (−0.27 kg). The T4 was significant in CRC1 Santa Gertrudis (0.13 kg; P < 0.01) and Brahman (−0.11 kg; P = 0.03) and not significant (P > 0.05) in any of the other breeds or in the pooled TEMP and TROP data sets, including no significant effects in CRC2 Brahman (−0.01 kg; P = 0.86) or Tropical Composite (0.03 kg; P = 0.59).

The effect of tenderstretching carcasses in CRC2 populations was that the tenderness markers were still significant, but the sizes of effects were generally halved. For T1, the estimated effects were −0.06 and −0.07 kg TS_SF for Brahman and Tropical Composite, respectively. Marker T2 in Tropical Composite reduced to −0.08 kg TS_SF and marker T3 in Brahman reduced to −0.15 kg TS_SF.

Effects of the tenderness markers on STN_SF are presented in Table 8. For CRC1 pooled TEMP, none of the markers had significant effects (P < 0.05), although T2 was significant (P < 0.10), with a −0.04-kg estimated effect. Within the temperate breeds, the only significant marker (P = 0.02) on STN_SF was T1 in Angus, with a −0.10-kg effect. For CRC1 TROP, T1 and T2 were significant for STN_SF, with −0.05- and −0.08-kg effects, respectively, and T4 approached significance (P = 0.08), with a 0.04-kg estimated size of effect. Within CRC1 tropical breeds, T1 effects were similar in direction and magnitude, but none was significant (P < 0.05) for the 3 breeds. For T2, the effects of this marker were significant for Santa Gertrudis and Belmont Red breeds (−0.15 and −0.06 kg, respectively). The T3 and T4 markers were significant (P < 0.05) only for Brahman, with −0.13- and +0.10-kg effects on STN_SF, respectively.

Additive genetic and phenotypic variances estimated with and without the tenderness markers fitted are presented for LTL_SF in Table 9 and for STN_SF in Table 10. In general, heritability estimates for LTL_SF and STN_SF were moderate, except for the smaller estimates of 8 and 10% for CRC1 TEMP. These estimates are in close agreement with the published results in Table 2, with slight differences likely due to differences in the methods of estimation used (i.e., univariate vs. multivariate). Inclusion of the 4 tenderness markers reduced the additive genetic variance of LTL_SF between 7.4 and 17.2%, representing an approximate genetic correlation (i.e., square root of genetic variance explained) of the combined effects of the markers and the trait of between 0.27 and 0.41. The combined effects of the 4 tenderness markers on the phenotypic variance of LTL_SF ranged between 1.5 and 4.7%. In CRC2 populations, the process of tenderstretching greatly reduced the additive genetic and the phenotypic variances of LTL_SF. The additive genetic variance explained by the markers in Brahman was small (1.8%), but for Tropical Composite, the markers explained 22.9% of the additive genetic variance. The variances explained by the combined effects of the 4 tenderness markers on STN_SF were 4.1 and 8.5% of the additive genetic variance in CRC1 TROP and TEMP, respectively.

**Marbling Markers**

Gene frequencies of the marbling markers and test of HWE are presented in Tables 5 and 6. For temperate breeds, the gene frequencies of the favorable allele were low (i.e., less than 0.30) for all marbling markers, particularly M2 and M3. There were similar frequencies for breeds in the tropical data sets except for M2, which was at more intermediate frequencies and were at high frequencies in Brahman (0.75 and 0.80) for the CRC1 and CRC2 populations. Estimates of HWE for the marbling markers showed that most were not significantly different (P < 0.05) from their expectation except for M2, which differed significantly (P < 0.05) from its
Table 5. Number of animals by genotype and estimated allele frequencies of 2-star allele for the 12 GeneSTAR markers\(^1\) by data set and breed

| Data set and breed\(^2\) | Variable\(^3\) | T1  | T2  | T3  | T4  | M1  | M2  | M3  | M4  | N1  | N2  | N3  | N4  |
|--------------------------|-----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| CRC1                     | AN              | 1,308 | 1,111 | 1,294 | 1,301 | 1,253 | 1,099 | 1,303 | 1,294 | 1,312 | 1,268 | 1,251 | 1,293 |
|                          | q               | 0.876 | 0.434 | 0.808 | 0.909 | 0.248 | 0.191 | 0.094 | 0.257 | 0.883 | 0.781 | 0.566 | 0.564 |
|                          | HE              | 991 | 904 | 975 | 1,000 | 955 | 885 | 990 | 989 | 933 | 971 | 948 | 979 |
|                          | q               | 0.824 | 0.212 | 0.813 | 1.000 | 0.127 | 0.016 | 0.097 | 0.197 | 0.865 | 0.960 | 0.590 | 0.455 |
|                          | SH              | 417 | 362 | 494 | 415 | 398 | 377 | 396 | 413 | 417 | 400 | 397 | 400 |
|                          | q               | 0.993 | 0.014 | 0.051 | 0.964 | 0.142 | 0.023 | 0.045 | 0.276 | 0.865 | 0.976 | 0.542 | 0.819 |
|                          | MG              | 420 | 389 | 414 | 421 | 396 | 340 | 418 | 416 | 421 | 411 | 403 | 417 |
|                          | q               | 0.868 | 0.518 | 0.791 | 0.849 | 0.361 | 0.181 | 0.043 | 0.132 | 0.932 | 0.555 | 0.510 | 0.311 |
|                          | TEMP            | 3,136 | 2,766 | 3,087 | 3,137 | 3,002 | 2,701 | 3,107 | 3,112 | 3,112 | 3,050 | 2,999 | 3,089 |
|                          | q               | 0.874 | 0.319 | 0.708 | 0.937 | 0.210 | 0.110 | 0.082 | 0.224 | 0.882 | 0.833 | 0.563 | 0.528 |
|                          | PT              | 727 | 728 | 625 | 715 | 684 | 742 | 738 | 741 | 737 | 735 | 736 | 736 |
|                          | q               | 0.922 | 0.242 | 0.646 | 0.949 | 0.345 | 0.278 | 0.147 | 0.201 | 0.834 | 0.855 | 0.656 | 0.541 |
|                          | SH              | 343 | 347 | 340 | 345 | 333 | 347 | 345 | 338 | 248 | 342 | 338 | 340 |
|                          | q               | 0.974 | 0.020 | 0.087 | 0.957 | 0.134 | 0.003 | 0.035 | 0.272 | 0.736 | 0.955 | 0.441 | 0.731 |
|                          | CRC1            | 864 | 656 | 853 | 864 | 859 | 654 | 860 | 864 | 866 | 860 | 859 | 863 |
|                          | q               | 0.572 | 0.039 | 0.173 | 0.524 | 0.011 | 0.750 | 0.003 | 0.050 | 0.908 | 0.990 | 0.957 | 0.782 |
|                          | SG              | 1,214 | 1,096 | 1,216 | 1,212 | 1,198 | 1,021 | 1,226 | 1,223 | 1,221 | 1,224 | 1,189 | 1,218 |
|                          | q               | 0.718 | 0.263 | 0.351 | 0.760 | 0.051 | 0.416 | 0.005 | 0.048 | 0.895 | 0.953 | 0.784 | 0.771 |
|                          | BE              | 1,460 | 1,289 | 1,451 | 1,452 | 1,412 | 1,267 | 1,447 | 1,446 | 1,454 | 1,436 | 1,417 | 1,446 |
|                          | q               | 0.775 | 0.426 | 0.593 | 0.931 | 0.049 | 0.315 | 0.076 | 0.136 | 0.741 | 0.953 | 0.646 | 0.665 |
|                          | TROP            | 3,538 | 3,041 | 3,520 | 3,528 | 3,469 | 2,942 | 3,533 | 3,533 | 3,541 | 3,520 | 3,465 | 3,537 |
|                          | q               | 0.706 | 0.284 | 0.408 | 0.773 | 0.040 | 0.446 | 0.034 | 0.084 | 0.835 | 0.962 | 0.770 | 0.730 |
|                          | CRC2            | 2,256 | 1,751 | 2,193 | 2,239 | 2,230 | 1,994 | 2,275 | 2,245 | 2,213 | 2,273 | 2,270 | 2,276 |
|                          | q               | 0.730 | 0.241 | 0.438 | 0.777 | 0.076 | 0.319 | 0.068 | 0.114 | 0.794 | 0.981 | 0.753 | 0.714 |
|                          | BR              | 1,955 | 1,584 | 1,914 | 1,946 | 1,935 | 1,577 | 1,964 | 1,949 | 1,952 | 1,965 | 1,959 | 1,960 |
|                          | q               | 0.647 | 0.038 | 0.163 | 0.444 | 0.016 | 0.801 | 0.003 | 0.047 | 0.922 | 0.992 | 0.951 | 0.842 |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. T1 to T4 = tenderness markers; M1 to M4 = marbling markers; N1 to N4 = feed-efficiency markers.

\(^2\)CRC = Cooperative Research Centre database; PT = progeny test program; AN = Angus; HE = Hereford; SH = Shorthorn; MG = Murray Grey; BR = Brahman; SG = Santa Gertrudis; BE = Belmont Red; TC = Tropical Composite; TEMP = pooled temperate breeds (AN, HE, SH, and MG); TROP = pooled tropically adapted breeds (BR, SG, and BE).

\(^3\)n = total number with a genotype; q = gene frequency of favorable 2-star allele (as defined by Catapult Genetics).
Table 6. Expected numbers by genotypes under Hardy-Weinberg equilibrium and significance of deviation from equilibrium ($\chi^2$) for the 12 GeneSTAR markers by breed and data set

| Data set and breed | Item | T1  | T2  | T3  | T4  | T5  | T6  | T7  | T8  | T9  | T10 | T11 | T12 | N1  | N2  | N3  | N4  |
|-------------------|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| CRC1              | AN   | 0.737 | 0.514 | 0.992 | 0.849 | 0.016* | 0.459 | 0.904 | 0.389 | 0.404 | 0.427 | 0.862 | 0.008* | 0.008* | 0.008* | 0.008* |
|                   | HE   | 0.037* | 0.032* | 0.979 | —   | 0.774 | 0.892 | 0.282 | 0.453 | 0.149 | 0.427 | 0.512 | 0.165 | 0.037* | 0.032* | 0.979 | —   |
|                   | SH   | 0.989 | 0.965 | 0.129 | 0.747 | 0.262 | 0.905 | 0.392 | 0.831 | 0.854 | 0.248 | 0.771 | 0.142 | 0.037* | 0.032* | 0.979 | —   |
|                   | MG   | 0.611 | 0.302 | 0.950 | 0.618 | 0.352 | 0.012* | 0.965 | 0.761 | 0.773 | 0.112 | 0.400 | 0.364 | 0.037* | 0.032* | 0.979 | —   |
|                   | TEMP | 0.365 | 0.000* | 0.000* | 0.533 | 0.868 | 0.590 | 1.000 | 0.608 | 0.055 | 0.000* | 0.931 | 0.439 | 0.365 | 0.000* | 0.000* | 0.533 |
|                   | PT   | 0.772 | 0.322 | 0.980 | 0.995 | 0.929 | 0.011* | 0.809 | 0.077 | 0.000* | 0.984 | 0.008* | 0.892 | 0.077 | 0.000* | 0.984 | 0.008* |
|                   | SH   | 0.001* | 0.029 | 0.956 | 0.904 | 1.000 | 0.999 | 0.000* | 0.016* | 0.000* | 0.016* | 0.765 | 0.444 | 0.001* | 0.029 | 0.956 | 0.904 |
|                   | CRC1 | 0.961 | 0.585 | 0.937 | 0.998 | 0.948 | 0.008* | 0.996 | 0.436 | 0.625 | 0.953 | 0.508 | 0.819 | 0.961 | 0.585 | 0.937 | 0.998 |
|                   | SG   | 0.999 | 0.848 | 0.076 | 0.849 | 0.998 | 0.778 | 0.983 | 0.208 | 0.904 | 0.554 | 0.759 | 0.977 | 0.999 | 0.848 | 0.076 | 0.849 |
|                   | BE   | 0.655 | 0.130 | 0.938 | 0.484 | 0.937 | 0.000* | 0.873 | 0.995 | 0.026* | 0.170 | 0.000* | 0.000* | 0.655 | 0.130 | 0.938 | 0.484 |
expectation in 4 breeds. This suggests a possible issue with the assigning of genotypes for this marker as indicated by the greater failure rate or possible violation of the underlying assumptions of HWE.

Estimated sizes of effects for the 4 marbling markers are presented in Table 11 for IMF and Table 12 for MARB. In general, none of the markers had significant effects (P < 0.05) on either IMF or MARB. There was no consistent direction of effects of the markers, with both positive and negative regression estimates for IMF and MARB. For Herefords, the effect of M1 on IMF was significant, with an estimate of −0.25% IMF/M1 star (i.e., opposite the claimed direction), and for Santa Gertrudis, M4 was estimated to have a significant positive effect on MARB (0.24 score/M4 star).

Feed-Efficiency Markers

Gene frequencies of the feed-efficiency markers and HWE test are presented in Tables 5 and 6. In all populations and breeds, gene frequencies were high to very high (>0.95) for the favorable alleles, especially for N1 and N2 in tropical data sets and N3 for Brahman. Gene frequencies were similar across breed samples from different data sets within this study (i.e., CRC1 Brahman and CRC2 Brahman, CRC1 Angus and Angus PT, CRC1 Shorthorn and Shorthorn PT, CRC1 Belmont Red and CRC2 Tropical Composite), except for Shorthorn PT, which were all slightly less, particularly N1, compared with the CRC1 Shorthorn population. In this case, the increased number of noncalled N1 genotypes in the PT indicates a possible problem of assigning the 0-star allele in this data set. Estimates of HWE for the feed-efficiency markers by breeds were generally not significantly different (P > 0.05) from their expectations; the exceptions were for 3 of the 4 markers in CRC1 Belmont Red and 2 of the markers in Angus and Shorthorn PT data sets. For the CRC1 TEMP population, the N3 marker was significant (P = 0.01), with an estimated coefficient of −0.14 kg/d per N3 star, and the N4 marker was also negative and significant (P < 0.10). The direction of the effects of the N1 and N2 markers was negative but smaller in magnitude than N3 and not significant (P = 0.36 and P = 0.45, respectively) for the favorable alleles.

| Item | T1 | T2 | T3 | T4 | M1 | M2 | M3 | M4 | N1 | N2 | N3 | N4 |
|------|----|----|----|----|----|----|----|----|----|----|----|----|
| TROP | χ² | 0.526 | 0.000* | 0.000* | 0.829 | 0.074 | 0.311 | 0.454 | 0.000* | 0.165 | 0.000* | 0.092 |
| 0    | 306 | 1,560 | 1,256 | 182 | 3,196 | 901 | 3,305 | 2,961 | 96 | 5 | 183 | 258 |
| 1    | 1,469 | 1,236 | 1,700 | 1,239 | 268 | 1,454 | 231 | 547 | 976 | 259 | 1,228 | 1,394 |
| 2    | 1,763 | 245 | 585 | 2,106 | 6 | 586 | 4 | 25 | 2,468 | 3,256 | 2,057 | 1,886 |
| CRC2 TC | χ² | 0.962 | 0.145 | 0.721 | 0.054 | 0.673 | 0.781 | 0.540 | 0.619 | 0.807 | 0.978 | 0.950 | 1.000 |
| 0    | 164 | 1,008 | 693 | 111 | 1,903 | 924 | 1,975 | 1,761 | 94 | 1 | 138 | 187 |
| 1    | 899 | 641 | 1,080 | 776 | 314 | 867 | 290 | 454 | 724 | 84 | 844 | 930 |
| 2    | 1,202 | 102 | 421 | 1,352 | 13 | 203 | 11 | 29 | 1,395 | 2,188 | 1,288 | 1,159 |
| BR   | χ² | 0.777 | 0.000* | 0.947 | 0.499 | 0.787 | 0.338 | 0.991 | 0.520 | 0.857 | 0.944 | 0.556 | 0.464 |
| 0    | 243 | 1,465 | 1,340 | 602 | 1,875 | 62 | 1,952 | 1,717 | 12 | 4 | 55 | 49 |
| 1    | 893 | 116 | 523 | 961 | 9 | 502 | 12 | 174 | 279 | 30 | 183 | 531 |
| 2    | 819 | 2 | 51 | 383 | 0 | 1,012 | 0 | 4 | 1,661 | 1,935 | 1,771 | 1,391 |

1GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. T1 to T4 = tenderness markers; M1 to M4 = marbling markers; N1 to N4 = feed-efficiency markers.
2CRC = Cooperative Research Centre database; PT = progeny test program; AN = Angus; HE = Hereford; SH = Shorthorn; MG = Murray Grey; BR = Brahman; SG = Santa Gertrudis; BE = Belmont Red; TC = Tropical Composite; TEMP = pooled temperate breeds (AN, HE, SH, and MG); TROP = pooled tropically adapted breeds (BR, SG, and BE).
3The numbers 0, 1, and 2 indicate copies of the favorable allele (referred to as stars).
*P < 0.05.
tive regression estimate (0.57 kg/d). For the other data sets, the 4 markers were not significant; however, N1 in CRC2 Tropical Composite was significant (\(P < 0.10\)), with a −0.12 kg/d estimate. Within CRC1 TROP, the N4 marker in Santa Gertrudis was significant (\(P < 0.10\)), with a −0.19 kg/d effect.

Estimated effects of the markers on DFI generally reflected the results for RFI. For CRC1 TEMP, N3 and N4 had significant negative (\(P = 0.03\) and \(P = 0.03\)) effects on DFI: −0.19 and −0.21 kg/d, respectively. However, for CRC1 TROP, N3 and N4 were significant (\(P < 0.10\)), with estimated effects of −0.18 and +0.19 kg/d, respectively. Further examination of breeds with CRC1 TEMP showed estimates with large SE as a result of the smaller number of records and greater gene frequencies. However, there were some significant results; marker N1 was significant with a negative estimate in Murray Grey (−2.00 kg/d; \(P = 0.01\)) and was consistent with the effect seen in this breed for RFI. For marker N3, the significant effect in CRC1 TEMP was mainly the result of Herefords, with a significant (\(P = 0.02\)) and large negative estimate (−0.44 kg/d) but with small and nonsignificant effects in the other 3 temperate breeds. Similarly, for breeds within CRC1 TROP, the Belmont Red had a significant and negative (−0.29 kg/d; \(P = 0.03\)) effect, but no significant effects were observed for Brahman or Santa Gertrudis. For N4, all CRC1 temperate breeds had negative nonsignificant effects.

Table 7. Estimated effects (b) of the 4 GeneSTAR tenderness markers\(^1\) (fitted jointly) on M. longissimus thoracis et lumbrorum shear force (kg) and tenderstretch shear force (kg) from the different data sets and breeds

| Data set and breed\(^2\) | T1 b | SE | P-value | T2 b | SE | P-value | T3 b | SE | P-value | T4 b | SE | P-value |
|-------------------------|------|----|--------|------|----|--------|------|----|--------|------|----|--------|
| CRC1                    |      |    |        |      |    |        |      |    |        |      |    |        |
| AN                      | −0.16* | 0.04 | <0.001 | −0.15* | 0.04 | <0.001 | −0.03 | 0.04 | 0.39 | −0.04 | 0.05 | 0.49 |
| HE                      | −0.18* | 0.06 | <0.01  | 0.04  | 0.05 | 0.42  | 0.01  | 0.05 | 0.88 | 0.02  | 0.07 | 0.80 |
| MG                      | −0.15* | 0.07 | 0.03   | −0.15* | 0.06 | <0.01 | 0.06  | 0.07 | 0.39 | 0.02  | 0.07 | 0.80 |
| SH                      | 0.19   | 0.36 | 0.60   | −0.65  | 0.38 | 0.09  | 0.06  | 0.18 | 0.74 | 0.22  | 0.21 | 0.29 |
| TEMP                    | −0.16* | 0.03 | <0.0001 | −0.09* | 0.03 | <0.001 | −0.03 | 0.03 | 0.32 | 0.00  | 0.04 | 0.93 |
| CRC1                    |      |    |        |      |    |        |      |    |        |      |    |        |
| BR                      | −0.13* | 0.05 | 0.01   | −0.22  | 0.15 | 0.14  | −0.18* | 0.07 | 0.01 | −0.11* | 0.05 | 0.03 |
| BE                      | −0.18* | 0.04 | <0.0001 | −0.16* | 0.04 | <0.001 | −0.10* | 0.04 | 0.02 | 0.05  | 0.06 | 0.41 |
| SG                      | −0.15* | 0.04 | <0.0001 | −0.20* | 0.05 | <0.0001 | −0.11* | 0.04 | <0.001 | 0.13* | 0.05 | <0.01 |
| TROP                    | −0.16* | 0.03 | <0.0001 | −0.17* | 0.03 | <0.0001 | −0.12* | 0.03 | <0.0001 | 0.01  | 0.03 | 0.86 |
| CRC2                    |      |    |        |      |    |        |      |    |        |      |    |        |
| TC                      | −0.19* | 0.05 | <0.001 | −0.22* | 0.07 | <0.01 | −0.07 | 0.06 | 0.21 | 0.03  | 0.06 | 0.59 |
| TC TS                   | −0.06* | 0.03 | 0.03   | −0.08* | 0.04 | 0.03  | −0.05* | 0.03 | 0.06 | −0.01 | 0.03 | 0.63 |
| BR                      | −0.15* | 0.06 | <0.01  | 0.02  | 0.14 | 0.87  | −0.27* | 0.07 | <0.001 | −0.01 | 0.06 | 0.86 |
| BR TS                   | −0.07* | 0.03 | 0.03   | −0.00  | 0.07 | 0.99  | −0.15* | 0.04 | <0.001 | −0.02 | 0.03 | 0.60 |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. T1 to T4 = tenderness markers.

\(^2\)CRC = Cooperative Research Centre database; AN = Angus; HE = Hereford; MG = Murray Grey; SH = Shorthorn; BR = Brahman; BE = Belmont Red; SG = Santa Gertrudis; TC = Tropical Composite; TS = tenderstretched side; TEMP = pooled temperate breeds (AN, HE, MG, and SH); TROP = pooled tropically adapted breeds (BR, BE, and SG).

*Significant at \(P < 0.05\).
Within CRC1 TROP, Belmont Red had a significant \( P = 0.02 \) positive effect (+0.33 kg/d) of the N4 on DFI.

**DISCUSSION**

Gene frequencies of the 12 markers differed across markers and breeds, and 86% were estimated to be HWE. Estimates within the same breed across populations were also similar. However, many of the markers were observed to have very large or small frequencies of the favorable allele in some breeds, and this has contributed to increased SE of the estimated regression coefficients. Also, evidence from lesser (<90%) call rates and failure of HWE indicate that genotype determination of some of the markers (e.g., M2 and T2) in some data sets may have affected the accuracy of the results.

Table 9. Estimated additive genetic \( (V_a) \) and phenotypic \( (V_p) \) variances and heritabilities \( (h^2 \pm SE) \) for M. longissimus thoracis et lumborum shear force (kg) and tenderstretch shear force (kg) with and without fitting 4 GeneSTAR tenderness markers\(^1\) as fixed effects

| Data set\(^2\) | Markers\(^3\) | \( V_a \) | \( V_p \) | \( h^2 \) \( \pm SE \) | \( V_a \) | \( V_p \) |
|--------------|-------------|--------|--------|----------------|--------|--------|
| CRC1 TEMP    | No          | 0.036  | 0.433  | 0.08 (0.04)    | 17.2   | 1.5    |
|              | Yes         | 0.030  | 0.426  | 0.07 (0.04)    |        |        |
| CRC1 TROP    | No          | 0.182  | 0.612  | 0.30 (0.06)    | 17.1   | 4.7    |
|              | Yes         | 0.151  | 0.583  | 0.26 (0.06)    |        |        |
| CRC2 BR      | No          | 0.382  | 1.125  | 0.34 (0.11)    | 7.4    | 2.0    |
|              | Yes         | 0.354  | 1.102  | 0.32 (0.10)    |        |        |
| CRC2 TC      | No          | 0.349  | 1.088  | 0.32 (0.10)    | 12.9   | 2.7    |
|              | Yes         | 0.305  | 1.059  | 0.29 (0.09)    |        |        |
| CRC2 BR TS   | No          | 0.087  | 0.273  | 0.32 (0.11)    | 1.8    | 1.8    |
|              | Yes         | 0.086  | 0.268  | 0.32 (0.11)    |        |        |
| CRC2 TC TS   | No          | 0.068  | 0.230  | 0.30 (0.11)    | 22.9   | 2.8    |
|              | Yes         | 0.053  | 0.224  | 0.24 (0.10)    |        |        |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia.

\(^2\)CRC = Cooperative Research Centre database; TEMP = pooled temperate breeds (Angus, Hereford, Murray Grey, and Shorthorn); TROP = pooled tropically adapted breeds (Brahman, Santa Gertrudis, and Belmont Red); BR = Brahman; TC = Tropical Composite; TS = tenderstretched side.

\(^3\)No = no markers fitted; Yes = 4 markers fitted jointly.

\(^4\)Expressed as percentage differences in model variance estimates.

\( (P > 0.05) \) effects for DFI, and within CRC1 TROP, Belmont Red had a significant \( P = 0.02 \) positive effect (+0.33 kg/d) of the N4 on DFI.

Many of the markers for tenderness and feed efficiency were not observed to be in HWE when considered in pooled populations, and this highlights that spurious results of marker effects may occur if breed is not correctly modeled in the analysis of multibreed data.

The locations of all 4 tenderness markers have been published, and 3 are SNP located within genes that code for 2 of the key enzymes involved in the post-mortem meat tenderization process (i.e., calpain and calpastatin). Gene frequency estimates for our populations were in general agreement with the review by Van Eenenma et al. (2007) for T1, T2, and T3. Estimates of gene frequencies across populations of the same breed in this study were also similar, suggesting little differences across the samples and consistent calling of marker alleles across studies. The estimated sizes of effects of the T1 marker were extremely consistent across

Table 10. Estimated additive genetic \( (V_a) \) and phenotypic \( (V_p) \) variances and heritabilities \( (h^2 \pm SE) \) for M. semitendinosus shear force (kg) with and without fitting 4 GeneSTAR tenderness markers\(^1\) as fixed effects

| Data set\(^2\) | Markers\(^3\) | \( V_a \) | \( V_p \) | \( h^2 \) \( \pm SE \) | \( V_a \) | \( V_p \) |
|--------------|-------------|--------|--------|----------------|--------|--------|
| CRC1 TEMP    | No          | 0.029  | 0.278  | 0.10 (0.04)    | 8.4    | 0.0    |
|              | Yes         | 0.026  | 0.278  | 0.09 (0.04)    |        |        |
| CRC1 TROP    | No          | 0.110  | 0.299  | 0.37 (0.06)    |        |        |
|              | Yes         | 0.106  | 0.230  | 0.36 (0.06)    | 4.1    | 1.0    |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia.

\(^2\)CRC = Cooperative Research Centre database; TEMP = pooled temperate breeds (Angus, Hereford, Murray Grey, and Shorthorn); TROP = pooled tropically adapted breeds (Brahman, Santa Gertrudis, and Belmont Red).

\(^3\)No = no markers fitted; Yes = 4 markers fitted jointly.

\(^4\)Expressed as percentage differences in model variance estimates.
data sets, and results from CRC1 data sets were somewhat expected given that a subset of CRC1 animals was used in discovery of this marker (Barendse, 2002). Results for T1 effects were in close agreement with the estimates of Van Eenennaam et al. (2007) and Casas et al. (2006) across a range of breeds. However, Casas et al. (2006) did not observe a significant difference in purebred Brahms, whereas in our study, we found significant effects in both the CRC1 Brahman (−0.13 kg) and CRC2 Brahman (−0.15 kg), which were very similar in magnitude to all other breeds. The estimates in Casas et al. (2006) for Brahms (n = 444) had large SE, and the difference in aging regimens between experiments (14 vs. 2 d) may have affected estimates of

Table 11. Estimated effects (b) of the 4 GeneSTAR marbling markers1 (fitted jointly) on intramuscular fat percentage from the different data sets and breeds

| Data set and breed2 | M1 | M2 | M3 | M4 |
|--------------------|----|----|----|----|
|                    | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value |
| CRC1               |    |    |         |    |    |         |    |    |         |    |    |         |
| AN                 | −0.03 | 0.08 | 0.70 | 0.05 | 0.10 | 0.62 | 0.10 | 0.12 | 0.40 | −0.07 | 0.08 | 0.36 |
| HE                 | −0.25* | 0.09 | 0.01 | −0.09 | 0.27 | 0.75 | 0.15 | 0.10 | 0.14 | −0.12 | 0.08 | 0.13 |
| MG                 | 0.07 | 0.17 | 0.66 | −0.13 | 0.24 | 0.59 | −0.42 | 0.37 | 0.25 | 0.27 | 0.23 | 0.25 |
| SH                 | −0.11 | 0.16 | 0.50 | 0.25 | 0.38 | 0.52 | 0.10 | 0.27 | 0.71 | 0.04 | 0.12 | 0.78 |
| TEMP               | −0.06 | 0.06 | 0.25 | −0.06 | 0.08 | 0.47 | 0.09 | 0.08 | 0.24 | −0.03 | 0.05 | 0.54 |
| CRC2               |    |    |         |    |    |         |    |    |         |    |    |         |
| BR                 | −0.15 | 0.23 | 0.52 | −0.01 | 0.07 | 0.89 | 0.29 | 0.46 | 0.53 | −0.17 | 0.11 | 0.12 |
| BE                 | 0.08 | 0.11 | 0.47 | 0.09 | 0.06 | 0.10 | 0.10 | 0.09 | 0.24 | 0.10 | 0.07 | 0.13 |
| SG                 | 0.06 | 0.10 | 0.55 | −0.08 | 0.05 | 0.10 | −0.41 | 0.29 | 0.16 | 0.15 | 0.10 | 0.12 |
| TROP               | −0.02 | 0.07 | 0.77 | 0.01 | 0.03 | 0.78 | 0.07 | 0.08 | 0.34 | 0.06 | 0.05 | 0.19 |
| CRC1               |    |    |         |    |    |         |    |    |         |    |    |         |
| BR                 | −0.15 | 0.17 | 0.38 | −1.44 | 1.37 | 0.29 | −0.15 | 0.26 | 0.56 | 0.05 | 0.12 | 0.66 |

1GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. M1 to M4 = marbling markers.
2CRC = Cooperative Research Centre database; AN = Angus; HE = Hereford; MG = Murray Grey; SH = Shorthorn; BR = Brahman; BE = Belmont Red; SG = Santa Gertrudis; TC = Tropical Composite; PT = progeny test program; TEMP = pooled temperate breeds (AN, HE, MG, and SH); TROP = pooled tropically adapted breeds (BR, BE, and SG).
*Significant at P < 0.05.

Table 12. Estimated effects (b) of the 4 GeneSTAR marbling markers1 (fitted jointly) on Meat Standards Australia marbling score from the different data sets and breeds

| Data set and breed2 | M1 | M2 | M3 | M4 |
|--------------------|----|----|----|----|
|                    | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value |
| CRC1               |    |    |         |    |    |         |    |    |         |    |    |         |
| AN                 | −0.02 | 0.06 | 0.77 | −0.05 | 0.06 | 0.36 | 0.04 | 0.07 | 0.58 | 0.01 | 0.05 | 0.83 |
| HE                 | −0.03 | 0.05 | 0.55 | 0.13 | 0.14 | 0.35 | −0.00 | 0.06 | 0.98 | 0.00 | 0.05 | 0.94 |
| MG                 | 0.12 | 0.09 | 0.21 | −0.14 | 0.13 | 0.91 | 0.06 | 0.25 | 0.82 | 0.14 | 0.13 | 0.28 |
| SH                 | 0.03 | 0.11 | 0.82 | 0.01 | 0.22 | 0.95 | 0.24 | 0.18 | 0.18 | −0.04 | 0.07 | 0.62 |
| TEMP               | 0.00 | 0.03 | 0.94 | −0.04 | 0.04 | 0.42 | 0.04 | 0.04 | 0.42 | 0.01 | 0.03 | 0.69 |
| CRC2               |    |    |         |    |    |         |    |    |         |    |    |         |
| TC                 | −0.02 | 0.04 | 0.60 | 0.03 | 0.03 | 0.34 | 0.04 | 0.04 | 0.42 | 0.03 | 0.04 | 0.44 |
| BR                 | 0.03 | 0.08 | 0.68 | 0.03 | 0.03 | 0.40 | −0.07 | 0.20 | 0.74 | −0.02 | 0.06 | 0.73 |
| SH                 | −0.13 | 0.10 | 0.19 | −1.23 | 0.78 | 0.12 | −0.21 | 0.15 | 0.16 | 0.11 | 0.07 | 0.11 |
| AN                 | −0.03 | 0.06 | 0.66 | 0.09 | 0.07 | 0.19 | 0.04 | 0.08 | 0.59 | −0.07 | 0.07 | 0.34 |

1GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. M1 to M4 = marbling markers.
2CRC = Cooperative Research Centre database; AN = Angus; HE = Hereford; MG = Murray Grey; SH = Shorthorn; BR = Brahman; BE = Belmont Red; SG = Santa Gertrudis; TC = Tropical Composite; PT = progeny test program; TEMP = pooled temperate breeds (AN, HE, MG, and SH); TROP = pooled tropically adapted breeds (BR, BE, and SG).
*Significant at P < 0.05.
the size of gene marker effects. Drinkwater et al. (2006) also confirmed the existence of T1 in a linkage mapping study using Brahman-influenced cattle. Barendse et al. (2007a) and Barendse et al. (2008) reported T1 genotype effects very much in agreement with the current results using a subset of the CRC1 tropical cattle. Morris et al. (2006) reported consistent direction of effects for T1 and T2 in *Bos taurus* cattle, but they reported the differences declined with increasing aging times (up to 28 d), particularly for T2.

Table 13. Estimated effects (b) of the 4 GeneSTAR feed-efficiency markers\(^1\) (fitted jointly) on residual feed intake (kg/d) from the different data sets and breeds

| Data set and breed | N1 |  |  |  |  |  |  |  |  |  |
|-------------------|----|---|---|---|---|---|---|---|---|---|
|                   | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value |
| **CRC1**          |    |    |          |    |    |          |    |    |          |    |    |          |
| AN                | 0.01| 0.14| 0.94     | −0.02| 0.11| 0.85     | −0.13| 0.09| 0.13     | −0.06| 0.09| 0.45     |
| HE                | −0.06| 0.13| 0.66     | 0.57| 0.32| 0.08     | −0.12| 0.11| 0.25     | −0.00| 0.10| 0.98     |
| MG                | −1.24*| 0.51| 0.02     | −0.25| 0.16| 0.12     | −0.22| 0.21| 0.30     | 0.03| 0.21| 0.89     |
| SH                | −0.01| 0.20| 0.96     | −0.05| 0.50| 0.93     | 0.09| 0.15| 0.54     | −0.25| 0.20| 0.22     |
| TEMP              | −0.07| 0.08| 0.36     | −0.06| 0.08| 0.45     | −0.14*| 0.05| 0.01     | −0.10| 0.06| 0.09     |
| **CRC2**          |    |    |          |    |    |          |    |    |          |    |    |          |
| BR                | −0.31| 0.11| 0.11     | 0.19| 0.54| 0.73     | 0.19| 0.27| 0.48     | −0.20| 0.13| 0.14     |
| BE                | −0.06| 0.08| 0.47     | 0.12| 0.16| 0.48     | −0.08| 0.07| 0.29     | 0.01| 0.08| 0.89     |
| SG                | 0.17| 0.13| 0.19     | −0.11| 0.23| 0.63     | −0.06| 0.09| 0.51     | −0.19| 0.10| 0.06     |
| TROP              | 0.01| 0.06| 0.92     | 0.10| 0.13| 0.42     | −0.05| 0.06| 0.35     | −0.07| 0.06| 0.18     |
| **CRC1**          |    |    |          |    |    |          |    |    |          |    |    |          |
| **CRC2**          |    |    |          |    |    |          |    |    |          |    |    |          |
| **TC**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **BR**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **BE**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **SG**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **TROP**          |    |    |          |    |    |          |    |    |          |    |    |          |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. N1 to N4 = feed-efficiency markers.

\(^2\)CRC = Cooperative Research Centre database; AN = Angus; HE = Hereford; MG = Murray Grey; SH = Shorthorn; BR = Brahman; BE = Belmont Red; SG = Santa Gertrudis; TC = Tropical Composite; PT = progeny test program; TEMP = pooled temperate breeds (AN, HE, MG, and SH); TROP = pooled tropically adapted breeds (BR, BE, and SG).

\(^*\)Significant at \(P < 0.05\).

Table 14. Estimated effects (b) of the 4 GeneSTAR feed-efficiency markers\(^1\) (fitted jointly) on daily feed intake (kg/d) from the different data sets and breeds

| Data set and breed | N1 |  |  |  |  |  |  |  |  |  |
|-------------------|----|---|---|---|---|---|---|---|---|---|
|                   | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value | b  | SE | P-value |
| **CRC1**          |    |    |          |    |    |          |    |    |          |    |    |          |
| AN                | −0.01| 0.22| 0.96     | −0.16| 0.18| 0.39     | −0.07| 0.14| 0.64     | −0.07| 0.14| 0.63     |
| HE                | 0.12| 0.22| 0.59     | 0.36| 0.56| 0.53     | −0.44*| 0.19| 0.02     | −0.22| 0.18| 0.23     |
| MG                | −2.00*| 0.77| 0.01     | −0.46| 0.24| 0.06     | −0.01| 0.32| 0.97     | −0.48| 0.32| 0.15     |
| SH                | −0.00| 0.35| 0.99     | −0.24| 0.93| 0.80     | −0.04| 0.26| 0.88     | −0.19| 0.34| 0.58     |
| TEMP              | −0.05| 0.13| 0.71     | −0.18| 0.14| 0.18     | −0.19*| 0.09| 0.03     | −0.21*| 0.09| 0.03     |
| **CRC2**          |    |    |          |    |    |          |    |    |          |    |    |          |
| **TC**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **BR**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **BE**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **SG**            |    |    |          |    |    |          |    |    |          |    |    |          |
| **TROP**          |    |    |          |    |    |          |    |    |          |    |    |          |

\(^1\)GeneSTAR markers, Catapult Genetics, Albion, Queensland, Australia. N1 to N4 = feed-efficiency markers.

\(^2\)CRC = Cooperative Research Centre database; AN = Angus; HE = Hereford; MG = Murray Grey; SH = Shorthorn; BR = Brahman; BE = Belmont Red; SG = Santa Gertrudis; TC = Tropical Composite; PT = progeny test program; TEMP = pooled temperate breeds (AN, HE, MG, and SH); TROP = pooled tropically adapted breeds (BR, BE, and SG).

\(^*\)Significant at \(P < 0.05\).
not have significant effects, in *Bos taurus* cattle and small effects in *Bos indicus*-derived breeds compared with purebred Brahman. Page et al. (2004) reported decreased shear force for T2 between the 2 homozygotes (0.6 kg) in 2 *Bos taurus* populations. Van Eenennaam et al. (2007) analyzed the effects of T2 and T3 as a combined 2-marker genotype and reported a −0.34- and −0.33-kg shear force difference between C:C and G:T (i.e., T2:T3) genotype in 2 validation analyses with mixed breeds including Brahman. A similar result was reported by White et al. (2005) in 2 populations of *Bos indicus*-influenced and *Bos Taurus*-only cattle. Their estimated effects of T3 were also significant and included a population of purebred Brahman. Barendse et al. (2007b), using a subset of the CRC1 temperate and tropical cattle from this study, also reported a significant effect of T3 only in tropically adapted breeds and found evidence of epistasis only in some breeds for T1 with T2 or T3. However, Casas et al. (2006) reported a significant interaction in one of the populations (i.e., GPE8) in their study. The estimates showed animals with the CC genotype (n = 3) at both markers were more tender than any other genotype group. However, they made the conclusion that there was no clear evidence of an interaction between T1 and T3 on shear force and that the 2 markers act additively.

Literature estimates of the effect of the T4 markers were limited to those of Barendse et al. (2008). Their discovery population was also the CRC1 tropical breeds data set used in this study, and results for the CAPN3:c.1558+225G>T SNP showed gene frequencies and estimated size of effects very similar to our results for T4, including the significant effect of the marker in the opposite direction in Santa Gertrudis cattle. However, the effect of T4 on shear force was not significant in the CRC2 Tropical Composite or Brahman data sets and provides further evidence that this marker may be in different phases across breeds.

The effects of the 4 markers on STN_SF were nonsignificant in the temperate breeds, and T1 and T2 were significant in the tropical breeds but with effects of generally less magnitude than those observed for LTL_SF. These results suggest the markers were having less effect on tenderness of the STN muscle and support the estimated genetic correlation between tenderness in the 2 muscles in these data, which was only moderate at 0.59 and 0.46 in temperate and tropical breeds, respectively (Johnston et al., 2003). However, with few exceptions, when the markers had an effect, they were acting to reduce shear force with increasing number of favorable alleles.

The tenderstretch processing had a large effect on the mean and variance of LTL_SF in the CRC2 carcasses, and this result has been fully documented in Wolcott et al. (2009). The sizes of effects of the tenderness markers were more than halved but were still significant and explained significant additive variance for Tropical Composite. However, the effect of tenderstretching on reducing the mean and variance of shear force suggests that the utility of the tenderness markers, and the role of genetics in general, is greatly reduced if this procedure were to become commonplace in the meat-processing sector.

The additive genetic variance explained by the markers was small (i.e., less than 20%) for LTL_SF across all data sets; however, even at these levels, the markers would add significant value to a genetic evaluation by increasing the accuracy of prediction, particularly when shear force phenotypes are not available. For some of the breeds, in which the gene frequencies of the favorable allele are currently low, the utility of the markers may increase over time if the frequencies increase by selection. The small variance explained by the current markers is likely due to the existence of other SNP within the calpain and calpastatin genes associated with tenderness (e.g., Page et al., 2004; Schenkel et al., 2006; Barendse et al., 2007a, 2008) and other genes and SNP that are associated with tenderness on other chromosomes (e.g., Stone et al., 2005; Davis et al., 2008). Furthermore, genetic correlations estimated in quantitative genetic analyses suggest other possible gene networks involved in the meat tenderness, such as temperament (Kadel et al., 2006), meat color (Wolcott et al., 2009), and marbling (Shackelford et al., 1994; Reverter et al., 2003).

Marbling markers were generally not significant or their effects were not consistent on either IMF or MARB. These results were across the range of breeds and experiments. The average level of marbling ranged from very small to moderate, and the heritabilities ranged from 0.17 to 0.64 across data sets. The lack of significant association for the M1 marker is contrary to the findings of Wood et al. (2006), whose results from a meta-analysis showed a significant association of the TG5 marker on marbling across several studies and breeds, including a subset of the CRC1 Angus from this study. Wood et al. (2006) included the results of Barendse et al. (2004) in which they reported a significant effect of TG5 on marbling score in feedlot cattle fed between 160 and 240 d. In a very small study, Thaller et al. (2003) also reported a significant association between TG5 and LM IMF in German Holsteins (n = 28). However, several studies have also reported no association between the marbling markers and measures of carcass marbling. Casas et al. (2005) found no association between TG5 marker and marbling score in Brahman; however, there were very few numbers of 1- and 2-star animals. Van Eenennaam et al. (2007) reported no association of M1 with US marbling score but the effect of the M1 marker approached significance for increased USDA quality grade in Charolais × Angus cattle. Rinken et al. (2006) reported no significant effect of TG5 on marbling score, IMF, quality grade, or percent low USDA choice and above in Simmental steers. Thaller et al. (2003) found no effect in a very small sample (n = 27) of German Charolais. Casas et
al. (2007), in a study of numerous breeds, reported no associations of polymorphisms in the thyroglobulin gene, including TG5, on marbling. However, they did find that animals of Wagyu inheritance with the TG5 TT genotype had significantly more marbling than CC or CT genotypes, which suggests a possible recessive mode of action. Casas et al. (2007) concluded that the TG5 marker is most likely not in linkage disequilibrium with other functional loci except in Wagyu. Our study contained no animals of Wagyu decent. The results of Shin and Chung (2007) also reported a significant recessive effect of the TG5 marker in Korean native cattle. However, in their study, the TT genotype was associated with reduced marbling score, further supporting the conclusions of Casas et al. (2006) regarding the likely lack of linkage disequilibrium of the marker and causative mutation. This is further supported by the results in our study for the M1 marker in Herefords for IMF.

Our results showed no significant effects of the M2 marker on IMF or marbling score across the populations studied, and this agrees with the only other study to evaluate this marker. Van Eenennaam et al. (2007) reported no association of M2 with US marbling score or USDA quality grade in Charolais × Angus cattle. Given the unknown identity of the M3 and M4 markers, this is the first study to report on these markers, and it has shown, in the populations studied, the markers had no significant effects on IMF or marbling score.

This study and many other studies have failed to show consistent effects of any of the marbling markers across a range of breeds and production systems. This may be due to several factors such as low linkage disequilibrium of the markers with the marbling traits outside the original discovery populations, differences in the level of marbling or production environment (e.g., number of days on feed), and possibly differences in the mode of action of the markers across breeds (e.g., dominance).

Results for the feed-efficiency markers were significant for the N3 marker in the CRC1 TEMP data set. This result was somewhat expected given that a subset of these animals was used in the whole genome association study of Barendse et al. (2007a), in which numerous SNP were identified to be associated with RFI, and subsequently 4 were commercialized as the feed-efficiency markers. However, the effects of the markers were not significant in the other 3 data sets, including the CRC1 tropical breeds that were also used in the marker discovery. It is not known which 4 of these markers were commercialized as the GeneSTAR feed-efficiency markers, so it is not possible to compare results to other studies. Although, there have been SNP identified in beef for RFI and DFI (Nkrumah et al., 2007; Sherman et al., 2009), and SNP for DFI have also been reported in other livestock species [e.g., dairy cattle (Liefers et al., 2002) and chickens (van Kaam et al., 1999)]. Finally, the high gene frequencies (i.e., for the favorable allele) observed in the populations used in this study for many of the 4 feed-efficiency markers would limit the utility in genetic evaluation and selection programs, particularly in breeds such as Brahman.

This study has estimated the effects of the 12 gene markers across a diverse range of breeds and production systems representing a large part of the Australian beef industry. The marbling and feed-efficiency GeneSTAR markers did not predict the expected differences in these data. Subsets of the tenderness markers predicted differences in meat tenderness, and the direction of their effects was generally consistent across breeds. The amount of variation explained by the 4 tenderness markers suggests they are useful for selection, and predicted breeding values would have low to moderate accuracies based on gene-marker data alone. Therefore, new procedures are being developed to use both phenotypic data (e.g., shear force) and the GeneSTAR tenderness gene markers to develop a BREDPLAN shear force EBV\textsuperscript{M}. Further increasing the accuracy of EBV\textsuperscript{M} from gene-marker data will require discovering additional SNP or chromosome segments that are associated with the traits. This study has demonstrated that the effects of gene markers need to be confirmed in independent data sets outside those used for discovery, and they need to be sufficiently large to estimate the size of effects and the amount of variance explained in each population or breed. The results also showed that the characterization of the target traits (e.g., shear force of LTL or STN), breeds, finishing, and processing procedures will be required to assess the economic value of the marker information.

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GeneSTAR marker frequencies and effects

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