

Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds.

3. Meat quality traits*

D. J. Johnston^{A,F}, A. Reverter^{A,E}, D. M. Ferguson^B, J. M. Thompson^C, and H. M. Burrow^D

Cooperative Research Centre for Cattle and Beef Quality

^AAnimal Genetics and Breeding Unit†, University of New England, Armidale, NSW 2351, Australia.

^BFood Science Australia, PO Box 3312, Tingalpa DC, Qld 4173, Australia.

^CDepartment of Animal Science, University of New England, Armidale, NSW 2351, Australia.

^DCSIRO Livestock Industries, Box 5545, Rockhampton Mail Centre, Qld 4702, Australia.

^ECurrent address: CSIRO Livestock Industries, Long Pocket Laboratories, 120 Meiers Road, Indooroopilly, Qld 4068, Australia.

^FCorresponding author; email: djohnsto@pobox.une.edu.au

Abstract. Meat quality measures, including objective measures of tenderness (shear force and compression), were taken on 2 muscles [*M. longissimus thoracis et lumborum* (LTL) and *M. semitendinosus* (ST)] from 7566 carcasses from temperate (TEMP) and tropically adapted (TROP) beef cattle breeds. Animals were finished to 1 of 3 market carcass weight end-points (220, 280, or 340 kg) either on pasture or in a feedlot, and in 2 different geographic regions for TROP. Both the phenotypic and genetic expressions of the traits were estimated at each market weight and for each finishing regime. Heritabilities and correlations between the traits were estimated for TEMP and TROP separately. Smaller additive variances and heritabilities were observed for temperate breeds compared with tropically adapted breeds for most of the traits studied. For TROP, the heritability of traits measured on the ST muscle [compression (ST_C), shear force (ST_SF), and L* Minolta lightness value (ST_L*)] was 0.27, 0.42, and 0.16, respectively, and for traits measured on the LTL muscle [compression (LTL_C), shear force (LTL_SF), L* Minolta lightness value (LTL_L*), a* Minolta redness value (LTL_a*), cooking loss % (LTL_CL%), and consumer assessed tenderness score (LTL_TEND)] 0.19, 0.30, 0.18, 0.13, 0.20, and 0.31, respectively. For TEMP, the heritability of traits measured on the ST muscle [ST_C, ST_SF, ST_L*, a* Minolta redness value (ST_a*), cooking loss % (ST_CL%)] was 0.12, 0.11, 0.17, 0.13, and 0.15, respectively, and of traits measured on the LTL muscle (LTL_C, LTL_SF, LTL_L, and LTL_TEND) 0.08, 0.09, 0.17 and 0.18, respectively. Genetic correlations were moderate to high for tenderness measures (shear force and compression) between muscles for the same tenderness measure (e.g. LTL_SF and ST_SF was 0.46 for TROP) and within a muscle for the different measures (e.g. ST_C and ST_SF was 0.83 for TROP). Phenotypic and genetic correlations between LTL_L* and all objective measures of tenderness were negative (e.g. LTL_SF and LTL_L* for TROP was -0.40). The genetic relationship between LTL_SF and LTL_TEND was -0.79 and -0.49 for TROP and TEMP, respectively. Finishing system affected the phenotypic expression of all traits. Pasture-finished, compared with feedlot-finished, animals had higher shear force and compression measures, darker meat colour, and lower sensory tenderness scores for both TEMP and TROP. For TROP, heifers had higher shear force and compression measures, lower sensory tenderness scores, and darker meat colour (lower L* values) than steers. Genetic correlations between markets were generally high and close to unity with the exception of the ST_L*, LTL_L*, ST_C, and ST_SF for TEMP. Geographic region had little effect on the phenotypic and genetic expression of meat quality traits for TROP. Genetic correlations between finishing regimes for all traits were positive and close to unity, with the exception of ST_C and LTL_SF for TEMP, and LTL_L* and LTL_CL% for TROP. Genetic improvement of meat quality traits is a possibility for tropically adapted breeds given the moderate heritabilities, adequate phenotypic variance, generally favourable genetic correlations between traits, and little evidence of genotype by environment interactions.

Additional keywords: beef tenderness, shear force, compression, cooking loss, G × E

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Introduction

In recent years there has been a vigorous assault on improving the consistency of beef quality, particularly tenderness, in Australia. This has been predicated on the need to arrest the negative trend in beef consumption but on a more positive note, the evidence that consumers will buy more and pay more for beef with guaranteed tenderness (Boleman *et al.* 1997; see review by Egan *et al.* 2001). In view of the goal, it is essential that the contributions of the genetic and non-genetic influences on beef quality are better characterised particularly under Australian production systems and markets.

From the published genetic parameters for beef quality traits (see reviews by Marshall 1999 and Burrow *et al.* 2001) there is considerable variability in the results across studies and therefore it is difficult to draw clear conclusions regarding their applicability under Australian conditions. Suffice to say, traits associated with carcass composition, particularly fatness traits (e.g. carcass yield %, subcutaneous fat thickness, and marbling), appear moderately to highly heritable. The same, however, cannot be said for the important trait of beef tenderness where the heritability estimates are much more variable (0.02–0.53). Confidence in these estimates is constrained somewhat by the small numbers of animals used—often only a few hundred. Secondly, it is not always clear as to whether the post-slaughter conditions were controlled. It is well recognised that the expression of traits, such as tenderness, is critically influenced by the post-slaughter conditions (Ferguson *et al.* 2001).

In view of the need to develop improved understanding of the relevance and magnitude of the genetic and non-genetic influences on beef quality traits under Australian production systems, the Cooperative Research Centre for Cattle and Beef Quality (Beef CRC) straightbreeding project was established (see Bindon 2001). Preliminary meat quality results from this project have been published by Robinson *et al.* (2001) and Johnston *et al.* (2001). This paper is the third in a series that reports on the outcomes of the Beef CRC straightbreeding project.

The objectives of this paper were to (1) quantify the effects of different market weight end-points and finishing regimes on the phenotypic expression of several meat quality traits in 2 muscles for temperate and tropically adapted breeds; (2) estimate genetic parameters, including heritabilities and genetic and phenotypic correlations for meat quality traits in temperate and tropically adapted breeds; and (3) determine the existence of genotype by environment interactions for meat quality traits. Results from this study are used in Reverter *et al.* (2003b) to estimate the genetic correlations with animal measures (Johnston *et al.* 2003) and abattoir carcass measures (Reverter *et al.* 2003a) on the same animals.

Materials and methods

Animals

Cattle used in this study were from the straightbreeding project of the Beef CRC. The design of the project and management of the cattle are described in Upton *et al.* (2001). In brief, the project was a large progeny test for carcass and meat quality traits from 4 temperate breeds (TEMP: Angus, Hereford, Shorthorn, and Murray Grey) and 3 tropically adapted breeds (TROP: Brahman, Belmont Red, and Santa Gertrudis). All sires used were performance recorded through BREEDPLAN, and within a breed, genetic linkages across herds and years 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 were born during the years 1993–1998 in 36 cooperator herds (23 for TEMP and 13 for TROP) throughout eastern Australia. Parentage and date of birth were recorded on all animals in the cooperator herds, and at weaning, the animals were delivered to CRC managed properties in central Queensland and north-eastern New South Wales (Bindon 2001; Upton *et al.* 2001).

Cattle were slaughtered between 1994 and 2000 when the mean weight of the slaughter group (i.e. animals in the same year, season, market weight, and finishing regime) reached approximately the assigned market liveweight. Animals were handled pre-slaughter using industry best practice and slaughtered at 7 different commercial abattoirs. Every effort was made to control the slaughter procedure to minimise extraneous variation, particularly for tenderness traits. This was essentially achieved through the application of electrical stimulation, either with low voltage (45 V for 40 s) within 5 min post-stunning, or high voltage (400–800 V) 40–60 min post-stunning via 2 rubbing rails. However, due to operational difficulties or equipment malfunction, there were some whole slaughter groups ($N = 12$) that were not stimulated. Also, within slaughter groups that were stimulated, if the stimulation procedure failed on a carcass (i.e. no visual sign of muscle tetany), this was recorded as non-stimulated ($N = 200$ carcasses).

Although every effort was made to ensure the pre- and post-slaughter procedures were standardised, there were some differences between abattoirs and slaughter groups. Examples of these include differences in transport distance to the abattoir and method of electrical stimulation. These factors were accounted for in the statistical analysis through the modelling of fixed effects. For a complete description of pre- and post-slaughter procedures see Perry *et al.* (2001).

Treatments

Cattle in this study were allocated to 1 of 6 finishing treatment groups for TEMP and 9 for TROP. Allocation was based on the design of Robinson (1995), in particular, sire progeny were balanced across treatments. Finishing treatments for TEMP included 3 target carcass weights [domestic 220 kg (DOM), Korean 280 kg (KOR), or Japanese 340 kg (JAP)]. Market weight was cross-classified with finishing regime of pasture (PAST) or feedlot (FLOT) finishing. The TEMP progeny were finished in north-eastern NSW and were denoted as either PAST_SOUTH or FLOT_SOUTH. For TROP, there were the 3 finishing regimes. The first 2 comprised pasture (PAST-NORTH) or feedlot (FLOT-NORTH) finishing in central Queensland. The third treatment, representing approximately one-third of the tropically adapted progeny, was relocated at weaning from central Queensland to north-eastern NSW for grow-out and feedlot finishing (FLOT-SOUTH). This treatment was used to generate a geographic region effect. Numbers of animals by breed, market weight, and finishing regimes are presented in Johnston *et al.* (2003).

Measurements

Meat quality measures were taken on 2 muscles: *M. longissimus thoracis et lumborum* (LTL) and *M. semitendinosus* (ST). Twenty to 24 h post-mortem, the whole ST and a 15-cm section of the LTL caudal from the 12/13th ribs were taken from the left side of the carcass and immediately frozen at -20°C for later analyses. A detailed description of the procedures used in the assessment of meat quality traits is provided by Perry *et al.* (2001). The following measures were taken on both muscles: Warner-Bratzler shear force of the LTL (LTL_SF) and ST (ST_SF), compression of the LTL (LTL_C) and ST (ST_C), cooking loss % of the LTL (LTL_CL%) and ST (ST_CL%), ultimate pH of the LTL (LTL_pH) and ST (ST_pH), Minolta L* value of the LTL (LTL_L*) and ST (ST_L*), Minolta a* value of the LTL (LTL_a*) and ST (ST_a*), and Minolta b* value of the LTL (LTL_b*) and ST (ST_b*).

A subset of the data (all slaughter groups between June 1996 and December 1998) had consumer assessments of palatability, performed by Meat Standards Australia (MSA), using a sample of the LTL aged for 14 days. Detailed descriptions of sample preparation, cooking procedures, and tasting protocols are presented in Polkinghorne *et al.* (1999). Consumer-assessed palatability traits of the LTL included tenderness (LTL_TEND), juiciness (LTL_JUIC), flavour (LTL_FLAV), overall acceptability (LTL_OACC), and MQ4 index of sensory scores (LTL_MQ4). See Table 1 for a complete description of all measurements and scores.

Statistical analyses

Data were initially examined to identify outliers. With the exception of shear force (LTL_SF) measurements, very few were found. Johnston *et al.* (2001) previously showed that differences in post-slaughter procedures influenced the variation in the measurements such as shear force. All LTL_SF records from 12 non-stimulated slaughter groups or individuals were removed. A preliminary analysis of LTL_SF, using a restricted maximum likelihood (REML) animal model in ASREML

(Gilmour *et al.* 1999), was used to identify outliers. The model contained a fixed contemporary group (CG) and was defined as the concatenation of the effects of herd of origin and slaughter group. Slaughter group accounted for the effects of year, season, sex, market weight, and finishing regime. Records greater than 3 residual standard deviations from their contemporary group mean ($N = 115$) were removed. An additional 7 LTL_SF records were removed that were over 9.0 kg shear that were not detected as outliers by the ASREML procedure. All but one of the records were from slaughter groups of less than 10 records. The final dataset for LTL_SF was 6828 records from 196 slaughter groups.

Preliminary univariate analyses were done in an attempt to reduce the number of traits for further analyses. Traits with heritabilities of 10% or less were not considered for further analyses. An exception was made for the objective measures LTL_SF, LTL_C, and LTL_CL% for TEMP because of their importance as tenderness measures and for comparison with the genetic parameters for the same traits for TROP.

Least square means

A series of analyses was run using the GLM procedure in SAS (SAS Institute Inc. 1988) to compute least square means (LSMEANS) for the meat quality traits by each of the design effects. Given the complexity of the design, the models were configured to include a combination of independent effects that allowed estimable solutions to be obtained for each of the important design effects (i.e. market group, finishing regime, market weight by finishing regime, sex, and sex by market (for TROP only). To estimate the LSMEANS for a particular design effect (e.g. market group) for each trait, the design effect was run as an independent effect in a model that included a second independent effect that accounted for all other design variables. Therefore, configuration of the model, to enable LSMEANS to be computed, ignored any abattoir or slaughter day effects associated with the design being investigated because slaughter day was completely nested within market weight and finishing treatments. Eqn 1 is an example of the fixed effect model used to analyse each dependent variable (ST_C, ST_SF, ST_L*, ST_a*,

Table 1. Description of meat quality measurements
Adapted from Perry *et al.* (2001). ST, *M. semitendinosus*; LTL, *M. longissimus thoracis et lumborum*

Code	Trait	Description
ST_SF, LTL_SF	Shear force (kg)	Modified Warner-Bratzler shear force (SF) of the ST and LTL using a triangulated 0.64-mm-thick blade pulled upward through the cooked sample at 100 mm/min at right-angles to the fibre direction. The mean for 6 subsamples was recorded
ST_C, LTL_C	Compression (kg)	Compression was measured as the product of hardness and cohesiveness of the cooked ST and LTL sample. A blunt cylindrical metal rod (diam. 6.3 mm) was driven into the sample at 50 mm/min, twice exactly in the same position. The mean for 6 subsamples was recorded
ST_CL%, LTL_CL%	Cooking loss (%)	The percentage difference in the pre- and post-cooked weights of a 245–255-g sample of ST and LTL (90 by 60 by 50 mm) cooked in a water bath (70°C) for 60 min and then cooled for 30 min
ST_pH, LTL_pH	Ultimate pH	pH measure of the ST and LTL sample using a digital pH meter 48 h post-slaughter
ST_L*, LTL_L*	L* value meat colour	L* colour space measurement (darkness–lightness) on the ‘bloomed’ meat surface of ST and LTL sample using a Minolta Chroma Meter
ST_a*, LTL_a*	a* value meat colour	a* colour space measurement (green–red) on the ‘bloomed’ meat surface of ST and LTL sample using a Minolta Chroma Meter
ST_b*, LTL_b*	b* value meat colour	b* colour space measurement (blue–yellow) on the ‘bloomed’ meat surface of ST and LTL sample using a Minolta Chroma Meter
LTL_TEND	Sensory tenderness score	Consumer-evaluated score: 0, very tough; 100, very tender
LTL_JUIC	Sensory juiciness score	Consumer-evaluated score: 0, very dry; 100, extremely juicy
LTL_FLAV	Sensory flavour score	Consumer-evaluated score: 0, extremely dislike; 100, extremely like
LTL_OACC	Sensory overall acceptability score	Consumer-evaluated score: 0, extremely dislike; 100, extremely like
LTL_MQ4	Sensory MQ4 score	MSA index: $0.4 \times \text{LTL_TEND} + 0.1 \times \text{LTL_JUIC} + 0.2 \times \text{LTL_FLAV} + 0.3 \times \text{LTL_OACC}$

ST_CL%, LTL_C, LTL_SF, and LTL_L*) to generate LSMEANS for market group effect for TEMP and TROP separately:

$$y_{ijk} = \mu + \text{mark}_j + \text{group}_k + e_{ijk} \quad (1)$$

where y_{ijk} is the observation on a dependent variable for animal i , μ is the overall mean, mark_j is the effect of the j th market weight group, group_k is the effect of the k th group that accounts for all other design variables including herd of origin, year, season, sex, and finishing regime, and e_{ijk} is random residual error.

Consumer-assessed palatability traits were measured on a subset of the data with no heifer data for TEMP, and only small numbers of slaughter groups existed within a market and finish category. Therefore, the previous model was altered to estimate LSMEANS. For each main effect fitted, the second independent effect included was the concatenated effect of herd, sex, and slaughter group nested within the main effect. For example, LTL_TEND LSMEANS for pasture and grain finishing were estimated using the following model:

$$y_{ijk} = \mu + \text{fin}_j + \text{group}_{kj} + e_{ijk} \quad (2)$$

where y_{ijk} is the observation on a consumer-assessed palatability trait for animal i , μ is the overall mean, fin_j is the effect of the j th finishing regime, group_{kj} is the effect of the k th group that accounts for all other design variables including herd of origin, year, season, sex, and slaughter group nested within fin_j , and e_{ijk} is random residual error.

To assess the magnitude of these effects, orthogonal contrasts were also estimated. Contrasts for sex were evaluated after removing steers finished to the Japanese market weight endpoint. For TROP, the effect of finishing regime was further investigated through orthogonal contrasts using animals finished in the North only. Breed means were not computed because the project was not designed to allow direct comparisons across breeds. This was primarily due to the fact that herds of origin were completely nested within breed, no TEMP cattle were raised in the subtropical environment, and the Shorthorn data were only based on steer progeny.

Variance component estimation

Genetic parameters were obtained from a 9-trait multivariate REML using analytical gradients with VCE 4.2.5 (Groeneveld and García-Cortés 1998). The traits included 8 objective measures of meat quality, and consumer assessed tenderness score. Given the vector y_i containing records on the i th trait, the animal model used can be expressed as follows:

$$y_i = X_i b_i + Z_i u_i + e_i \quad (3)$$

with

$$\text{Var} \begin{bmatrix} u_i \\ e_i \end{bmatrix} = \begin{bmatrix} A\sigma_A^2 & 0 \\ 0 & I\sigma_E^2 \end{bmatrix}$$

where X_i is a known incidence matrix relating observations in y_i to the linear CWT covariate and CG fixed effects in vector b_i (the number of levels of CG was 585 and 580 for TEMP and TROP, respectively); Z_i is a known incidence matrix relating observations in y_i to random additive genetic values in u_i ; e_i are unknown vectors of random temporary environmental effects; A is Wright's numerator relationship matrix between all animals using 3 generations of pedigree obtained from Australia's National Beef Recording Scheme database; I is an identity matrix; σ_A^2 is the additive direct genetic variance; and σ_E^2 is the residual error variance.

Genetic parameters for the 5 consumer-assessed palatability traits were estimated in a series of 10 bivariate analyses, for TEMP and TROP separately. The same animal model was used as described previously and a representation of the bivariate model used is presented in

Johnston *et al.* (2003). The number of levels of CG was 183 and 289 for TEMP and TROP, respectively.

To assess the magnitude of genotype \times environment interactions, each trait was analysed by treating it as a different trait in a multivariate analysis for the design variables of market weight group and finishing regime. For all genetic analyses the KOR and JAP market animals were pooled and termed export (EXP) due to relatively low numbers in the JAP market weight treatment group, particularly in TROP. However, the original market weight group was still used to define CG. Only CG with 3 or more records were used in the estimation analyses. For each trait, records from DOM and EXP were considered as 2 traits. For TEMP, records from the different finishing regimes (FLOT and PAST) were also considered as 2 traits. For TROP, the data were run using trivariate analyses with each of the 3 finishing regimes considered as different traits, i.e. PAST-NORTH, FLOT-NORTH, and FLOT-SOUTH. The same animal model described previously was used for these bi- and tri-variate estimations. A representation of the bivariate model used is presented in Johnston *et al.* (2003).

Results and discussion

Summary statistics for each trait are presented in Tables 2 and 3 for TEMP and TROP, respectively. The numbers of records were reasonably consistent across traits; however, only about one-third of the animals had consumer-assessed palatability traits. Several traits had h^2 of $\leq 10\%$ and were not considered in any further analyses. For TEMP these included LTL_pH (0.05 ± 0.03), LTL_CL% (0.09 ± 0.04), LTL_a* (0.03 ± 0.03), LTL_b* (0.02 ± 0.03), ST_b* (0.09 ± 0.04), and ST_pH (0.05 ± 0.03); and for TROP, LTL_pH (0.02 ± 0.03), ST_a* (0.08 ± 0.03), ST_b* (0.05 ± 0.03), ST_CL% (0.09 ± 0.03), and ST_pH (0.10 ± 0.04).

Table 2. Unadjusted means, standard deviations, and ranges for meat quality traits for temperate breeds
See Table 1 for description of traits

Trait	N	Mean	s.d.	Min.	Max.
ST_C (kg)	3350	2.04	0.33	1.10	3.63
ST_SF (kg)	3357	4.78	0.72	2.80	7.56
ST_CL% (%)	3585	21.77	1.95	7.60	33.15
ST_pH	3585	5.56	0.14	5.00	6.91
ST_L*	3540	47.07	3.44	28.67	56.26
ST_a*	3540	24.00	3.35	12.23	39.84
ST_b*	3539	16.13	2.09	5.92	27.00
LTL_C (kg)	3358	1.63	0.30	0.74	3.06
LTL_SF (kg)	3322	4.12	0.82	2.01	8.75
LTL_CL% (%)	3338	20.91	2.36	11.77	36.70
LTL_pH	3343	5.51	0.12	5.00	6.76
LTL_L*	3568	39.57	2.97	26.45	55.26
LTL_a*	3568	23.48	2.83	12.94	34.85
LTL_b*	3568	12.58	1.73	4.60	19.33
LTL_TEND	1152	59.19	14.63	15.30	91.50
LTL_JUIC	1152	59.42	12.62	22.17	89.50
LTL_FLAV	1152	59.98	11.16	23.67	89.00
LTL_OACC	1152	59.14	12.44	20.50	91.17
LTL_MQ4	1152	59.07	12.35	25.50	90.02

Table 3. Unadjusted means, standard deviations, and ranges for meat quality traits for tropically adapted breeds

See Table 1 for description of traits

Trait	N	Mean	s.d.	Min.	Max.
ST_C (kg)	3597	2.13	0.36	1.04	3.82
ST_SF (kg)	3587	4.76	0.64	2.78	7.24
ST_CL% (%)	3831	23.72	2.04	15.87	32.65
ST_pH	3835	5.58	0.10	5.35	6.40
ST_L*	3830	48.09	4.08	25.68	60.10
ST_a*	3830	24.33	4.26	12.10	48.95
ST_b*	3830	16.49	2.29	7.21	33.66
LTL_C (kg)	3589	1.77	0.28	1.04	3.53
LTL_SF (kg)	3506	4.62	0.99	2.34	8.93
LTL_CL% (%)	3585	22.32	2.02	10.51	33.57
LTL_pH	3587	5.56	0.10	5.16	6.67
LTL_L*	3561	38.51	3.16	25.42	50.94
LTL_a*	3798	22.63	3.14	10.55	53.99
LTL_b*	3798	11.90	1.79	2.49	20.20
LTL_TEND	1585	46.78	15.41	4.20	89.80
LTL_JUIC	1585	48.99	13.16	10.50	89.33
LTL_FLAV	1585	51.42	11.61	14.50	87.00
LTL_OACC	1585	48.76	13.16	11.33	84.00
LTL_MQ4	1585	48.50	12.98	9.53	84.97

Least square means

Significant market weight and finishing regime effects ($P < 0.001$) were observed for all meat quality traits for TEMP. Similarly for TROP, market weight, finishing regime, and sex were significant for all traits with the exception of market weight for the consumer-assessed palatability traits and sex for LTL_C. Least square means for each of these effects are presented in Tables 4 and 8 (TEMP) and Tables 6 and 9 (TROP). Orthogonal contrasts and coefficients of

determination (R^2) are shown in Tables 5, 7, and 10. The range in R^2 was 0.29–0.57 for the 70 models used.

Tenderness and consumer palatability scores

Pasture-finished cattle had significantly higher (tougher) means for both objective measures of tenderness on the 2 muscles (LTL_C, LTL_SF, ST_C, and ST_SF) and lower consumer-assessed tenderness score (TEMP 61.9 and 59.3, TROP 47.8 and 40.9, for feedlot and pasture finishing, respectively). Conflicting reports exist on the effect of forage v. feedlot diets on tenderness. Differences in levels of fatness, carcass weights, and processing conditions (e.g. use of electrical stimulation) make comparisons across studies difficult. Gazzola *et al.* (1999) reported that steaks from pasture-fed steers were tougher (0.56 kg higher LTL_SF) than those from feedlot-finished steers. In their study, both groups were slaughtered at a similar liveweight (*c.* 625 kg). In contrast, Mandell *et al.* (1997) reported significantly lower SF for silage-fed yearling Charolais-cross steers compared with animals fed high moisture corn when finished to constant rib fat thickness endpoints. Dubeski *et al.* (1997) concluded that shear force was more sensitive to the rate of gain than to the diet. A similar conclusion was drawn by Muir *et al.* (1998b) in their review of the subject. Others (Harper 1999; Oddy *et al.* 2001) have promoted the view that the pattern of growth rather than the overall rate of growth may be more important in the context of beef tenderness/toughness. Certainly, large difference in growth paths existed in our study, particularly between feedlot- and pasture-finished groups. However, Perry *et al.* (2002) reported only a small effect of growth rate differences on consumer-assessed palatability scores.

Table 4. Least square means for meat quality traits for temperate breeds

See Table 1 for description of traits. DOM, domestic market weight; KOR, Korean market weight; JAP, Japanese market weight; FLOT, feedlot finishing; PAST, pasture finishing; SOUTH, temperate northern NSW; NORTH, subtropical central Qld

Levels	ST_C	ST_SF	ST_L*	ST_a*	ST_CL%	LTL_C	LTL_SF	LTL_L*
<i>Market weight (M)</i>								
DOM	2.06	4.59	46.92	22.01	21.59	1.67	4.15	39.48
KOR	2.04	4.79	46.33	24.86	21.39	1.66	4.23	39.38
JAP	1.98	4.82	45.40	25.66	21.15	1.57	4.07	39.94
<i>Finishing regime (F)</i>								
FLOT-SOUTH	1.92	4.50	47.48	23.45	21.75	1.55	3.94	41.06
PAST-SOUTH	2.14	4.96	45.53	24.67	21.17	1.74	4.35	38.16
<i>M × F</i>								
DOM-FLOT	1.97	4.49	47.97	21.79	22.00	1.60	4.05	40.76
DOM-PAST	2.14	4.70	45.61	22.32	20.95	1.74	4.21	38.08
KOR-FLOT	1.95	4.53	47.23	24.26	21.43	1.57	3.88	40.52
KOR-PAST	2.13	5.08	45.15	25.62	21.20	1.74	4.61	38.17
JAP-FLOT	1.82	4.53	45.94	24.91	21.28	1.45	3.95	41.66
JAP-PAST	2.16	5.14	44.58	26.55	20.88	1.70	4.21	38.12

Table 5. Solutions from orthogonal contrasts of main effects on meat quality traits for temperate breeds
See Table 1 for description of traits. See Table 4 for description of levels. All contrasts significantly different from zero (at $P = 0.05$); n.s., not significant

Contrast	ST_C	ST_SF	ST_L*	ST_a*	ST_CL%	LTL_C	LTL_SF	LTL_L*
<i>Market weight</i>								
R^2	0.33	0.34	0.34	0.49	0.29	0.36	0.29	0.37
DOM v. KOR	n.s.	-0.20	0.59	-3.65	0.43	n.s.	-0.08	n.s.
DOM v. JAP	0.08	-0.23	1.53	-2.85	0.19	0.10	0.07	-0.45
JAP v. KOR	-0.06	n.s.	-0.94	0.80	-0.24	-0.08	-0.16	0.56
<i>Finishing regime</i>								
R^2	0.39	0.41	0.36	0.53	0.35	0.48	0.34	0.38
PAST v. FLOT	0.23	0.46	-1.95	1.22	-0.57	0.19	0.41	-2.89

Table 6. Least square means meat quality traits for tropically adapted breeds
See Table 1 for description of traits. See Table 4 for description of levels

Levels	ST_C	ST_SF	ST_L*	LTL_C	LTL_SF	LTL_L*	LTL_a*	LTL_CL%
<i>Market weight (M)</i>								
DOM	2.14	4.75	48.50	1.78	4.83	38.59	20.66	22.59
KOR	2.17	4.85	47.27	1.85	4.78	38.09	23.03	22.26
JAP	2.12	4.90	46.60	1.82	4.67	37.99	24.42	22.46
<i>Sex</i>								
Heifer	2.21	4.87	48.01	1.78	4.80	38.05	22.21	22.29
Steer	2.07	4.69	48.79	1.79	4.64	38.94	21.79	22.54
<i>Sex \times M</i>								
Heifer-DOM	2.22	4.86	48.46	1.77	4.88	38.32	20.97	22.64
Steer-DOM	2.05	4.70	48.84	1.77	4.71	39.05	20.48	22.69
Heifer-KOR	2.22	4.96	47.05	1.83	4.81	37.73	23.34	22.04
Steer-KOR	2.10	4.77	48.14	1.83	4.66	38.76	22.92	22.45
<i>Finishing regime (F)</i>								
FLOT-NORTH	2.00	4.59	48.50	1.70	4.64	39.38	22.66	22.13
FLOT-SOUTH	1.93	4.72	50.25	1.67	4.57	39.96	22.19	22.91
PAST-NORTH	2.36	5.03	45.18	1.98	5.02	36.37	22.19	22.40
<i>M \times F</i>								
DOM-FN	2.04	4.57	49.20	1.66	4.60	39.66	20.47	22.09
DOM-FS	1.88	4.63	50.92	1.63	4.48	40.68	20.86	22.92
DOM-PN	2.42	5.03	45.91	1.96	5.23	36.48	19.71	22.71
KOR-FN	2.05	4.65	47.67	1.76	4.73	38.85	23.01	22.08
KOR-FS	1.95	4.74	49.30	1.69	4.57	39.61	22.50	22.65
KOR-PN	2.39	5.06	44.59	2.00	4.99	36.49	22.57	22.13
JAP-FN	1.94	4.61	46.81	1.72	4.62	39.15	24.84	22.82
JAP-FS	1.94	4.79	48.96	1.63	4.37	39.56	23.60	22.71
JAP-PN	2.32	5.17	42.87	2.05	5.03	35.47	24.84	22.19

Relatively small differences were observed for the effect of market weight on tenderness and these were not consistent between the 2 muscles. For TROP and TEMP, ST_SF increased with increasing market weight and hence age, whereas LTL_SF was lower in JAP than KOR or DOM in both TEMP and TROP. These trends were not observed in the compression measurements. Age-related decreases in tenderness have generally been ascribed to an increase in connective tissue toughness due to increased collagen cross-linking (Harper 1999). The compression measurement is believed to be a more sensitive measure of connective tissue differences (Harris and Shorthose 1988), yet there were

minimal changes in ST_C or LTL_C as market weight, and therefore animal age, increased. Thus, one conclusion that might be drawn is that the age-related changes in connective tissue toughness have not been large. This is perhaps further supported by the consumer-assessed tenderness results where once again no linear trend of increasing market weight on tenderness was apparent for TROP. For TEMP, KOR (LTL_TEND = 58.6) and JAP (LTL_TEND = 60.3) did not differ significantly for tenderness; however, DOM showed a significant increase in tenderness (LTL_TEND = 63.1). This is unlikely to be of practical importance given the size of the effect relative to the standard deviation of the trait (Table 2).

Table 7. Solutions from orthogonal contrasts of main effects on meat quality traits for tropically adapted breeds
See Table 1 for description of traits. See Table 4 for description of levels. All contrasts significantly different from zero (at $P = 0.05$); n.s., not significant

Contrast	ST_C	ST_SF	ST_L*	LTL_C	LTL_SF	LTL_L*	LTL_a*	LTL_CL%
<i>Market weight</i>								
R^2	0.48	0.32	0.45	0.46	0.40	0.46	0.56	0.32
DOM v. KOR	-0.03	-0.10	1.89	-0.07	n.s.	0.50	-2.37	0.33
DOM v. JAP	n.s.	-0.15	1.22	-0.04	0.17	0.61	-3.76	n.s.
JAP v. KOR	-0.04	n.s.	-0.67	-0.03	-0.11	n.s.	1.39	0.20
<i>Sex</i>								
R^2	0.50	0.33	0.43	0.44 ^A	0.39	0.48	0.55	0.35
Heifer v. steer	0.14	0.18	-0.77	–	0.16	-0.89	0.42	-0.25
<i>Finishing regime</i>								
R^2	0.48	0.32	0.45	0.46	0.40	0.46	0.57	0.38
PAST v. FLOT	0.36	0.44	-3.31	0.28	0.38	-3.01	-0.47	0.27
FN v. FS	0.08	-0.13	-1.76	0.03	n.s.	-0.58	0.47	-0.77

^AMain effect was not significant.

Table 8. Least square means for consumer assessed palatability traits for temperate breeds
See Table 1 for description of traits. See Table 4 for description of levels

Levels	LTL_TEND	LTL_JUIC	LTL_FLAV	LTL_OACC	LTL_MQ4
<i>Market weight</i>					
DOM	63.1	58.9	59.7	60.2	60.8
KOR	58.6	60.2	59.9	58.8	58.6
JAP	60.3	62.4	61.8	60.6	60.6
<i>Finishing regime</i>					
FLOT-SOUTH	61.9	61.2	62.4	61.8	61.6
PAST-SOUTH	59.3	60.2	59.2	58.3	58.6

Table 9. Least square means for consumer assessed palatability traits for tropically adapted breeds
See Table 1 for description of traits. See Table 4 for description of levels

Levels	LTL_TEND	LTL_JUIC	LTL_FLAV	LTL_OACC	LTL_MQ4
<i>Market weight</i>					
DOM	46.4	48.0	50.6	48.1	47.9
KOR	45.0	47.7	50.0	47.3	46.9
JAP	45.1	48.8	50.8	47.1	47.3
<i>Finishing regime</i>					
FLOT-NORTH	47.8	49.9	52.1	49.2	49.3
FLOT-SOUTH	48.7	50.7	53.4	51.0	50.5
PAST-NORTH	40.9	44.1	46.5	43.2	43.2
<i>Sex</i>					
Heifer	43.5	46.8	49.2	46.8	46.2
Steer	47.5	48.6	51.5	48.6	49.0

Overall, these results support those of Dubeski *et al.* (1997), in that as slaughter weight, and hence slaughter age, increased there were negligible effects on meat tenderness in heifers and steers ranging from 10 to 42 months of slaughter age.

The effect of market weight on consumer palatability traits was not significant for TROP. In contrast, for TEMP, JAP groups were 2–3 points higher for juiciness and flavour

scores than DOM and KOR, which may reflect differences observed for IMF% (Reverter *et al.* 2003a).

Heifers from TROP had significantly higher shear force and compression than steers, with the exception of LTL_C. Heifers had lower consumer palatability scores by about 2–4 points than steers. In general, the effect of geographic region on tenderness traits and consumer palatability traits for

Table 10. Solutions from orthogonal contrasts of main effects on consumer assessed palatability traits for temperate and tropically adapted breeds

See Table 1 for description of traits. See Table 4 for description of levels. All contrasts significantly different from zero (at $P = 0.05$); n.s., not significant

Effect	Contrast	LTL_TEND	LTL_JUIC	LTL_FLAV	LTL_OACC	LTL_MQ4
<i>Temperate breeds</i>						
Market weight	R^2	0.49	0.42	0.39	0.44 ^A	0.46
	DOM v. KOR	4.42	n.s.	n.s.	–	2.20
	DOM v. JAP	2.73	–3.45	–2.15	–	n.s.
	JAP v. KOR	n.s.	2.19	1.92	–	2.00
Finishing regime	R^2	0.49	0.42	0.39	0.44	0.46
	PAST v. FLOT	–2.66	–0.93	–3.21	–3.52	–3.02
<i>Tropically adapted breeds</i>						
Market weight	R^2	0.49 ^A	0.48 ^A	0.41 ^A	0.47 ^A	0.48 ^A
Sex	R^2	0.47	0.47	0.40	0.45	0.46
	Heifer v. steer	–4.07	–1.83	–2.29	–2.84	–3.01
Finishing regime	R^2	0.49	0.49	0.41	0.47	0.48
	PAST v. FLOT	–6.91	–5.82	–5.59	–5.99	–6.12
	FN v. FS	n.s.	n.s.	n.s.	–1.83	n.s.

^AMain effect was not significant.

TROP was small. However, ST_SF was higher in the FLOT-SOUTH (4.72 kg) than the FLOT-NORTH group (4.59 kg).

Cooking loss %

For TEMP, carcasses from DOM had slightly higher ST_CL% than KOR and JAP market weight groups; similar trends were observed for LTL_CL% for TROP. Only small differences were observed for the effect of pasture v. feedlot finishing on cooking loss. For TROP, a geographic region effect was observed where the FLOT-SOUTH group had a higher cooking losses (LTL_CL% = 22.91%) than the FLOT-NORTH group (22.13%). In general, the magnitudes of the differences for cooking loss % were small. French *et al.* (2001) also reported no dietary treatment effects (combinations of grass silage, concentrates, and pasture) on LTL cooking loss %.

Meat colour (L^* and a^* values)

Cattle finished on pasture had significantly lower (darker) LTL_L* and ST_L* values than those from the feedlot for both TEMP and TROP. French *et al.* (2000, 2001) reported no differences in L^* values between dietary treatments (combinations of grass silage, concentrates, and pasture). However, Bennett *et al.* (1995) reported darker meat in forage-fed animals than concentrate-fed animals, but the forage-fed animals were older at slaughter. Several authors have suggested higher muscle myoglobin content in pasture-fed animals as a possible explanation (Bidner *et al.* 1986; Varnam and Sutherland 1995) but it could also simply be that myoglobin content increases with age (Young and West 2001). Muir *et al.* (1998a, 1998b) concluded that improved lean colour was generally associated with younger animals. However, in the present study, little or no difference was

observed in LTL_L* with increasing market weights and, hence, age, although increasing market weight resulted in lower (i.e. darker) ST_L* for both TEMP and TROP and higher (i.e. redder) ST_a* for TEMP and higher LTL_a* for TROP. The observed difference in meat colour between feedlot and pasture in this study may also be in part due to more marbling in the feedlot-finished group (see Reverter *et al.* 2003a) and this could lead to increased meat brightness (Muir *et al.* 1998b).

Heifers had significantly darker, redder meat than steers. Page *et al.* (2001) reported similar results. For TROP, the FLOT-SOUTH group had higher ST_L* and LTL_L* (i.e. brighter meat) than FLOT-NORTH.

Genetic parameters

Consumer-assessed palatability traits had higher heritabilities for TROP than TEMP, but all scores were highly correlated both phenotypically and genetically (>0.93) for both TEMP and TROP (Tables 11 and 12). For TROP, LTL_TEND and LTL_MQ4 had the highest heritabilities (0.31 ± 0.09 and 0.32 ± 0.09 , respectively) of the sensory traits. Therefore, for all further analyses with objective measures, only LTL_TEND was used. For all objectively measured traits, TROP had higher heritabilities than TEMP. For TROP, the heritabilities for LTL_C, LTL_SF, LTL_L*, and LTL_TEND were 0.19, 0.30, 0.18, and 0.31, respectively, compared with 0.08, 0.09, 0.17, and 0.18 for TEMP. ST_C, ST_SF, and ST_L* were 0.27, 0.42, and 0.16, respectively, for TROP, and 0.12, 0.11, and 0.17 for TEMP. ST_CL% had a heritability of 0.15 in TEMP and LTL_CL% had a heritability of 0.20 in TROP. Finally, ST_a* and LTL_a* had a heritability of 0.13 in both TEMP and TROP (Tables 13 and 14). Standard errors on

Table 11. Heritabilities (diagonal) and genetic (above) and phenotypic (below) correlations between consumer-assessed palatability traits for temperate breeds

See Table 1 for description of traits. Heritabilities pooled over all bivariate estimates. Standard errors of heritability and genetic correlation estimates ranged from 0.04 to 0.08 and from 0.08 to 0.21, respectively

	LTL_TEND	LTL_JUIC	LTL_FLAV	LTL_OACC	LTL_MQ4
LTL_TEND	0.10	1.00	0.93	1.00	n.c.
LTL_JUIC	0.78	0.15	0.99	1.00	n.c.
LTL_FLAV	0.77	0.77	0.05	0.99	0.99
LTL_OACC	0.86	0.81	0.92	0.10	n.c.
LTL_MQ4	n.c.	n.c.	0.90	n.c.	0.13

n.c., Non-convergence.

Table 12. Heritabilities (diagonal) and genetic (above) and phenotypic (below) correlations between consumer-assessed palatability traits for tropically adapted breeds

See Table 1 for description of traits. Heritabilities pooled over all bivariate estimates. Standard errors of heritability and genetic correlation estimates ranged from 0.07 to 0.09 and from 0.01 to 0.06, respectively

	LTL_TEND	LTL_JUIC	LTL_FLAV	LTL_OACC	LTL_MQ4
LTL_TEND	0.31	0.93	1.00	1.00	1.00
LTL_JUIC	0.77	0.20	0.97	0.98	0.96
LTL_FLAV	0.76	0.77	0.23	1.00	1.00
LTL_OACC	0.86	0.81	0.91	0.27	1.00
LTL_MQ4	0.95	0.85	0.95	0.96	0.32

Table 13. Additive genetic variances (V_a), heritabilities (diagonal), and genetic (above) and phenotypic (below) correlations between meat quality traits for temperate breeds

See Table 1 for description of traits. Standard errors of heritability and genetic correlation estimates ranged from 0.01 to 0.02 and from 0.04 to 0.11, respectively

	V_a	ST_C	ST_SF	ST_L*	ST_a*	ST_CL%	LTL_C	LTL_SF	LTL_L*	LTL_TEND
ST_C	0.01	0.12	0.67	-0.30	0.29	0.22	0.60	0.31	-0.13	-0.78
ST_SF	0.03	0.30	0.11	-0.51	-0.06	-0.17	0.17	0.59	-0.04	-0.42
ST_L*	1.23	-0.01	0.00	0.17	-0.18	0.31	-0.15	-0.37	0.76	0.18
ST_a*	0.67	0.09	0.02	-0.03	0.13	0.21	0.11	0.19	-0.54	-0.06
ST_CL%	0.35	0.12	0.07	0.30	0.18	0.15	0.25	0.07	-0.19	-0.47
LTL_C	0.00	0.18	0.12	0.03	0.07	0.11	0.08	0.45	-0.10	-0.90
LTL_SF	0.04	0.05	0.13	-0.19	-0.08	-0.06	0.25	0.09	-0.23	-0.49
LTL_L*	0.86	-0.03	-0.01	0.42	0.00	0.13	-0.04	-0.18	0.17	0.12
LTL_TEND	23.60	-0.08	-0.14	-0.04	0.03	-0.06	-0.21	-0.27	0.03	0.18

Table 14. Additive genetic variances (V_a), heritabilities (diagonal), and genetic (above) and phenotypic (below) correlations between meat quality traits for tropically adapted breeds

See Table 1 for description of traits. Standard errors of heritability and genetic correlation estimates ranged from 0.02 to 0.04 and from 0.04 to 0.09, respectively

	V_a	ST_C	ST_SF	ST_L*	LTL_C	LTL_SF	LTL_L*	LTL_a*	LTL_CL%	LTL_TEND
ST_C	0.02	0.27	0.83	-0.21	0.63	0.21	-0.28	0.09	0.28	-0.60
ST_SF	0.13	0.32	0.42	-0.23	0.65	0.46	-0.29	0.02	0.35	-0.73
ST_L*	1.50	-0.04	-0.04	0.16	-0.24	-0.25	0.64	0.25	0.11	0.12
LTL_C	0.01	0.17	0.17	-0.08	0.19	0.38	-0.39	-0.14	0.46	-0.70
LTL_SF	0.19	0.06	0.19	-0.16	0.24	0.30	-0.40	-0.60	-0.11	-0.79
LTL_L*	0.97	-0.06	-0.06	0.30	-0.17	-0.22	0.18	0.24	-0.01	0.54
LTL_a*	0.55	-0.01	-0.01	0.09	-0.05	-0.22	0.09	0.13	0.15	0.22
LTL_CL%	0.49	0.03	0.05	0.04	0.28	0.15	-0.11	0.10	0.20	-0.15
LTL_TEND	45.95	-0.06	-0.21	0.08	-0.26	-0.36	0.14	0.06	-0.13	0.31

heritability estimates ranged from 0.01 to 0.04. In a recent review, Burrow *et al.* (2001) reported weighted heritability estimates (predominantly from the LTL) for *Bos taurus* groups and *Bos indicus/Bos taurus* groups, respectively, of 0.21 and 0.26 for shear force, taste panel tenderness 0.19 and 0.23, taste panel juiciness 0.20 and 0.12, and taste panel flavour 0.02 and 0.07. In an earlier review, Marshall (1999) reported mean heritability estimates of 0.25, 0.29, 0.17, 0.26, and 0.24 for shear force, L* value, a* value, pH, and water loss. The results from the present study are also consistent with the preliminary tenderness genetic estimates on a subset of these data (approximately half the data), published by Robinson *et al.* (2001). The moderate heritabilities and phenotypic variances for TROP suggest that scope exists for genetic improvement in meat quality traits. Ferguson *et al.* (2000) showed that electrical stimulation reduced the differences in shear force between animals with increasing Brahman content. However, in our study, significant amounts of genetic variation still existed within TROP after the use of electrical stimulation. Results for the temperate breeds suggest limited scope for the genetic improvement of meat quality traits under best industry practice management systems employed by the Beef CRC, which concurs with the earlier findings of Robinson *et al.* (2001).

Phenotypic correlations (r_p) were generally lower than genetic correlations. The magnitude and direction of the correlations were similar for TEMP and TROP (see Tables 13 and 14). The r_p values between LTL_SF and LTL_TEND and between LTL_L* and ST_L* were -0.27 and 0.42 for TEMP and -0.36 and 0.30 for TROP, respectively. Phenotypic correlations across muscles (LTL, ST) or methods (SF, C) were generally low and suggest that tenderness in one muscle (or method) is not a good phenotypic predictor of tenderness in the other muscle (or method). Harris and Shorthose (1988) and Shackelford *et al.* (1995) reported similar conclusions.

Genetic correlations between shear force and compression measures were positive, with higher correlations observed for the ST (0.83 ± 0.04 for TROP and 0.67 ± 0.07 for TEMP) than the LTL (0.38 ± 0.05 for TROP and 0.45 ± 0.05 for TEMP). Genetic correlations between the muscles for the same measure were 0.63 ± 0.06 for compression and 0.46 ± 0.05 for SF for TROP and 0.60 ± 0.07 and 0.59 ± 0.07 for TEMP. Therefore, selection for tenderness in one muscle is likely to result in a commensurate improvement in the other muscle. Likewise for SF and C, selection for one trait will have favourable correlated improvements genetically in the other. These effects will be more useful for improving overall tenderness in TROP given the higher heritabilities. Robinson *et al.* (2001) reported generally lower genetic correlations between the same measure on the different muscles using a subset of these data.

Genetic correlations of LTL_TEND with compression and shear force measurements were high and negative for TROP and TEMP. For TROP, the genetic correlations of LTL_TEND with LTL_SF, ST_SF, LTL_C, and ST_C were -0.79 ± 0.04 , -0.73 ± 0.04 , -0.70 ± 0.04 , and -0.60 ± 0.06 , respectively. This shows that the objective measures of tenderness (measured 24 h post-slaughter) and consumer-assessed tenderness (after 14 days aging) were genetically similar traits. In his review, Marshall (1999) reported that the average genetic correlation (from 9 estimates) between shear force and sensory taste panel tenderness was -0.86 . Aging time was not always documented but it is expected that in the majority of the studies, shear force and sensory scores were determined on 14-day-aged samples.

Muscle colour (LTL_L*) was negatively genetically correlated with all measures of tenderness for TEMP and TROP. For TROP, LTL_L* was genetically correlated with LTL_SF (-0.40 ± 0.07) and with LTL_TEND (0.54 ± 0.07). In addition, LTL_a* was correlated genetically with LTL_SF (-0.60 ± 0.06) and with LTL_TEND (0.22 ± 0.08). Genetic correlations of LTL_L* and ST_L* were positive for TROP (0.64 ± 0.06) and TEMP (0.76 ± 0.05). These results indicate that correlated improvement in LTL (and ST) tenderness could be achieved through indirect selection on LTL_L* and LTL_a* colour. If single-trait selection was practiced, theoretically, the accuracy of direct selection on LTL_TEND would be 0.56 compared with the indirect single-trait selection on LTL_SF, LTL_L*, and LTL_a*, which would be 0.43, 0.23 and 0.08, respectively. No other literature estimates were found for these genetic relationships; however, several studies have reported similar phenotypic or residual correlations between shear force and L* colour (Dubeski *et al.* 1997; Wulf *et al.* 1997; Wulf and Page 2000). Correlations between cooking loss % and other traits varied between TEMP and TROP. For TROP, LTL_CL% was positively correlated with LTL_C, ST_C, and ST_SF but slightly negatively with LTL_SF (-0.11). For TEMP, the genetic correlations between ST_CL% and all other traits were generally small with the exception of a -0.47 correlation with LTL_TEND. Further work is required to investigate the usefulness of colour measures as a phenotypic predictor of tenderness.

Market weight effect

Additive variances and heritabilities varied between market and between TEMP and TROP (Tables 15 and 16). In general, additive variances for tenderness measures were similar or higher in DOM compared with EXP, with the exception of LTL_C for TROP. For TEMP, the additive variance for LTL_L* in DOM was considerably higher (1.96 units²) than in export (0.63 units²), although the phenotypic variances were similar.

Genetic correlations between market groups for TROP were unity for ST_C, ST_SF, LTL_a*, and LTL_CL%,

Table 15. Additive genetic variances (V_a), heritabilities (h^2), and genetic correlations (r_g) by market weight and finishing regime for meat quality traits for temperate breeds

See Table 1 for description of traits. See Table 4 for a description of levels

Level		ST_C	ST_SF	ST_L*	ST_a*	ST_CL%	LTL_C	LTL_SF	LTL_L*
<i>Market weight^A</i>									
DOM	V_a	0.02	0.07	0.65	0.17	0.37	0.002	0.06	1.96
	h^2	0.31	0.28	0.09	0.04	0.13	0.04	0.13	0.49
EXP	V_a	0.01	0.03	1.79	1.09	0.39	0.003	0.03	0.63
	h^2	0.12	0.10	0.24	0.21	0.19	0.10	0.07	0.12
	r_g	0.43	0.42	0.69	1.00	0.88	1.00	1.00	0.49
<i>Finishing regime^B</i>									
FLOT-SOUTH	V_a	0.01	0.02	1.26	1.01	0.25	0.002	0.02	0.66
	h^2	0.24	0.08	0.21	0.20	0.13	0.07	0.06	0.14
PAST-SOUTH	V_a	0.01	0.04	1.35	0.47	0.57	0.003	0.07	0.98
	h^2	0.10	0.12	0.15	0.09	0.21	0.08	0.13	0.18
	r_g	0.54	1.00	1.00	0.92	0.84	1.00	0.79	1.00

^AStandard errors were not able to be approximated as a result of the unity correlations; s.e.s of remaining heritability and genetic correlation estimates ranged from 0.03 to 0.10 and from 0.17 to 0.32, respectively.^BStandard errors were not able to be approximated as a result of the unity correlations; s.e.s of remaining heritability and genetic correlation estimates ranged from 0.04 to 0.06 and from 0.25 to 0.36, respectively.**Table 16. Additive genetic variances (V_a), heritabilities (h^2), and genetic correlations (r_g) by market weight, finishing regime, and geographic region for meat quality traits for tropically adapted breeds**

See Table 1 for description of traits. See Table 4 for a description of levels

Level		ST_C	ST_SF	ST_L*	LTL_C	LTL_SF	LTL_L*	LTL_a*	LTL_CL%
<i>Market weight^A</i>									
DOM	V_a	0.026	0.12	1.90	0.006	0.28	0.83	0.40	0.52
	h^2	0.34	0.45	0.22	0.14	0.41	0.17	0.11	0.20
EXP	V_a	0.017	0.13	1.43	0.010	0.16	1.13	0.61	0.48
	h^2	0.23	0.40	0.14	0.21	0.27	0.20	0.13	0.20
	r_g	1.00	1.00	0.79	0.82	0.89	0.71	1.00	1.00
<i>Finishing regime^B</i>									
FLOT-NORTH	V_a	0.01	0.15	3.01	0.009	0.26	1.31	0.31	0.56
	h^2	0.18	0.52	0.29	0.22	0.47	0.20	0.07	0.23
PAST-NORTH	V_a	0.03	0.18	1.79	0.008	0.16	0.99	0.69	0.85
	h^2	0.30	0.54	0.16	0.13	0.20	0.21	0.17	0.31
	r_g	1.00	0.80	0.89	1.00	1.00	0.68	1.00	0.69
<i>Geographic region^C</i>									
FLOT-SOUTH	V_a	0.02	0.08	0.69	0.007	0.18	1.44	0.72	0.43
	h^2	0.30	0.30	0.09	0.18	0.33	0.26	0.17	0.20
FLOT-NORTH	V_a	0.01	0.15	3.01	0.009	0.26	1.31	0.31	0.56
	h^2	0.18	0.52	0.29	0.22	0.47	0.20	0.07	0.23
	r_g	0.95	0.82	0.90	1.00	0.86	0.84	1.00	0.80

^AStandard errors were not able to be approximated as a result of the unity correlations; s.e.s of remaining heritability and genetic correlation estimates ranged from 0.03 to 0.08 and from 0.10 to 0.21, respectively.^BStandard errors were not able to be approximated as a result of the unity correlations; s.e.s of remaining heritability and genetic correlation estimates ranged from 0.04 to 0.06 and from 0.04 to 0.20, respectively.^CStandard errors were not able to be approximated as a result of the unity correlations; s.e.s of remaining heritability and genetic correlation estimates ranged from 0.06 to 0.10 and from 0.13 to 0.16, respectively.

whereas genetic correlations between market weights for LTL_C, LTL_SF, LTL_L*, and ST_L* were 0.82, 0.89, 0.71, and 0.79, respectively. For TEMP, the genetic correlations between market weights for LTL_C, LTL_SF, and ST_a* were unity, but were 0.43 ± 0.22 , 0.42 ± 0.25 , 0.69 ± 0.33 , 0.88 ± 0.29 , and 0.49 ± 0.17 for ST_C, ST_SF, ST_L*,

ST_CL%, and LTL_L*, respectively. No other literature estimates were found relating to the effect of market weight on the genetic expression of meat quality traits. The results showed changes in the genetic expression of meat quality traits with market weight but the genetic correlations were generally high, particularly for TROP. Some re-ranking of

sires across market weights may be expected for ST measures and LTL_L* for TEMP and LTL_L* for TROP breeds but the impact of such a re-ranking in a breeding program will depend on the distribution of records across market weights.

Finishing regime effect

Additive variances and heritability for all measures for TEMP were higher in pasture than feedlot finishing, with the exception of ST_C and ST_a*. Similarly, for TROP, tenderness measures on the ST muscle, LTL_a*, and LTL_CL% were more heritable in pasture than grain finishing. But for other measures on the LTL (LTL_C, LTL_SF, LTL_L*) and ST_L*, additive variances and heritabilities were higher for Feedlot North than the Pasture North group. Geographic region had little effect on the genetic expression of meat quality traits, with the exception of ST_L*, which had a higher additive variance and heritability in Feedlot North carcasses than the Feedlot South group.

Genetic correlations between finishing regime for TEMP were very high and close to unity for LTL_C, LTL_L*, ST_SF, ST_L*, and ST_a* but lower for LTL_SF (0.72 ± 0.36), ST_C (0.54 ± 0.25), and ST_CL% (0.84 ± 0.25); however, all standard errors were large. For TROP, the genetic correlations between pasture and feedlot were high for LTL_C, LTL_SF, LTL_a*, ST_C, and ST_L* but lower for LTL_L* (0.68 ± 0.16), LTL_CL% (0.69 ± 0.14), and ST_SF (0.80 ± 0.09). Genetic correlations for traits across geographic regions were all >0.80 , with standard errors of 0.13 – 0.16 , and suggest little evidence of genotype \times region interactions.

Conclusions

This study has added greatly to the knowledge of the genetic and phenotypic influences on meat quality in temperate and tropically adapted cattle breeds under Australian production and market systems. We emphasise that the results were generated under a given set of pre- and post-slaughter protocols that reflected best practice Australian processing conditions. Extrapolation of results beyond these given conditions is likely to generate incorrect conclusions.

Results for the temperate breeds suggest that limited scope exists for the genetic improvement of meat quality. In contrast, opportunities for genetic improvement for the tropically adapted breeds appear possible given the moderate heritabilities, adequate phenotypic variance, favourable genetic correlations between traits, and little evidence of genotype by environment interactions. However, the ability of the current seedstock industry to routinely measure these traits on large numbers of animals is limited. This may be overcome by selecting an easy-to-measure correlated trait(s) or genetic markers if they exist, or through the restructuring of the seedstock industry to allow large scale, ongoing

progeny testing programs that include the collection of meat quality records. However, the collection of samples and methods for measuring meat quality traits will also need advancing if this is to be an option.

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References

- Bennett LL, Hammond AC, Williams MJ, Kunkle WE, Johnson DD, Treston RL, Miller MF (1995) Performance, carcass yield, and carcass quality characteristics of steers finished on *Rhizoma Peanut (Arachis glabrata)*-tropical grass pasture or concentrate. *Journal of Animal Science* **73**, 1881–1887.
- Bidner TD, Schupp AR, Mohamad AB, Rumore NC, Montgomery RE, Bagley CP, McMillin KW (1986) Acceptability of beef from Angus-Hereford or Angus-Hereford-Brahman steers finished on all-forage or a high energy diet. *Journal of Animal Science* **63**, 381–387.
- Bindon BM (2001) Genesis of the Cooperative Research Centre for the Cattle and Beef Industry: integration of resources for beef quality research (1993–2000). *Australian Journal of Experimental Agriculture* **41**, 843–853.
- Boleman SJ, Boleman SL, Miller RK, Taylor JF, Cross HR, Wheeler TL, Koohmaraie M, Shakelford SD, Miller MF, West RL, Johnson DD, Savel JM (1997) Consumer evaluation of beef of known categories of tenderness. *Journal of Animal Science* **75**(6), 1521–1524.
- Burrow HM, Moore SS, Johnston DJ, Barendse W, Bindon BM (2001) Quantitative and molecular genetic influences on properties of beef. *Australian Journal of Experimental Agriculture* **41**, 893–919.
- Dubesi PL, Aalhus JL, Jones SD, Robertson WM, Dyck RS (1997) Meat quality of heifers fattened to heavy weights to enhance marbling. *Canadian Journal of Animal Science* **77**, 635–643.
- Egan AF, Ferguson DM, Thompson JM (2001) Consumer requirements for beef and their implications for the Australian beef industry. *Australian Journal of Experimental Agriculture* **41**, 893–919.
- Ferguson DM, Bruce HL, Thompson JM, Egan AF, Perry D, Shorthose WR (2001) Factors affecting beef palatability—farmgate to chilled carcass. *Australian Journal of Experimental Agriculture* **41**, 879–891.
- Ferguson DM, Jiang S, Hearnshaw H, Rymill SR, Thompson JM (2000) Effect of electrical stimulation on protease activity and tenderness of *M. longissimus* from cattle with different proportions of *Bos indicus* content. *Meat Science* **55**, 265–272.
- French P, O'Riordan EG, Monahan FJ, Caffrey PJ, Mooney MT, Troy DJ, Moloney AP (2001) The eating quality of meat of steers fed grass and/or concentrates. *Meat Science* **57**, 379–386.

- French P, O'Riordan EG, Monahan FJ, Caffrey PJ, Vidal M, Mooney MT, Troy DJ, Moloney AP (2000) Meat quality of steers finished on autumn grass, grass silage or concentrate-based diets. *Meat Science* **56**, 173–180.
- Gazzola C, O'Neill CJ, Frisch JE (1999) Comparative evaluation of the meat quality of beef cattle breeds of Indian, African and European origins. *Animal Science* **69**, 135–142.
- Gilmour AR, Cullis BR, Welham SJ, Thompson R (1999) ASREML. Biometrics, Bulletin No. 3, NSW Agriculture, Orange, Australia.
- Groeneveld E, García-Cortéz LA (1998) VCE4.0, a (co)variance component package for frequentists and Bayesians. In 'Proceedings of the 6th World Congress on Genetics Applied Livestock Production'. Armidale. Vol. 27, pp. 455–458.
- Harper GS (1999) Trends in skeletal muscle biology and the understanding of toughness in beef. *Australian Journal of Agricultural Research* **50**, 1105–1129.
- Harris PV, Shorthose WR (1988) Meat texture. In 'Developments in Meat Science—4'. (Ed. RA Lawrie) p. 245 (Elsevier Applied Science Publishers: London)
- Johnston DJ, Reverter A, Burrow HM, Oddy VH, Robinson DL (2003). Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 1. Animal measures. *Australian Journal of Agricultural Research* **54**, 107–118.
- Johnston DJ, Reverter A, Robinson DL, Ferguson DM (2001) Sources of variation in mechanical shear force measures of tenderness in beef from tropically adapted genotypes, effects of data editing and their implications for genetic parameter estimation. *Australian Journal of Experimental Agriculture* **41**, 991–996.
- Mandell IB, Gullet EA, Buchanan-Smith JG, Campbell CP (1997) Effects of diet and slaughter endpoint on carcass composition and beef quality in Charolais cross steers. *Canadian Journal of Animal Science* **77**, 403–414.
- Marshall DM (1999) The genetics of meat quality. In 'The genetics of cattle'. (Eds R Fries, A Ruvinsky) p. 605 (CABI: Wallingford, UK)
- Muir PD, Deakin JM, Bown MD (1998b) Effects of forage- and grain-based feeding systems on beef quality: A review. *New Zealand of Agricultural Research* **41**, 623–635.
- Muir PD, Smith NB, Wallace GJ, Cruckshank GJ, Smith DR (1998a) The effect of short-term grain feeding on liveweight gain and beef quality. *New Zealand of Agricultural Research* **41**, 517–526.
- Oddy VH, Harper GS, Greenwood PL, McDonagh MB (2001) Nutritional and developmental effects on the intrinsic properties of muscles and how they relate to the eating quality of beef. *Australian Journal of Experimental Agriculture* **41**, 921–942.
- Page JK, Wulf DM, Schwotzer TR (2001) A survey of muscle color and pH. *Journal of Animal Science* **79**, 678–687.
- Perry D, Shorthose WR, Ferguson DM, Thompson JM (2001) Methods used in the CRC program for the determination of carcass yield and beef quality. *Australian Journal of Experimental Agriculture* **41**, 893–919.
- Perry D, Thompson JM, Reverter A, Johnston DJ (2002) Effect of growth rate on palatability in beef cattle. In 'Proceeding of the 48th International Congress of Meat Science and Technology'. Rome, Italy, Vol. 48, pp. 276–277. (ICoMST: Rome)
- Polkinghorne R, Watson R, Porter M, Gee A, Scott, J, Thompson J (1999) Meat Standards Australia, a 'PACCP' based beef grading scheme for consumers. 1. The use of consumer scores to set grade standards. In 'Proceeding of the 45th International Congress of Meat Science and Technology'. Yokohama, Japan, Vol. 45. Pp. 14–15. (ICoMST: Yokohama)
- Reverter A, Johnston DJ, Perry D, Goddard ME, Burrow HM (2003a) Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 2. Abattoir carcass traits. *Australian Journal of Agricultural Research* **54**, 119–134.
- Reverter A, Johnston DJ, Ferguson DM, Perry D, Goddard ME, Burrow HM, Oddy VH, Thompson JM, Bindon BM (2003b) Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 4. Correlations among animal, abattoir carcass, and meat quality traits. *Australian Journal of Agricultural Research* **54**, 149–158.
- Robinson DL (1995) Design of the CRC straightbreeding genetics experiments. *Proceedings of the Australian Association Animal Breeding Genetics* **11**, 541–545.
- Robinson DL, Ferguson DM, Oddy VH, Perry D, Thompson J (2001) Genetic and environmental influences on beef tenderness. *Australian Journal of Experimental Agriculture* **41**, 997–1003.
- SAS Institute Inc (1988) 'SAS procedures guide. Release 6.03 edition.' (SAS Institute Inc.: Cary, NC)
- Shackelford SD, Wheeler TL, Koohmaraie M (1995) Relationship between shear force and trained sensory panel tenderness ratings of 10 major muscles from *Bos indicus* and *Bos taurus* cattle. *Journal of Animal Science* **73**, 3333–3340.
- Upton W, Burrow HM, Dundon A, Robinson DL, Farrell EB (2001) Cooperative Research Centre breeding program design, measurements and database—methods that underpin CRC research results. *Australian Journal of Experimental Agriculture* **41**, 943–952.
- Varnam AH, Sutherland JP (1995) The colour of meat. In 'Meat and meat products-technology, chemistry and micro biology'. p. 26 (Chapman and Hall: London)
- Wulf DM, O'Connor SF, Tatum JD, Smith GC (1997) Using objective measures of muscle color to predict beef longissimus tenderness. *Journal of Animal Science* **75**, 684–692.
- Wulf DM, Page JK (2000) Using measurements of muscle color, pH, and electrical impedance to augment the current USDA beef quality grading standards and improve the accuracy and precision of sorting carcasses into palatability groups. *Journal of Animal Science* **78**, 2595–2607.
- Young OA, West J (2001) Meat color. In 'Meat science and applications'. (Eds YH Hui, W Nip RW Rogers, OA Young) p. 53 (Marcel Dekker Inc.: New York)

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