

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

4. Correlations among animal, carcass, and meat quality traits*

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Abstract. Beef cattle data from temperate (TEMP, $n = 3947$) and tropically adapted (TROP, $n = 4137$) breeds were analysed to compute estimates of genetic and phenotypic correlations between animal, abattoir carcass, and meat quality measures. Live animal traits included: liveweight (S2LWT), scanned subcutaneous rump fat depth (S2P8), scanned eye muscle area (S2EMA), flight time (S1FT), and finishing average daily gain (FADG). Carcass traits included: hot carcass weight (CWT), retail beef yield percentage (RBY), intramuscular fat percentage (IMF), subcutaneous rump fat depth (P8), eye muscle length by width (ELW), and meat colour score (MEATC). Meat quality measures taken on 2 muscles [*M. longissimus thoracis et lumborum* (LTL) and *M. semitendinosus* (ST)] included: shear force of LTL (LTL_SF) and ST (ST_SF); compression of the ST (ST_C); cooking loss % of the LTL (LTL_CL%) and ST (ST_CL%); Minolta LTL L* (LTL_L*), a* (LTL_a*), ST a* (ST_a*); and consumer-assessed LTL tenderness score (LTL_TEND). Genetic and phenotypic correlations between animal measures and related carcass traits were moderate to very high for TEMP and TROP. Genetic correlations between S2LWT and CWT were 0.89 and 0.82, between S2P8 and P8 0.80 and 0.88, and between S2EMA and ELW 0.62 and 0.68, for TEMP and TROP, respectively. Genetic correlations between animal measures and other carcass traits varied; moderate genetic correlations were estimated between S2P8 and RBY (−0.57, −0.19 for TEMP, TROP) and S2P8 and IMF (0.39, 0.23 for TEMP, TROP). Genetic correlations between animal and meat quality measures were moderate to low. For TEMP, moderate genetic correlations were estimated between S2P8 and LTL_TEND (0.38), FADG and ST_a* (−0.49), and FADG and LTL_TEND (0.45); and for TROP, S1FT and LTL_SF (−0.54), and S2EMA and LTL_L* (−0.46). Phenotypic correlations between animal and meat quality were generally low and close to zero. Several moderate to high genetic correlations existed between carcass and meat quality traits. In general, fatness measures were genetically correlated with tenderness (e.g. IMF and LTL_TEND 0.61, 0.31 for TEMP, TROP). CWT was genetically correlated with meat colour (CWT and LTL_L* 0.66, 0.60 for TEMP, TROP) and objective tenderness measures (CWT and ST_C −0.52, −0.22 for TEMP, TROP). Once again phenotypic correlations between carcass and meat quality were low, indicating that few phenotypic predictors of meat quality traits were identified. Several of the genetic correlations show that both animal and abattoir carcass traits may be of use as indirect measures for carcass and meat quality traits in multiple trait genetic evaluation systems.

Additional keywords: beef, carcass quality, genetic correlation, phenotypic correlation.

*This paper is the last of a series of four papers presented in this issue.

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Introduction

Improvement of carcass and meat quality traits is vital to Australia's beef industry, as both our domestic and overseas customers are placing greater emphasis on aspects of meat quality (Egan *et al.* 2001). Results presented in the first 3 papers of this series (Johnston *et al.* 2003a, 2003b; Reverter *et al.* 2003) have established that many of the traits associated with carcass yield, fatness, marbling, and meat tenderness are heritable and can be improved by selection. This was particularly the case for many of the carcass traits and meat tenderness for the tropically adapted breeds. However, in order to incorporate these traits in a genetic evaluation scheme and to design appropriate breeding programs, genetic and phenotypic correlations between existing and new traits are required. The genetic correlations can also be used to identify correlated measures that can be used as indirect selection criteria for, often difficult and costly to measure, carcass and meat quality traits.

This paper is the last in a series of 4 papers and reports genetic and phenotypic relationships between measures of animal, carcass, and meat quality traits from the straightbreeding project of the Cooperative Research Centre for Cattle and Beef Quality (Beef CRC). A total of 17 and 18 traits for temperate and tropically adapted breeds, respectively, were selected from all of the animal, carcass, and meat quality measurements, and genetic and phenotypic correlations were estimated between all possible trait combinations.

Materials and methods

Animals

Details of the design of the breeding program and complete management of the animals were described by Upton *et al.* (2001). Briefly, cattle were classified by breed into 2 groups: temperate (TEMP) and tropically adapted (TROP). TEMP breeds included Angus, Hereford, Murray Grey, and Shorthorn. TROP breeds included Brahman, Belmont Red, and Santa Gertrudis. Cooperating herds provided the Beef CRC on average with 25 fully pedigreed progeny born from 1993 to 1998 from each of 4 home-bred sires per year, as well as generating linkages across herds through the use of 2 additional link sires per year (about 12 progeny per link sire). Calves were purchased by the Beef CRC at weaning from 34 herds throughout eastern Australia. Additionally, records on 320 straightbred Brahman steers and heifers derived from the Beef CRC crossbreeding project (Upton *et al.* 2001) from 2 additional herds were also included in the analyses. All sires 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 number of sires used was 232 and 163 for TEMP and TROP, respectively. Table 1 details the distribution of animals by main effects within TEMP and TROP.

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. Cattle were assigned to 1 of 3 target-market carcass-weight groups (domestic 220 kg, Korean 280 kg, and Japanese 340 kg). Market

Table 1. Number of animals by the design variables for temperate and tropically adapted breeds

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; TEMP, temperate breeds; TROP, tropically adapted breeds

Treatment	Level	Breed group	
		TEMP	TROP
Breed	Angus	1843	—
	Hereford	1136	—
	Murray Grey	456	—
	Shorthorn	512	—
	Brahman	—	1220
	Belmont Red	—	1581
	Santa Gertrudis	—	1336
Sex	Steer	3507	2369
	Heifer	440	1768
Market weight	DOM	1428	1556
	KOR	1358	1774
	JAP	1161	807
Finishing regime	FLOT-SOUTH	2124	1383
	PAST-SOUTH	1823	75
	FLOT-SOUTH	—	1319
	PAST-SOUTH	—	1360

weight group was cross-classified with finishing regime of pasture or feedlot. TEMP progeny were finished in temperate environments of north-eastern New South Wales (NSW). For TROP, there were 3 finishing regimes. The first 2 comprised pasture or feedlot 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. 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 in 58 slaughter groups. Every effort was made to control the slaughter procedure, including the use of electrical stimulation, to minimise extraneous variation, particularly for tenderness traits.

Measurements

A total of 20 traits were selected from all of the animal (Johnston *et al.* 2003a), carcass (Reverter *et al.* 2003), and meat quality (Johnston *et al.* 2003b) measurements studied. Criteria for selection of traits included ease of measurement, magnitude of genetic variance and heritability, and likelihood of being included as either selection or objective criteria in genetic evaluation programs. A comprehensive description of traits selected for this study is provided in Table 2.

Five animal measurements were selected: flight time measured immediately post-weaning for TROP only (S1FT), liveweight (S2LWT), ultrasound-scanned subcutaneous fat depth at the P8 site (S2P8), scanned eye muscle area (S2EMA) measured at the start of finishing period, and average daily gain measured during the finishing period (FADG). Carcass traits included: hot carcass weight (CWT), retail beef yield percentage (RBY), intramuscular fat percentage (IMF), subcutaneous fat depth at the P8 site (P8), eye muscle length by width (ELW), and meat colour score (MEATC). Meat quality measures were taken on 2 muscles: *M. longissimus thoracis et lumborum* (LTL) and *M. semitendinosus* (ST). A detailed description of the procedures used in the assessment of the meat quality traits is provided by Perry *et al.*

Table 2. Description of traits included in the analyses

Acronym	Description
<i>Animal</i>	
S1FT	Post-weaning measure of flight time (s*100). Electronically recorded time taken for an animal to cover 1.7 m after leaving a weighing crush (Burrow <i>et al.</i> 1988)
S2LWT	Measure of liveweight (kg) at the start of the finishing period
S2P8	Measure of ultrasound scanned ^A rump fat depth at the P8 site (mm) at the start of the finishing period
S2EMA	Measure of ultrasound scanned ^A LTL area (cm ²) at the start of the finishing period
FADG	Average daily gain measured during the whole finishing period (kg/day)
<i>Carcass</i>	
CWT	Hot carcass weight (kg)
RBV	Retail beef yield as a percentage of carcass weight. Measures were produced from the total weight of 17 trimmed boneless retail primal cuts, plus the weight of adjusted manufacturing trim, expressed as a percentage of recovered left-side weight
IMF	Percentage of intramuscular fat measured either through near-infrared spectroscopy or by the ether-extracted fat method
P8	Subcutaneous fat thickness at the P8 site (mm)
ELW	Eye muscle length by width (cm ²) measured by multiplying LTL length by LTL width.
MEATC	AUS-MEAT ^B scored meat colour measured on the exposed LTL muscle at the quartering site and assessed in the chilled carcass and scored against reference standards. Re-coded into continuous numeric scales from 1 (bright-light red) to 6 (dark red)
<i>Meat quality</i>	
LTL_a*	a* colour space chromaticity measurement (green–red) on the ‘bloomed’ meat surface of <i>M. longissimus thoracis et lumborum</i> (LTL) using a Minolta Chroma Meter
LTL_L*	L* colour space lightness measurement (black–white) on the ‘bloomed’ meat surface of LTL using a Minolta Chroma Meter
LTL_CL%	Cooking loss percentage. The percentage difference in the pre- and post- cooked weights of a 245–255 g sample of LTL (90 by 60 by 50 mm) cooked in a waterbath (70°C) for 60 min and then cooled for 30 min
LTL_SF	Modified Warner-Bratzler shear force (kg) of the LTL using a 4-mm flat blade pulled upward through the sample at 100 mm/min at right angles to the fibre direction
LTL_TEND	Consumer-assessed tenderness score: 0, very tough; 100, very tender
ST_a*	a* colour space chromaticity measurement (green–red) on the ‘bloomed’ meat surface of <i>M. semitendinosus</i> (ST) using a Minolta Chroma Meter
ST_CL%	Cooking loss percentage of the ST. Same measurement procedure as for LTL_CL%
ST_C	Compression (kg) measured as the product of hardness and cohesiveness of the cooked ST 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 of 6 samples was recorded
ST_SF	Modified Warner-Bratzler shear force (kg) of the ST. Same procedure as for LTL_SF

^AAll ultrasound scanning was performed by accredited technicians using an Aloka 500 scanner (Upton *et al.* 1999).

^BAUS-MEAT (1996).

(2001). In this analysis, a subset of 9 meat quality measurements from the total of 19 analysed by Johnston *et al.* (2003b) was used. Objectively measured traits included: shear force of the LTL (LTL_SF) and ST (ST_SF), compression of the ST (ST_C), cooking loss % of the LTL (LTL_CL%) only for TROP and ST (ST_CL%) only for TEMP, Minolta L* value of the LTL (LTL_L*), and Minolta a* value of the LTL (LTL_a*) only for TROP and ST (ST_a*) only for TEMP. Finally, the consumer-assessed tenderness score (LTL_TEND) was also included in this analysis.

Table 3 presents summary statistics for the traits involved in this study for TEMP and TROP. Data edits including identification of outliers, re-coding of scored traits into continuous numeric scales, and treatment of missing values were described in the previous 3 papers in this series.

Estimation of genetic parameters

The aim of these analyses was to obtain estimates of genetic and phenotypic correlations between traits across the 3 categories (animal, carcass, and meat quality) separately for TEMP and TROP. However, with 17 traits for TEMP and 18 for TROP, estimation of genetic

parameters with a unique multivariate analysis was computationally unfeasible. Therefore, a series of trivariate analyses was performed for all possible 3-way combinations of animal, carcass, and meat quality traits. This strategy resulted in a total of 168 and 210 trivariate analyses for TEMP and TROP, respectively.

The animal model used for the analysis of animal, carcass, and meat quality traits was described by Johnston *et al.* (2003a), Reverter *et al.* (2003), and Johnston *et al.* (2003b), respectively. The model for FADG included the covariate of age at the commencement of finishing, the fixed effect of contemporary group defined as the combined effects of herd of origin, sex, and slaughter group, and the random effects of additive genetic and temporary residual. Because the study by Johnston *et al.* (2003a) did not include FADG for either TEMP or TROP, nor the covariances between S1FT and the other animal measurements taken at the end of the backgrounding period, 2 additional multivariate analyses were performed as follows: a tetra-variate for TEMP including S2LWT, S2P8, S2EMA, and FADG; and a penta-variate for TROP including S1FT, S2LWT, S2P8, S2EMA, and FADG. In all cases, genetic parameters were obtained by REML using the VCE 4.2.5 software by Groeneveld and García-Cortés (1998).

Table 3. Summary statistics for animal, carcass, and meat quality traits for temperate and tropically adapted breeds

Summary statistics for animal, carcass, and meat quality traits adapted from Johnston *et al.* (2003a), Reverter *et al.* (2003), and Johnston *et al.* (2003b), respectively. See Table 2 for trait definition and units

Traits	Temperate breeds			Tropically adapted breeds		
	<i>n</i>	Mean	s.d.	<i>n</i>	Mean	s.d.
<i>Animal</i>						
S1FT (s*100)	—	—	—	3594	123.33	52.66
S2LWT (kg)	3771	361.53	63.95	3851	350.61	60.75
S2P8 (mm)	3485	4.41	2.62	2630	3.69	2.39
S2EMA (cm ²)	3355	49.06	7.76	2629	49.62	8.17
FADG (kg/day)	3612	1.04	0.39	3849	0.94	0.45
<i>Carcass</i>						
CWT (kg)	3852	269.13	54.87	4002	260.59	51.07
RBV (%)	1930	67.03	3.69	1315	67.39	3.16
IMF (%)	3594	4.64	2.23	3902	2.84	1.40
P8 (mm)	3643	10.19	4.57	3658	11.30	5.11
ELW (cm ²)	1635	81.59	15.90	2077	78.46	11.94
MEATC (units)	3761	2.48	0.74	3902	2.55	0.82
<i>Meat quality</i>						
LTL_a* (units)	—	—	—	3798	22.63	3.14
LTL_L* (units)	3568	39.57	2.97	3561	38.51	3.16
LTL_CL% (%)	—	—	—	3585	22.32	2.02
LTL_SF (kg)	3322	4.12	0.82	3506	4.62	0.99
LTL_TEND (score)	1152	59.15	14.63	1585	46.78	15.41
ST_a* (units)	3540	24.00	3.35	—	—	—
ST_CL% (%)	3585	21.77	1.95	—	—	—
ST_C (kg)	3350	2.04	0.33	3597	2.13	0.36
ST_SF (kg)	3357	4.78	0.72	3587	4.76	0.64

For TEMP and TROP, complete genetic and residual covariance matrices were built. The block diagonal elements corresponding to animal measurements were the REML estimates resulting from the previously reported tetra- and penta-variate analyses for TEMP and TROP, respectively. The block diagonal elements corresponding to the 6 carcass traits were from the estimates reported in Reverter *et al.* (2003) and the block diagonal elements corresponding to the 7 meat quality measurements were from the estimates reported in Johnston *et al.* (2003b). Finally, the block off-diagonal elements corresponding to correlations between animal and carcass, animal and meat quality, and carcass and meat quality measurements, were obtained from the means of the estimates from each of the trivariate analyses in which each trait was involved.

Results and discussion

Tables 4 and 5 present, for TEMP and TROP, the heritabilities (h^2), genetic (r_g) and phenotypic (r_p) correlations, and phenotypic variances for animal, carcass, and meat quality traits. Both matrices were positive definite as tested by a cholesky factorisation.

Correlation between animal measurements and carcass traits

Estimates of r_g and r_p between animal measurements and carcass traits were consistent across TEMP and TROP, as was the increased magnitude of the estimates of r_g compared with r_p . For TEMP, the average standard error of r_g estimates

was 0.15 and variability among estimates of a particular r_g was small regardless of the third trait involved in the analysis. For TROP, the average standard error of r_g estimates was 0.12, slightly smaller than that of TEMP as family size for TROP was also larger than for TEMP (24.6 and 16.6 progeny per sire on average for TROP and TEMP, respectively).

Estimates of r_g between the animal measurements and related carcass traits measured at the start of finishing (average age 467 and 581 days for TEMP and TROP, respectively) and at slaughter (average age 627 and 767 days for TEMP and TROP, respectively) were strong to very strong (0.89, 0.80, and 0.62 for r_g between S2LWT and CWT, S2P8 and P8, and S2EMA and ELW, respectively, for TEMP; and 0.82, 0.88, and 0.68 for TROP). These estimates are in agreement with the genetic correlations between animal ultrasound scans traits and carcass P8 and eye muscle area reported by several workers (Baud *et al.* 1998; Moser *et al.* 1998; Reverter *et al.* 2000; Crews and Kemp 2001). Koots *et al.* (1994) reported a weighted genetic correlation between yearling weight and carcass weight of 0.91. These correlations show the value of measuring indicator traits on the live animal, in some cases quite early in their life, to genetically improve carcass traits in the breeding objective.

Table 4. Heritabilities, genetic and phenotypic correlations, and phenotypic variance (V_p) for animal, carcass, and meat quality measurements in temperate breeds
See Table 2 for trait definition and units. Heritabilities are on the diagonal and shown in italics. Genetic and phenotypic correlations are shown above and below diagonal, respectively

	Animal				Carcass				Meat quality								
	S2LWT	S2P8	S2EMA	FADG	CWT	RBY	IMF	P8	ELW	MEATC	LTL_L*	LTL_SF	LTL_TEND	ST_a*	ST_CL%	ST_C	ST_SF
S2LWT	0.50	0.17	0.53	0.88	0.89	-0.20	0.08	-0.28	0.02	0.18	0.10	-0.02	0.09	-0.09	-0.01	-0.14	0.29
S2P8	0.30	0.39	0.20	0.17	0.06	-0.57	0.39	0.80	-0.40	-0.08	-0.23	-0.26	0.32	0.12	0.04	-0.08	0.05
S2EMA	0.50	0.20	0.33	0.32	0.52	0.16	-0.17	-0.06	0.62	-0.01	0.24	0.04	-0.09	-0.09	0.03	-0.05	0.10
FADG	0.18	-0.07	0.02	0.17	0.75	-0.10	-0.02	0.01	-0.01	0.08	0.08	0.22	0.28	-0.42	-0.22	-0.17	0.00
CWT	0.80	0.20	0.40	0.43	0.39	0.06	-0.12	-0.39	0.45	-0.46	0.66	-0.20	0.06	-0.56	-0.04	-0.52	-0.30
RBY	-0.05	-0.39	0.14	0.04	0.18	0.57	-0.38	-0.48	0.44	-0.02	0.16	0.24	-0.26	-0.09	0.01	0.34	-0.05
IMF	-0.08	0.19	-0.11	-0.01	-0.19	-0.31	0.38	0.34	-0.12	0.03	-0.15	-0.38	0.61	0.17	-0.25	-0.41	-0.32
P8	-0.07	0.41	-0.01	-0.04	-0.19	-0.40	0.16	0.36	-0.29	0.06	-0.03	-0.40	0.57	0.07	0.13	-0.26	-0.16
ELW	-0.02	-0.04	0.39	-0.03	0.32	0.14	-0.17	-0.14	0.30	-0.16	0.44	0.27	0.09	0.03	0.05	-0.17	-0.24
MEATC	0.10	-0.03	0.02	-0.07	-0.20	-0.03	-0.01	0.05	-0.06	0.11	-0.29	0.03	-0.01	-0.05	-0.14	0.21	0.58
LTL_L*	0.00	-0.01	0.02	0.13	0.42	0.04	0.06	-0.01	0.04	-0.30	0.17	-0.23	0.12	-0.54	-0.19	-0.13	-0.04
LTL_SF	-0.03	-0.07	-0.03	-0.02	-0.11	0.03	-0.11	-0.02	0.03	0.14	-0.18	0.09	-0.49	0.19	0.07	0.31	0.58
LTL_TEND	-0.05	0.04	-0.05	0.03	-0.09	-0.09	0.20	0.00	0.00	0.02	0.03	-0.27	0.18	-0.06	-0.47	-0.78	-0.42
ST_a*	0.03	0.08	0.03	-0.14	-0.21	-0.06	0.07	0.07	-0.01	-0.13	0.00	-0.08	0.03	0.13	0.21	0.29	-0.06
ST_CL%	-0.01	-0.05	0.02	0.02	0.01	0.11	-0.07	-0.05	0.03	-0.20	0.13	-0.06	-0.06	0.18	0.15	0.22	-0.17
ST_C	0.04	-0.01	0.02	-0.05	-0.20	-0.04	-0.07	-0.04	-0.02	-0.05	-0.03	0.05	-0.08	0.09	0.12	0.12	0.68
ST_SF	0.08	0.05	0.01	-0.08	-0.16	-0.11	-0.01	0.00	-0.03	-0.01	-0.01	0.12	-0.14	0.02	0.07	0.30	0.11
V _p	1027.35	2.52	23.33	0.03	505.56	3.99	2.10	7.95	76.79	0.26	5.12	0.43	130.55	5.14	2.27	0.06	0.28

Table 5. Heritabilities, genetic and phenotypic correlations, and phenotypic variance (V_P) for animal, carcass, and meat quality measurements in tropically adapted breeds. See Table 2 for trait definition and units. Heritabilities are on the diagonal and shown in italics. Genetic and phenotypic correlations are shown above and below diagonal, respectively

	Animal					Carcass					Meat quality							
	S1FT	S2LWT	S2P8	S2EMA	FADG	CWT	RBV	IMF	P8	ELW	MEATC	LTL_a*	LTL_L*	LTL_SF	LTL_TEND	ST_C	ST_SF	
S1FT	0.29	0.01	0.16	-0.03	0.09	0.05	0.11	-0.05	0.18	-0.03	-0.18	0.15	-0.07	0.19	-0.48	0.37	-0.05	-0.17
S2LWT	0.04	0.30	-0.42	0.29	0.28	0.82	0.20	-0.21	-0.22	-0.19	0.10	-0.29	-0.12	0.30	-0.04	-0.03	0.08	0.02
S2P8	0.05	0.16	0.21	-0.08	-0.33	-0.41	-0.19	0.23	0.88	-0.42	0.00	0.28	0.19	0.20	0.08	-0.13	-0.12	0.19
S2EMA	0.02	0.39	0.10	0.22	-0.14	0.20	0.16	-0.58	-0.07	0.68	0.39	-0.28	-0.44	-0.17	0.01	-0.29	0.28	0.34
FADG	0.08	0.17	0.02	0.01	0.22	0.67	-0.04	0.02	0.13	-0.19	-0.51	-0.16	0.36	0.24	-0.12	0.16	0.00	-0.03
CWT	0.05	0.82	0.12	0.34	0.60	0.36	0.16	-0.03	-0.17	-0.28	-0.55	-0.51	0.60	0.44	-0.21	0.00	-0.22	-0.15
RBV	0.02	0.01	-0.20	0.17	-0.12	-0.03	0.50	-0.43	-0.28	0.25	-0.18	0.07	0.14	0.22	-0.14	0.05	-0.07	-0.09
IMF	-0.02	-0.11	0.14	-0.08	0.11	0.09	-0.27	0.39	0.22	-0.15	-0.29	0.30	0.38	-0.17	-0.09	0.31	-0.34	-0.31
P8	0.03	-0.10	0.44	-0.04	0.11	-0.11	-0.22	0.12	0.30	-0.19	-0.05	0.15	0.19	0.13	0.04	0.21	-0.17	-0.04
ELW	-0.01	-0.10	-0.17	0.33	-0.08	0.08	0.13	-0.13	-0.13	0.32	0.15	0.07	-0.28	-0.19	-0.14	-0.08	-0.15	-0.03
MEATC	-0.03	0.09	-0.03	0.04	-0.12	-0.17	-0.02	-0.08	0.00	0.04	0.11	-0.27	-0.83	-0.14	0.34	-0.41	0.23	0.17
LTL_a*	-0.02	-0.07	0.07	0.05	-0.01	-0.18	-0.07	0.16	0.07	0.03	-0.10	0.13	0.24	0.15	-0.60	0.22	0.09	0.02
LTL_L*	0.05	0.01	0.03	-0.04	0.16	0.37	-0.04	0.14	0.05	-0.03	-0.31	0.03	0.18	-0.01	-0.40	0.54	-0.28	-0.29
LTL_CL%	-0.01	0.07	-0.03	-0.06	-0.02	0.21	0.17	-0.10	-0.07	-0.03	-0.04	0.10	-0.11	0.19	-0.11	-0.15	0.27	0.35
LTL_SF	-0.01	-0.02	-0.02	-0.01	-0.07	-0.16	0.00	-0.12	-0.02	0.02	0.10	-0.22	-0.22	0.15	0.30	-0.79	0.21	0.46
LTL_TEND	0.06	0.07	0.04	-0.01	0.04	0.04	-0.17	0.19	0.02	-0.03	-0.03	0.05	0.14	-0.13	-0.36	0.31	-0.59	-0.73
ST_C	-0.02	0.02	-0.05	0.04	-0.11	-0.31	-0.03	-0.11	-0.04	-0.01	0.02	-0.01	-0.06	0.03	0.06	-0.06	0.27	0.83
ST_SF	-0.05	0.03	0.03	0.05	-0.10	-0.18	-0.06	-0.05	-0.05	-0.05	0.07	-0.01	-0.06	0.05	0.19	-0.21	0.03	0.42
V _p	2065.52	800.42	2.31	28.79	0.04	546.70	4.30	0.96	14.33	78.19	0.31	4.27	5.53	2.51	0.63	147.42	0.07	0.30

Other medium to strong genetic correlations that were consistent across TEMP and TROP include: the negative correlations between S2LWT and P8, S2P8 and both RBY and ELW, and the positive correlations between S2P8 and IMF, and S2EMA and both CWT and RBY. The correlations of S2P8 with RBY and IMF were consistent with the correlations reported by Reverter *et al.* (2003) between abattoir-measured P8 fat depth and those traits. S1FT showed weak genetic associations with carcass traits except with P8 ($r_g = 0.18 \pm 0.06$) and MEATC ($r_g = -0.18 \pm 0.12$).

For TEMP, the phenotypic variance for FADG averaged $0.03 \text{ kg}^2/\text{day}^2$ and the heritability was estimated at 0.17 ± 0.03 . For TROP, the phenotypic variance for FADG averaged $0.04 \text{ kg}^2/\text{day}^2$ and the heritability was estimated at 0.22 ± 0.04 . For both TEMP and TROP, FADG showed a strong to very strong positive genetic and phenotypic association with CWT. The small r_g estimated between FADG and IMF (-0.02 and 0.02 for TEMP and TROP, respectively) contrasts with reported estimates of 0.24 (Mukai *et al.* 1995) and 0.44 (Johnston *et al.* 1999). The estimate of Mukai *et al.* (1995) was obtained for gain of bulls on test and steer marbling score. Interestingly, the estimate of Johnston *et al.* (1999) was obtained from a subset of the TEMP data used in the present analysis but was for a slightly longer period of gain and only used data from export market weight finished steers.

For TROP, the strongest r_g between an animal measurement and IMF was that for S2EMA, averaging -0.58 and varying minimally across the 7 trivariate analyses where this pair of traits was analysed. This estimate is in agreement with the negative estimate (-0.15) observed between carcass ELW and IMF when both traits were adjusted for carcass weight. The r_g values between S2LWT and IMF and P8 were also negative for TROP. These results suggest that for TROP, heavier cattle with larger eye muscle areas at the start of finishing, adjusted for age, when slaughtered had genetically less IMF and P8 and higher retail yield ($r_g = 0.20$) after adjusting for carcass weight. In contrast for TEMP, the r_g values between S2EMA and IMF and between S2LWT and IMF were -0.17 and 0.08 , respectively. These correlations indicate that heavier TEMP cattle at the start of finishing are genetically lower yielding ($r_g = -0.20$) with less P8 fat ($r_g = -0.28$) after adjusting for carcass weight. The strongest estimate of r_g between an animal measurement and IMF for TEMP was that for S2P8 (average = 0.39). Again, this estimate is in agreement with the 0.34 reported between carcass P8 and IMF by Reverter *et al.* (2003).

Estimates of r_g that were inconsistent across TEMP and TROP include those between the following pairs of traits: S2LWT and RBY (-0.20 and 0.20 for TEMP and TROP, respectively), S2P8 and CWT (0.06 and -0.41), S2EMA and MEATC (-0.01 and 0.39), and FADG and MEATC (0.08 and -0.51). Similar inconsistencies across TEMP and TROP were reported by Reverter *et al.* (2003) at the carcass level

for RBY, P8, and MEATC. The inconsistencies in magnitude and direction of the correlations are likely to be due to genetic differences between TEMP and TROP but could also be the result of differences in age at measurement and the effect of the environment on the expression of the traits.

Correlation between animal measurements and meat quality traits

Estimates of r_g and r_p between animal measurements and meat quality traits were generally consistent across TEMP and TROP (Tables 4 and 5). Meat tenderness measurements were genetically correlated with FADG. Selection for increased growth rate would be associated with genetic improvement in several of the meat quality traits, with the exception of LTL_SF (0.22) for TEMP and LTL_CL% (0.24) for TROP. However, the phenotypic correlations between growth rate and LTL_TEND were close to zero. This result is in agreement with the conclusion of Perry *et al.* (2002), from separate analysis of the same data, that reported only a small effect of growth rate differences on consumer palatability scores.

Moderate genetic correlations between S2EMA and several meat quality traits were estimated for TROP ranging from -0.44 with LTL_L* to 0.34 with ST_SF. Selection for increased S2EMA would result in unfavourable changes in meat quality traits, particularly darker meat and lower ST tenderness. Interestingly, a similar correlation existed between ELW and LTL_L* but correlations between ELW and ST tenderness measures were small and slightly negative. Further, S2EMA correlations with muscle lightness and colour were inconsistent across TEMP and TROP. However, this disagreement was already observed between S2EMA and MEATC. Marshall (1999) in his review reported a positive genetic correlation between sensory panel tenderness and LTL area (0.21).

The genetic correlations between S1FT (measured only in TROP) and the meat tenderness assessments of LTL_SF, LTL_TEND, and ST_SF were found to be moderate to high. This outcome is very important for Australia's northern breeding industry. Given the ease of measurement on the live animal, along with the observed estimate of h^2 (0.31 ; Table 7 and Johnston *et al.* 2003a), and the genetic correlations with tenderness, S1FT measured post-weaning could be included in a genetic improvement scheme as an indirect measure of meat tenderness and also as a measure to improve temperament. However, this has to be tempered somewhat by the fact that these associations were virtually non-existent at the phenotypic level. Under extensive management systems, temperament affects productivity of beef enterprises through increased production costs and possibly through losses in carcass and meat quality as a result of high levels of pre-slaughter stress (Burrow *et al.* 1991, 1999; Burrow 1997). However, evidence for the latter effect has been equivocal. Burrow *et al.* (1999) analysed data from 3 calf

crops and reported a negative relationship between flight speed score and LTL_SF in Year 1 but positive relationships in Years 2 and 3. In our study the phenotypic correlation was zero. However, Voisinet *et al.* (1997) reported that as temperament score increased from calm to excitable, shear force measurements and the incidence of borderline dark cutters increased.

For TEMP, variability was found in the estimate of r_g between S2LWT and LTL_L*, which was 0.60 ± 0.09 when CWT was the third trait in the model and zero otherwise. This result is likely to be caused by the high genetic correlation between CWT and LTL_L* ($r_g = 0.66$) and also between CWT and S2LWT ($r_g = 0.89$) and these estimates varied minimally with the third trait included. A similar scenario was observed with the estimate of r_g between FADG and LTL_L*, which was 0.46 ± 0.14 when CWT was the third trait and zero otherwise.

Inconsistent across TEMP and TROP were the estimates of r_g between LTL tenderness measurements and S2P8. For TEMP, the relationship was positive between S2P8 and LTL_TEND ($r_g = 0.32$) but slightly negative for TROP (-0.13 , Table 5). This could be reflecting the relationship that was observed between IMF and tenderness, particularly since the LTL_TEND was measured using untrained panelists that were unable to distinguish between the attributes of tenderness, juiciness, and flavour (Johnston *et al.* 2003b).

Correlation between carcass measurements and meat quality traits

As seen previously for the correlations of animal measures with carcass and meat quality measurements, most estimates of r_g and r_p between carcass measurements and meat quality traits were consistent across TEMP and TROP and the r_g estimates were of stronger magnitude than those for r_p .

Heavier carcasses were genetically associated with increased muscle lightness (CWT and LTL_L*, 0.66 and 0.60 for TEMP and TROP) and decreased a* colour. Moderate r_g existed between tenderness measures (LTL_SF, ST_SF, and LTL_TEND) and CWT and fatness measures (P8 and IMF). Similarly, this was also found between LTL_TEND and RBY for TEMP. These estimates are in agreement with those reviewed by Marshall (1999) who reported genetic correlations of sensory panel tenderness with CWT, fat thickness, and IMF of 0.24, 0.10, and 0.30, respectively. In summary, the genes responsible for heavier, more marbled carcasses are some of the same genes as, or closely linked to, those responsible for more tender meat, particularly for TEMP. In their reviews of the research literature, Marshall (1999) and Burrow *et al.* (2001) revealed that improvement in shear force (i.e. tenderness) would be genetically associated with increases in intramuscular fat and with little effect on muscling. Further, Marshall (1999)

concluded that the genetic correlation estimates between shear force and subcutaneous fatness or lean yield have varied considerably across studies, with the mean values indicating slight antagonisms.

Phenotypic correlations between fatness and tenderness measures were in the same direction as the genetic correlations but were of much smaller magnitude. The slight positive estimates of r_p between IMF and LTL_TEND (0.20 and 0.19 for TEMP and TROP) support the hypothesis that higher marbling decreases the risk of obtaining steaks with inferior tenderness (Smith *et al.* 1987; Jones and Tatum 1994). However, it is also likely that the relationship is more indirect in origin. For example, more marbling could simply mean less protein to shear through, therefore, more tender meat. For TEMP, the estimate of -0.40 for the r_g between P8 and LTL_SF could be associated with the relationship between IMF and tenderness. However, the phenotypic correlation was zero. In contrast, Jones and Tatum (1994) reported that steaks from carcasses with less than 0.5 cm fat thickness had higher LTL_SF values than did steaks produced by carcasses with 0.5 cm fat thickness or more. It is possible that phenotypic associations reported between fatness and shear force were influenced by processing conditions. For example, carcasses that are fatter and heavier cool slower; therefore, the chance of cold shortening is reduced compared with lighter, leaner carcasses if no electrical stimulation is used. However, in our study, electrical stimulation was applied, which should have minimised (not necessarily negated) the influence of carcass weight and fatness. Likewise, in the study of Jones and Tatum (1994), carcasses were also electrically stimulated.

The r_g between MEATC and ST_SF was 0.58 and 0.17 for TEMP and TROP, respectively. In contrast, the estimate of r_g between LTL_L* and ST_SF was only -0.04 and -0.29 for TEMP and TROP, respectively. However, the correlation between MEATC and LTL_L* was only -0.29 for TEMP but -0.83 for TROP. The lower association for TEMP was attributed to limited variation in scores used (i.e. 92% of records were either muscle colour score 0 or 1), and a heritability estimate of only 0.11 ± 0.03 (Reverter *et al.* 2003). For TROP, Table 5 shows r_g of 0.34, -0.41 , and 0.17 between MEATC and LTL_SF, LTL_TEND, and ST_SF, respectively.

Conclusions

Genetic and phenotypic correlations between animal measures and related carcass traits were moderate to very high for TEMP and TROP. Genetic correlations between animal measures and other carcass traits varied; moderate genetic correlations were estimated between ultrasound scan fat depth and carcass retail beef yield and intramuscular fat. Genetic correlations between animal and meat quality measures were generally moderate to low. For TEMP,

moderate genetic correlations were estimated between consumer tenderness score and scan fatness and finishing average daily gain. For TROP, flight time was genetically correlated with tenderness. Several moderate to high genetic correlations existed between carcass and meat quality traits. In general, fatness measures were genetically correlated with tenderness and CWT was genetically related to meat colour and objective tenderness measures. Phenotypic correlations between animal and carcass measures with meat quality traits were low and close to zero, indicating that few phenotypic predictors of carcass and meat quality were identified. Important genetic correlations existed between traits and could be used as selection criteria in multiple trait genetic evaluation systems or formation of breeding objectives to improve carcass and meat quality traits.

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