

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

2. Abattoir carcass traits*

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Abstract. A total of 11 abattoir carcass measures were recorded on 7854 carcasses in temperate (TEMP) and tropically adapted (TROP) beef breeds. Breeds for TEMP included Angus, Hereford, Murray Grey, and Shorthorn; Brahman, Belmont Red, and Santa Gertrudis accounted for TROP breeds. Measurements included carcass weight (CWT), retail beef yield percentage (RBY), intramuscular fat percentage (IMF), subcutaneous fat depth at the P8 site (P8) and at 12/13th rib (RIB), eye muscle length by width (ELW), deep butt temperature (DBTEMP), fat colour score (FATC), meat colour score (MEATC), marbling score (MARB), and carcass muscle score (MUSC). Animals were finished to 3 different market weight endpoints, either on pasture or in a feedlot, and in different geographic regions for the TROP breeds. Both the phenotypic and genetic expressions of the traits were estimated at each level of market weight endpoint and finishing regime. Heritabilities (h^2) and genetic (r_g) and phenotypic (r_p) correlations between traits were estimated for TEMP and TROP separately. The design effects of market weight endpoint and finishing regimes were the most important sources of variation for continuously measured traits. Main effects for the scored traits were finishing regime for FATC and MEATC and market weight endpoint for MARB and MUSC. Feedlot finished cattle had the whitest FATC and the lightest MEATC. For TEMP, estimates of h^2 for CWT, RBY, IMF, P8, RIB, ELW, DBTEMP, FATC, MEATC, MARB, and MUSC were 0.39, 0.57, 0.38, 0.36, 0.27, 0.30, 0.10, 0.05, 0.11, 0.17, and 0.14, respectively. In comparison, h^2 for the same order of traits for TROP were 0.36, 0.50, 0.39, 0.30, 0.41, 0.32, 0.04, 0.09, 0.11, 0.25, and 0.11. The direction and magnitude of r_g between traits were similar for TEMP and TROP, particularly between CWT, RBY, IMF, P8, and RIB. Genetic correlations of RBY were moderate and negative with all measures of fatness, including IMF (-0.38 TEMP and -0.43 TROP). Positive r_g existed between all measures of fatness, with MARB and IMF close to unity. Negative r_g was estimated between CWT and all fat measurements. Also negative were the r_g and r_p estimates between CWT and MEATC. For all traits in both TEMP and TROP, domestic weight carcasses exhibited lower additive variance than export market carcasses. However, genetic correlations between traits across market weight endpoints were positive and close to unity, with the exception of RBY for TROP. For TEMP breeds, genetic correlations between finishing regimes were close to unity. However, possible genotype by environment interactions were found for TROP for P8, MEATC, and MARB between finishing in different geographic regions, and between feedlot and pasture finished animals for RBY and MEATC. Genetic improvement of carcass traits is a possibility given the moderate heritabilities, moderate to strong genetic correlations, and little evidence of genotype by environment interactions.

Additional keywords: beef cattle, marbling, genetic parameters, $G \times E$.

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Introduction

The importance of carcass traits to the beef cattle industry is increasing, especially with the introduction of more detailed carcass specification systems and the payment of premiums for products satisfying the requirements of specific markets. 'Australian beef breeders are faced with the challenge of using vastly diverse production environments and systems to produce cattle that are both productive and profitable and beef products that satisfy consumer requirements' (Burrow *et al.* 2001). Breeding stock, bulls and cows, are usually selected based on their performance on pasture, although their offspring may be intended for finishing in a feedlot. Consequently, if there is a large genotype by environment ($G \times E$) interaction (feedlot *v.* pasture), the efficiency of this selection would be severely reduced. Also, cattle producers would like to select bulls and cows whose progeny would be suited to a range of market endpoints such as light weight domestic markets and heavier weight, export markets. Again, if there is a large $G \times E$ interaction (domestic *v.* export market weights), it would be necessary to select breeding stock specifically for the target market. Wilton and Goddard (1996) showed that economic weights and subsequent selection index weights depend on both average genotypic means and management (feeding and market programs) factors. Therefore, knowledge of genetic and non-genetic influences on beef production and quality is needed. Since December 1998, Australian beef seedstock breeders have had estimated breeding values (EBV) for abattoir carcass traits from BREEDPLAN Version 4.1 (Johnston *et al.* 1999a), including carcass weight, retail beef yield percentage, intramuscular fat percentage, fat depth, and eye muscle area, to use as selection criteria.

From 1994 to 2000 the Cooperative Research Centre for Cattle and Beef Quality (Beef CRC) backgrounded, finished, and slaughtered 7854 straightbred steers and heifers. Several preliminary genetic studies of carcass traits were reported (Ferguson *et al.* 1997; Johnston *et al.* 1999b; Reverter *et al.* 2000).

The objectives of this study were (1) to identify the magnitude of major design effects, (2) to estimate genetic parameters for up to 11 abattoir-measured carcass traits, and (3) to assess the magnitude and extent of $G \times E$ interaction between feedlot and pasture finished animals, between domestic and export market weight endpoints, and, for tropically adapted breeds, between temperate and subtropical finishing environments. Separate analyses were performed for temperate and tropically adapted breeds.

This paper is second in a series that reports on the genetic and phenotypic characterisation of animal traits (Johnston *et al.* 2003a), meat quality traits (Johnston *et al.* 2003b), and correlations among animal, carcass, and meat quality traits (Reverter *et al.* 2003) from temperate and tropically adapted breeds.

Materials and methods

Animals

Data ($n = 7534$) generated from the straightbreeding project of the Beef CRC were extracted from the Beef CRC database (Reverter *et al.* 2001). Details of the design of the breeding program and complete management of the animals are 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 from each of 4 homebred sires per year, as well as generating linkages across herds by the use of 2 additional link sires per year (about 12 progeny per link sire). The Beef CRC purchased calves at weaning from 34 herds throughout eastern Australia. Additionally, abattoir records on 320 straightbred Brahman steers and heifers derived from the Beef CRC crossbreeding project (see Upton *et al.* 2001) from 2 additional herds were also included in the analyses.

Treatments

All TEMP cattle were finished in the temperate environments in northern NSW, Australia. TROP steers and heifers were finished in both subtropical (North) and temperate (South) environments in the proportion of 65% to 35%, respectively. Cattle were managed under 2 finishing regimes (pasture and feedlot) to representative market liveweights of 400 (domestic), 520 (Korean), and 600 kg (Japanese, steers only) at slaughter. Animals were slaughtered when the mean of the slaughter group reached their assigned market weight. Slaughter group defined animals from the same year, season, market weight group, and finishing regime. Distribution of animals by main effects within TEMP and TROP is presented in Johnston *et al.* (2003a). There were only 75 animals from TROP steers finished at pasture in temperate environments and hence they were not included in final analyses. Cattle were slaughtered in 58 separate cohort groups at 7 different commercial abattoirs between December 1994 and March 2000.

Slaughter protocols and measurements

A detailed description of all pre- and post-slaughter methods and measurement protocols is presented in Perry *et al.* (2001). In brief, animals were slaughtered at commercial abattoirs with the majority being slaughtered within 30 h of dispatch from their finishing property. Standard pre- and post-slaughter procedures were used throughout the project. Carcasses were placed in chillers within 1 h of stunning and Achilles-hung. The left side of each carcass was quartered between 20 and 24 h after slaughter. Until mid-1998, carcasses were quartered at the 12/13th rib. Subsequently, they were quartered at the 10/11th rib. For all analyses the change in quartering site was accounted for in the fixed effects. All measurements were taken by trained CRC staff with the exception of the scored traits that were made by qualified AUS-MEAT assessors using AUS-MEAT standard reference chips (AUS-MEAT 1996).

Eleven abattoir traits were used in this paper and included: hot carcass weight (CWT), retail beef yield percentage (RBY), intramuscular fat percentage (IMF), subcutaneous rump fat depth at the P8 site (P8), subcutaneous fat depth between the 12th and 13th ribs (RIB), eye muscle length by width (ELW), fat colour score (FATC), meat colour score (MEATC), marbling score (MARB), carcass muscle score (MUSC), and deep butt temperature (DBTEMP). All scored traits were re-coded into continuous numeric scales. A comprehensive description of traits and units is provided in Table 1.

Table 1. Description of continuous and discrete traits included in the analyses

Acronym	Description
<i>Continuous</i>	
AGE	Slaughter age, days
CWT	Hot carcass weight, kg. Carcasses were dressed according to AUS-MEAT standard specifications (AUS-MEAT 1998)
RBY	Retail beef yield, %. 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. The 17 primal cuts used were as follows: cube roll, chuck roll, chuck tender, blade, point end brisket, navel end brisket, intercostals, shin, topside, outside flat, thick flank, rump, striploin, tenderloin, thin flank, eye round, and shank. Subcutaneous fat was trimmed to 10 mm, and for 7 cuts, it was further trimmed to a maximum coverage of 3 mm of subcutaneous fat, and accessible intermuscular fat was removed (see Perry <i>et al.</i> 2001 for full description)
IMF	Intramuscular fat, %. Percentage of intramuscular fat was measured either through near-infrared spectroscopy or by the ether-extracted fat method in a sample of the <i>longissimus thoracis et lumborum</i> (LTL) that was taken caudal to the quartering site
P8	Subcutaneous rump fat thickness at the P8 site, mm. The P8 site is located over the gluteus muscle on the rump, at the intersection of a line through the pin bone parallel to the chine and its perpendicular through the third sacral crest assessed on the chilled carcass
RIB	Subcutaneous rib fat thickness, mm. Taken at the quartering site between the 12th and the 13th ribs over the LTL muscle assessed on the chilled carcass
ELW	Eye muscle length by width, cm ² . Taken at the quartering site by multiplying LTL length by LTL width
DBTEMP	Deep butt temperature, °C. Measured through the obturator foramen to the centre of the butt, 20 h post-mortem and immediately before quartering
<i>Discrete</i>	
FATC	Fat colour score. AUS-MEAT fat colour score of the intermuscular fat lateral to the LTL assessed in the chilled carcass. Re-coded into continuous numeric scales from 1 (white) to 5 (yellow)
MEATC	Meat colour score. AUS-MEAT meat colour score ⁷ of the exposed LTL and assessed in the chilled carcass. Re-coded into continuous numeric scales from 1 (bright-light red) to 6 (dark red)
MARB	Marbling score. AUS-MEAT marbling score of the exposed LTL on a 0–6 scale assessed in the chilled carcass. Re-coded into continuous numeric scales from 1 (original score, 0) to 4 (original scores, 3 and 4)
MUSC	Muscle score. A visually appraised muscle score on a 15-point scale (least muscling, E–, E, E+; A–, A, A+) assessed on the chilled carcass. Re-coded into continuous numeric scales from 1 to 6 as follow: 1 (least muscling, original code, D), 2 (original code, D+), 3 (original code, C–), 4 (original code, C), 5 (original code, C+), 6 (original codes, B+, B, B–)

Statistical analyses

The data were initially examined to identify outliers. A preliminary analysis of the 11 traits, using a restricted maximum likelihood (REML) animal model in ASREML (Gilmour *et al.* 1999), was used to identify outliers based on records >3 standard deviations from their contemporary group mean. Contemporary group (CG) was defined as the concatenation of the effects: herd of origin, sex, and slaughter group. Very few outliers were found but not deleted because they tended to be in small CG where one or more extreme records could affect the mean and residual variance. Finally, animals ($n = 143$) with unknown date of birth were assigned a slaughter age from the least square mean of CG.

Least square means

Least square means (LSMEANS) for treatment effects were estimated separately for TEMP and TROP using the GLM Procedure of SAS (SAS 1988). 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. Five design variables were identified: herd of origin with 36 levels, sex (steer or heifer), year-season with 11 levels, finishing (feedlot or pasture; North or South), and market weight endpoint (domestic, Korean, or Japanese). Effects for which LSMEANS were estimated included sex by market interaction, finishing, market, and finishing by market interaction. Eqn 1 is an example of the fixed effect model used to analyse the dependent variables of AGE, CWT, RBY, IMF, P8, RIB, ELW, FATC, MEATC,

MARB, MUSC, DBTEMP 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, sex, year, season, and finishing regime, 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 breeds, 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.

Relationships between scored traits (FATC, MEATC, MARB, and MUSC) and their related continuous traits were assessed using a simple fixed effect model. LSMEANS were compared with results from multivariate analyses where the scored traits were treated as linear. The fixed effect model used is presented by Eqn 2. LSMEANS were computed for each of the continuous traits of AGE, CWT, RBY, IMF, P8, RIB, ELW, and DBTEMP for each level of the scored trait:

Table 2. Summary statistics for continuous abattoir carcass traits for temperate and tropically adapted breeds
See Table 1 for trait definition and units

Trait	<i>N</i>	Mean	s.d.	Min.	Max.
<i>Temperate breeds</i>					
AGE (days)	3852	629.61	127.52	343.00	964.00
CWT (kg)	3852	269.13	54.87	122.00	445.50
RBY (%)	1930	67.03	3.69	54.00	77.16
IMF (%)	3594	4.64	2.23	1.23	18.94
P8 (mm)	3643	10.19	4.57	1.00	34.00
RIB (mm)	3543	8.21	4.45	1.00	34.00
ELW (cm ²)	1635	81.59	15.90	41.81	142.50
DBTEMP (°C)	3411	17.60	3.76	5.80	29.00
<i>Tropically adapted breeds</i>					
AGE (days)	4002	766.03	169.18	381.00	1332.00
CWT (kg)	4002	260.59	51.07	120.50	428.00
RBY (%)	1315	67.39	3.16	58.50	76.77
IMF (%)	3902	2.84	1.40	0.08	13.19
P8 (mm)	3658	11.30	5.11	1.00	38.00
RIB (mm)	3664	6.16	3.42	1.00	24.00
ELW (cm ²)	2077	78.46	11.94	43.70	132.13
DBTEMP (°C)	3472	15.81	3.66	5.30	27.60

$$y_{ijklm} = \mu + CG_i + FATC_j + MEATC_k + MARB_l + MUSC_n + e_{ijklm} \quad (2)$$

where y_{ijklm} is the observation on a continuous dependent variable for animal i , μ is the overall mean, CG_i is the effect of the i th contemporary group (as defined earlier), $FATC_j$ is the effect of fat colour score, $MEATC_k$ is the effect of meat colour score, $MARB_l$ is the effect of marble score, $MUSC_n$ is the effect of carcass muscle score, and e_{ijklm} is random residual error.

Variance components

Genetic parameters were obtained simultaneously for the 11 carcass traits by multivariate REML using analytical gradients with VCE 4.2.5 (Groeneveld and García-Cortés 1998). 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

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

where X_i is a known incidence matrix relating observations in y_i to the linear CWT covariate (or AGE covariate for i = carcass weight) and CG fixed effects in vector b_i ; the number of levels of CG was 587 and 532 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 for each breed to produce a pedigree file with 9217 and 7793 animals for TEMP and TROP, respectively; I is an identity matrix; σ_A^2 is the additive direct genetic variance; and σ_E^2 is the residual error variance.

To assess the magnitude of G × E interactions, each carcass trait was analysed by treating it as a different trait for feedlot and pasture

finishing regimes, and for domestic and export (jointly Korean and Japanese) market weight endpoints. 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.* (2003a).

Results and discussion

Summary statistics including number of records, mean, standard deviation, minimum, and maximum for continuously measured traits are given in Table 2, and the distribution of the scored traits by finishing regime (pasture and feedlot) and market weight endpoint (domestic and export) is presented in Table 3. All animals had CWT observed and the majority had IMF, P8, RIB, and DBTEMP records (Table 2). Measurements with the least number of records included ELW and RBY and were the result of changing abattoirs. For the scored traits, Table 3 shows that FATC, MEATC, and MARB presented right-skewed distributions. This skewness was stronger in feedlot-finished animals for FATC and MEATC and in domestic market weight endpoint for MARB. MUSC presented a bimodal density, although this bimodality was less apparent in feedlot-finished animals.

Least square means

Tables 4 and 5 present numbers of observations and LSMEANS for each trait for TEMP and TROP, respectively. Results from the orthogonal contrasts are given in Table 6. For both TEMP and TROP, the design effects of market weight endpoint and finishing regimes were important sources of variation for most traits. Sex had a significant effect for TROP for various traits. LSMEANS for steers by Japanese market weight endpoint are the same as the main effect of market at the Japanese weight endpoint. Steers had 17.4 kg heavier CWT, 4.11 cm² larger ELW, and 2.06% more RBY than heifers. In contrast, heifers from TROP had 0.65% more IMF, 3.06 mm more P8, and 1.75 mm more RIB than steers for TROP. For TEMP, sex was not important for any trait except for P8 (heifers being fatter by 2.72 mm) and ELW (heifers having a smaller ELW by 3.52 cm²). When only feedlot-finished animals were evaluated, the sex effect for P8 and ELW for TEMP was no longer significant. However, sex comparisons should be treated with caution because of low numbers of heifers for TEMP causing the LSMEANS to have large standard errors.

Market weight effect

By design, the mean target CWT for each market (220, 280, and 340 kg for domestic, Korean, and Japanese, respectively) was achieved for both TEMP and TROP. Heavier market weight endpoints were also associated with reduced RBY, and increased fatness (IMF, P8, and RIB), ELW, and DBTEMP. Indeed, market had a significant effect on all traits except the scored measures of FATC, MEATC, and MUSC. Cattle managed to the domestic market weight

Table 3. Distribution (%) of discrete abattoir carcass traits for temperate and tropically adapted breeds and by finishing regime (pasture and feedlot) and market weight endpoint (domestic and export)

See Table 1 for trait definition and units; number of records for FATC, MEATC, MARB, and MUSC was 3757, 3761, 2384, and 3772, respectively, for temperate breeds, and 3902, 3902, 3458, and 3874, respectively, for tropically adapted breeds

Re-coded level	Pooled	Temperate breeds				Tropically adapted breeds				
		Finishing		Market		Pooled	Finishing		Market	
		Pasture	Feedlot	Domestic	Export			Pasture	Feedlot	Domestic
<i>FATC</i>										
1	70.2	42.6	92.8	76.1	66.8	74.5	45.7	89.1	78.8	71.3
2	16.6	30.8	4.9	19.5	15.0	15.2	31.4	7.0	12.4	17.2
3	8.6	16.4	2.3	4.0	11.3	6.8	13.6	3.3	3.4	9.0
4	3.4	7.4	0.0	0.3	5.1	2.5	6.4	0.6	3.1	2.2
5	1.2	2.7	0.0	0.1	1.8	1.0	2.9	0.0	2.2	0.2
<i>MEATC</i>										
1	0.1	0.0	0.2	0.0	0.2	1.4	0.0	2.1	3.4	0.1
2	62.7	46.8	75.8	65.3	61.2	57.6	32.5	70.1	60.5	55.1
3	29.3	38.6	21.6	26.4	30.9	29.8	43.9	23.3	27.4	32.2
4	5.7	10.0	2.3	6.0	5.6	8.4	17.1	3.6	6.4	9.4
5	1.3	2.9	0.1	1.4	1.3	1.8	4.4	0.4	1.6	1.9
6	0.8	1.7	0.0	0.9	0.7	1.0	2.1	0.5	0.6	1.3
<i>MARB</i>										
1	36.1	51.9	21.6	65.8	24.7	64.1	75.9	57.5	84.8	53.0
2	36.3	33.2	39.1	30.1	38.6	25.6	17.4	30.3	13.9	31.9
3	20.3	10.5	29.3	4.1	26.5	9.0	6.1	10.7	1.3	13.2
4	7.3	4.4	10.0	0.0	10.2	1.2	0.6	1.5	0.0	1.9
<i>MUSC</i>										
1	13.0	19.4	7.4	17.1	10.8	15.7	24.2	10.9	10.3	18.7
2	3.2	4.3	2.1	5.3	2.0	2.9	4.5	2.3	5.2	1.7
3	18.5	20.0	17.1	26.7	14.0	17.3	21.2	15.5	23.5	13.7
4	54.1	48.3	59.3	43.9	59.6	47.7	36.5	53.5	45.6	48.9
5	9.6	7.0	12.0	6.1	11.5	14.3	12.6	15.2	14.8	14.0
6	1.6	1.0	2.1	0.9	2.0	2.1	1.0	2.6	0.6	3.0

had a MARB of 1 [i.e. the lowest (re-coded) marble score] in 65.8% and 84.8% of animals for TEMP and TROP, respectively (Table 3). For TROP, the effect of market weight across all traits was consistent with those for TEMP animals, except that no effect was observed on MUSC. Also for TEMP, and in spite of the apparent trend on FATC with market weight endpoints (Table 4), the effect of market (domestic v. export) was significantly different for all traits except for FATC and MEATC. Similar results were reported by Dubeski *et al.* (1997) with Angus and Hereford heifers reporting IMF means of 6.93, 8.94, and 9.86% at slaughter weights of 500, 590, and 680 kg, respectively. With Charolais cross steers, Mandell *et al.* (1997) also reported increased levels of IMF and reduced lean yield with increasing backfat slaughter endpoints.

Finishing regime effect

For both TEMP and TROP, feedlot-finished animals were fatter (as measured from IMF, MARB, and RIB) and with lower RBY. For TEMP, the effect of finishing regime was a significant source of variation for all traits except P8 and

DBTEMP. Feedlot-finished carcasses had the whitest FATC score (score = 1) in 92.8% and 89.1% of carcasses and a MEATC of 2 (i.e. very light) in 75.8% and 70.0% of carcasses for TEMP and TROP, respectively (Table 5). In agreement with Strachan *et al.* (1993), Cranwell *et al.* (1996), McCaughey and Cliplef (1996), Schnell *et al.* (1997), and Muir *et al.* (1998), animals finished on grain had significantly whiter fat and brighter meat than animals finished at pasture. Similar results were reported by Bennett *et al.* (1995) with tropical grass pasture or concentrate. The authors concluded that meat colour of pasture-finished steers was darker with creamier coloured fat. The effects of finishing on carcass traits were similar between TROP and TEMP. However, a slight difference in CWT for TEMP was observed between finishing regimes but simply reflected differences in final liveweight (Johnston *et al.* 2003a) that occurred as a result of management constraints. The large observed difference in MEATC, particularly between TROP feedlot and pasture (-0.66 of a score), could be the result of large differences in age at slaughter (-224 days). Older animals often have higher myoglobin concentrations

Table 4. Temperate breeds: least-square means by main design effects and for each trait
 See Table 1 for trait definition and units. Sex: H, heifer, S, steer. Market: D, domestic; K, Korean; J, Japanese. Finish: FS, feedlot south; PS, pasture south

	AGE (days)	CWT (kg)	RBV (%)	IMF (%)	P8 (mm)	RIB (mm)	ELW (cm ²)	FATC (units)	MEATC (units)	MARB (units)	MUSC (units)	DBTEMP (°C)
	<i>Sex × market</i>											
H × D	489	198	68.98	3.60	8.20	6.40	74.12	1.39	2.75	1.19	3.27	15.39
H × K	675	278	65.85	5.48	14.52	10.15	82.81	1.66	2.34	2.24	3.78	17.05
S × D	502	210	69.60	3.00	6.49	4.84	78.16	1.37	2.47	1.25	3.04	14.76
S × K	673	283	65.72	4.82	10.79	8.55	85.81	1.61	2.47	1.96	3.63	18.23
	<i>Market</i>											
D	504	205	69.33	3.25	7.22	5.50	76.43	1.38	2.59	1.22	3.14	15.03
K	693	281	65.78	5.11	12.39	9.23	84.52	1.63	2.41	2.08	3.69	17.73
J	745	321	63.69	6.13	12.42	10.75	88.42	1.69	2.51	2.45	3.59	19.48
	<i>Finish</i>											
FS	593	269	65.77	5.25	11.40	9.71	86.51	1.10	2.31	2.06	3.65	17.13
PS	677	252	67.62	3.97	9.37	6.53	77.97	1.99	2.70	1.60	3.26	17.00
	<i>Finish × market</i>											
FS × D	485	216	68.60	3.64	8.35	6.75	79.34	1.07	2.18	1.39	3.43	15.40
FS × K	627	286	64.93	5.73	12.88	10.72	91.02	1.15	2.34	2.31	3.85	17.23
FS × J	687	332	62.29	7.23	14.15	13.12	91.18	1.08	2.47	2.77	3.70	19.98
PS × D	518	194	70.07	2.87	6.09	4.26	73.52	1.70	3.00	1.05	2.84	14.66
PS × K	730	276	66.62	4.48	11.90	7.75	78.03	2.12	2.48	1.84	3.54	18.22
PS × J	809	310	65.08	5.02	10.70	8.38	85.65	2.30	2.54	2.13	3.48	18.97

Table 5. Tropically adapted breeds: least-square means by main design effects and for each trait
 See Table 1 for trait definition and units; Sex: H, heifer, S, steer. Market: D, domestic; K, Korean, J, Japanese. Finish: FS, feedlot south; PN, pasture north; FN, feedlot north

	AGE (days)	CWT (kg)	RBV (%)	IMF (%)	P8 (mm)	RIB (mm)	ELW (cm ²)	FATC (units)	MEATC (units)	MARB (units)	MUSC (units)	DBTEMP (°C)
<i>Sex × market</i>												
H × D	630	207	68.15	2.46	9.59	4.95	73.15	1.28	2.34	1.24	3.42	13.04
H × K	840	265	64.93	3.31	14.33	7.52	79.29	1.71	2.65	1.67	3.47	16.48
S × D	616	224	69.60	1.87	7.40	3.61	77.22	1.52	2.42	1.19	3.49	12.99
S × K	801	282	67.60	2.60	10.40	5.36	83.44	1.31	2.47	1.44	3.44	15.81
<i>Market</i>												
D	624	216	68.87	2.16	8.50	4.28	75.18	1.40	2.38	1.22	3.46	13.02
K	823	274	66.27	2.96	12.37	6.44	81.37	1.51	2.56	1.55	3.46	16.14
J	913	320	64.82	3.45	12.90	7.42	84.79	1.37	2.71	1.80	3.40	18.28
<i>Finish</i>												
FN	698	263	66.47	2.64	12.98	6.43	80.29	1.18	2.35	1.51	3.80	14.64
FS	675	257	66.70	3.51	9.38	6.24	81.45	1.17	2.20	1.62	3.55	16.97
PN	915	260	68.10	2.06	10.46	4.64	76.99	1.96	3.00	1.28	2.98	14.35
<i>Finish × market</i>												
FN × D	575	215	67.88	2.03	10.22	4.68	75.85	1.18	2.28	1.23	3.71	12.27
FN × K	763	279	66.10	2.79	14.38	7.13	82.26	1.18	2.40	1.57	3.86	15.18
FN × J	809	324	64.41	3.56	15.50	8.53	85.23	1.19	2.37	1.94	3.88	18.31
FS × D	538	216	68.55	3.05	7.39	5.26	77.05	1.06	2.08	1.29	3.34	15.22
FS × K	745	272	65.68	3.62	10.58	6.69	82.67	1.36	2.33	1.71	3.61	17.83
FS × J	789	311	65.02	4.22	10.97	7.32	87.82	1.04	2.20	2.10	3.86	18.71
PN × D	772	216	70.18	1.42	7.87	2.89	72.65	1.96	2.79	1.12	3.32	11.55
PN × K	960	270	67.01	2.46	12.15	5.49	79.17	2.00	2.95	1.39	2.90	15.50
PN × J	1144	325	65.12	2.57	12.25	6.42	81.33	1.88	3.55	1.37	2.45	17.81

Table 6. Solutions from orthogonal contrasts to test for main design effect and for each trait for temperate and tropically adapted breeds

See Table 1 for trait definition and units. All contrasts are significantly different from zero (at $P = 0.05$); n.s., not significant

Contrast	AGE (days)	CWT (kg)	RBV (%)	IMF (%)	P8 (mm)	RIB (mm)	ELW (cm ²)	FATC (units)	MEATC (units)	MARB (units)	MUSC (units)	DBTEMP (°C)
<i>Pooled data</i>												
Feedlot-pasture	-137.9	8.0	-1.55	0.79	n.s.	1.93	5.46	-0.83	-0.55	0.30	0.54	0.50
Domestic-export	-212.9	-80.7	3.62	-1.54	-4.54	-3.31	-8.32	n.s.	n.s.	-0.69	n.s.	-3.64
Heifer-steer ^A	n.s.	-13.2	-1.27	n.s.	2.94	1.53	-3.99	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Temperate breeds</i>												
Feedlot-pasture	-83.6	17.4	-1.85	1.28	n.s.	3.18	8.54	-0.89	-0.39	0.46	0.40	n.s.
Domestic-export	-207.5	-90.1	4.32	-2.22	-5.18	-4.28	-9.51	n.s.	n.s.	-0.99	-0.52	-3.33
Heifer-steer ^A	n.s.	n.s.	n.s.	n.s.	2.72	n.s.	-3.52	n.s.	n.s.	n.s.	n.s.	n.s.
<i>(Only feedlot finished)</i>												
Heifer-steer ^A	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.31	n.s.	n.s.	-1.81
<i>Tropically adapted breeds</i>												
Feedlot-pasture	-237.9	n.s.	-1.51	1.01	n.s.	1.70	3.88	-0.79	-0.73	0.28	0.70	1.45
Domestic-export	-219.8	-73.2	3.05	-0.96	-4.05	-2.49	-7.32	n.s.	n.s.	-0.42	n.s.	-3.84
North-South	140.0	n.s.	n.s.	-1.16	2.32	n.s.	n.s.	0.40	0.47	n.s.	n.s.	-2.47
Heifer-steer ^A	n.s.	-17.4	-2.06	0.65	3.06	1.75	-4.11	n.s.	n.s.	n.s.	n.s.	n.s.
<i>(Only Northern finished)</i>												
Feedlot-pasture	-223.9	n.s.	-1.62	0.58	2.48	1.79	n.s.	-0.78	-0.66	0.23	0.82	0.29
Heifer-steer ^A	n.s.	-18.7	n.s.	0.61	3.66	1.95	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>(Only feedlot finished)</i>												
North-South	n.s.	n.s.	n.s.	-0.87	3.56	n.s.	n.s.	n.s.	0.14	n.s.	n.s.	-2.33
Heifer-steer ^A	n.s.	-16.8	-1.86	0.66	2.19	1.53	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

^AOnly domestic and Korean market weight endpoints considered in sex contrasts.

(Faustman 1994). Approximately 80–90% of the total meat pigment is due to the oxygen-binding protein myoglobin. Thus colour differences in meat are related to the myoglobin content of muscle fibres and to the chemical state of the iron atom found in the myoglobin molecule (Faustman 1994).

The North *v.* South contrast for TROP cattle revealed a significant effect for IMF, P8, and MEATC. Northern-finished animals expressed less IMF by 1.16%, more P8 by 2.32 mm, and darker MEATC by 0.47 scored units. When only feedlot-finished animals were considered in the North *v.* South contrast, these differences still remained, although with lesser magnitude for IMF and MEATC and bigger for P8 (Table 6). In agreement with Oddy *et al.* (1997), at the same CWT, Northern-finished cattle were older and fatter at the P8 site than Southern-fed steers and heifers.

Scored traits

Results from LSMEANS of continuously measured variables by levels of discrete variables revealed that MARB was positively associated with CWT and the other fat measurements, and negatively associated with RBY. However, some of these associations might not be linear. For instance, LSMEANS for RBY at MARB score of 1, 2, 3, and 4 were 67.19, 66.59, 66.20, and 65.82%, respectively, for TEMP, and 66.90, 66.22, 65.62, and 65.25%, respectively, for TROP. In common with previous studies (Cameron *et al.* 1994; Baud *et al.* 1998a), IMF was found to increase with the level of MARB. LSMEANS for IMF at MARB scores from 1 to 4 were 3.93, 4.52, 5.73, and 7.53% for TEMP, and 2.25, 2.91, 3.91, and 5.26% for TROP. This indicates that MARB may be a different trait to IMF. As suggested by Baud *et al.* (1998b), an alternative explanation could be that error in the measurement of MARB causes the regression of MARB on IMF to be rather flat, so that for any particular level of IMF there might be many MARB scores. To further investigate this hypothesis a simple regression analysis of MARB on IMF for TEMP and TROP by finishing regime yielded the following equations:

$$\text{MARB} = 1.06 + 0.22 \times \text{IMF} \quad (R^2 = 0.37)$$

and

$$\text{MARB} = 0.38 + 0.35 \times \text{IMF} \quad (R^2 = 0.44)$$

for TEMP finished in feedlot and pasture, respectively; and

$$\text{MARB} = 0.73 + 0.27 \times \text{IMF} \quad (R^2 = 0.24)$$

and

$$\text{MARB} = 0.68 + 0.29 \times \text{IMF} \quad (R^2 = 0.28)$$

for TROP finished in feedlot and pasture, respectively. These regressions show a bigger difference for the effect of pasture

versus grain finishing on MARB for TEMP than for TROP animals.

No association was found between FATC or MEATC and the continuous traits. MUSC not only presented an unusual distribution of records across levels (Table 3), but also seemed to be related to fat traits only. At MUSC score of 1, LSMEANS for IMF, P8, and RIB in TEMP were 5.16%, 8.99 mm, and 7.47 mm, respectively. The same values at MUSC score of 5 were 5.74%, 10.79 mm, and 9.14 mm, respectively. These results contrast with those reported by Perry *et al.* (1993a, and 1993b) who found a negative correlation between P8 and MUSC and a positive association between MUSC and RBY. For both TEMP and TROP, ELW and DBTEMP were only related to MUSC, and RBY was only related to MARB.

Genetic parameters

Estimates of additive genetic variance (V_A), heritability (h^2), and genetic (r_g) and phenotypic (r_p) correlations for all traits and for TEMP and TROP breeds are shown in Tables 7 and 8, respectively. For TEMP breeds, estimates of h^2 for CWT, RBY, IMF, P8, RIB, ELW, DBTEMP, FATC, MEATC, MARB, and MUSC were 0.39, 0.57, 0.38, 0.36, 0.27, 0.30, 0.10, 0.05, 0.11, 0.17, and 0.14, respectively. In comparison, h^2 for the same order of traits for TROP were 0.36, 0.50, 0.39, 0.30, 0.41, 0.32, 0.04, 0.09, 0.11, 0.25, and 0.11. Standard errors associated with estimates of h^2 from Table 7 averaged 0.04 and ranged from 0.02 for FATC to 0.07 for RBY. Larger standard errors were observed for estimates of r_g , averaging 0.15 and ranging from 0.04 for the r_g between IMF and MARB to 0.29 for the r_g between CWT and FATC. Similar standard errors were associated with estimates of h^2 and r_g for TROP (Table 8). The large standard errors resulted from the relatively few numbers of records for some traits. This was particularly true for those parameters relating to RBY, which had the fewest number of observations (Table 2). However, some small standard errors associated with extreme estimates (i.e. close to boundaries) can be attributed to positive definite software constraints.

A comprehensive review of h^2 estimates in beef cattle published from 1946 to 1991 was undertaken by Koots *et al.* (1994a) and more recently for carcass and meat quality by Burrow *et al.* (2001). The authors reported a weighted mean h^2 estimate of 0.23 for carcass weight on an age-constant basis and 0.48, 0.36, 0.46, and 0.41 for cutability, marbling, backfat, and eye muscle area on a weight-constant basis, respectively. These values are of similar magnitude to our estimates for the comparable traits of CWT, RBY, IMF, RIB, and ELW, respectively. The exception is CWT where our estimates were considerably larger (0.39 and 0.36 for TEMP and TROP, respectively). Lower estimates were recently reported by Shanks *et al.* (2001) on Simmental-sired cattle ranging from 0.12 for RBY and MARB on a weight-constant

Table 7. Temperate breeds: multivariate REML estimates of additive genetic variance (V_A), heritability, and genetic and phenotypic correlations for each trait
See Table 1 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

	V_A	CWT	RBY	IMF	P8	RIB	ELW	FATC	MEATC	MARB	MUSC	DBTEMP
CWT	199.14	<i>0.39</i>	0.06	-0.12	-0.39	-0.39	0.45	-0.08	-0.46	-0.15	0.10	-0.22
RBY	2.25	0.18	<i>0.57</i>	-0.38	-0.48	-0.65	0.44	-0.21	-0.02	-0.39	0.20	-0.39
IMF	0.80	-0.19	-0.31	<i>0.38</i>	0.34	0.21	-0.12	0.03	0.03	0.96	0.12	0.29
P8	2.83	-0.19	-0.40	0.16	<i>0.36</i>	0.82	-0.29	0.28	0.06	0.22	-0.02	0.47
RIB	1.82	-0.19	-0.40	0.17	0.48	<i>0.27</i>	-0.13	0.43	0.21	0.12	-0.17	0.45
ELW	23.17	0.32	0.14	-0.17	-0.14	-0.20	<i>0.30</i>	0.21	-0.16	-0.14	0.16	-0.52
FATC	0.01	-0.07	-0.04	0.03	0.02	0.03	-0.00	<i>0.05</i>	-0.12	0.11	0.70	-0.00
MEATC	0.03	-0.20	-0.03	-0.01	0.04	0.03	-0.06	-0.03	<i>0.11</i>	0.05	-0.53	0.31
MARB	0.06	-0.18	-0.19	0.46	0.08	0.10	-0.09	0.00	-0.02	<i>0.17</i>	0.19	0.11
MUSC	0.10	0.11	0.05	-0.02	0.03	0.03	0.09	-0.01	-0.03	-0.01	<i>0.14</i>	-0.16
DBTEMP	0.32	-0.14	-0.07	0.07	0.07	0.03	-0.06	0.03	0.00	0.03	0.05	<i>0.10</i>

Table 8. Tropically adapted breeds: multivariate REML estimates of additive genetic variance (V_A), heritability, and genetic and phenotypic correlations for each trait
See Table 1 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

	V_A	CWT	RBY	IMF	P8	RIB	ELW	FATC	MEATC	MARB	MUSC	DBTEMP
CWT	197.46	<i>0.36</i>	0.16	-0.03	-0.17	-0.42	-0.28	-0.02	-0.55	-0.20	-0.15	0.29
RBY	2.14	-0.03	<i>0.50</i>	-0.43	-0.28	-0.29	0.25	0.00	-0.18	-0.56	0.53	0.41
IMF	0.37	0.09	-0.27	<i>0.39</i>	0.22	0.20	-0.15	0.02	-0.29	0.89	-0.32	0.09
P8	4.33	-0.11	-0.23	0.12	<i>0.30</i>	0.79	-0.19	0.22	-0.06	0.19	0.09	-0.70
RIB	2.87	-0.13	-0.31	0.14	0.49	<i>0.41</i>	-0.10	0.01	0.18	0.13	-0.13	-0.66
ELW	25.41	-0.11	0.13	-0.13	-0.13	-0.13	<i>0.32</i>	0.12	0.15	-0.23	-0.18	-0.01
FATC	0.02	-0.13	-0.03	0.01	0.02	0.02	0.06	<i>0.09</i>	-0.16	-0.05	-0.19	0.07
MEATC	0.03	-0.17	-0.02	-0.08	0.00	-0.00	0.04	0.02	<i>0.11</i>	-0.22	-0.09	-0.26
MARB	0.08	-0.01	-0.17	0.48	0.07	0.06	-0.01	0.01	-0.08	<i>0.25</i>	-0.10	0.06
MUSC	0.08	-0.02	0.12	-0.03	-0.01	0.01	-0.01	0.04	-0.04	-0.01	<i>0.11</i>	0.01
DBTEMP	0.10	-0.06	-0.02	0.02	0.03	0.01	-0.02	-0.01	-0.04	-0.01	0.06	<i>0.04</i>

basis to 0.32 for CWT on an age-constant basis. In their study, RBY was measured from an estimate of the yield of closely trimmed, boneless retail cuts from the round, loin, rib, and chuck.

Most r_g estimates were consistent across TEMP and TROP and in agreement with reported figures from studies made with subsets of these data (Ferguson *et al.* 1997; Johnston *et al.* 1999b; Reverter *et al.* 2000). For both TEMP and TROP, negative r_g values were found between CWT and all fat measurements, and between RBY and all fat measurements. Both FATC and MEATC not only had low heritability but they did not significantly influence any other variable (as seen from LSMEANS analyses previously discussed). There was a moderate to strong negative r_g between MEATC and CWT, suggesting that the genes with the potential to produce heavier carcasses at a constant age are the same genes as, or closely linked to, those with the potential to produce brighter lean meat. Estimates of h^2 for DBTEMP were low for both TEMP and TROP and thus its r_g with other traits is difficult to interpret and must be treated with caution.

Estimates of r_g and r_p between ELW and CWT were different across TEMP and TROP. These were clearly positive for TEMP (0.45 and 0.32 for r_g and r_p , respectively) but slightly negative for TROP (-0.28 and -0.11 for r_g and r_p , respectively). The weighted average r_g estimate between eye muscle area and CWT given in the review of Koots *et al.* (1994b) is 0.48 when both traits are adjusted to an age-constant basis. Also, Shanks *et al.* (2001) reported that the r_g of this same pair of traits was high and positive at all end points. However, the authors did not explore the scenario in which CWT is age-adjusted and eye muscle area is carcass weight-adjusted. The estimates of Reverter *et al.* (2000) with a subset of these data were -0.35 and -0.16 for Angus and Hereford, respectively.

Genetic relationships between IMF, MARB, fat thickness, and RBY are of particular interest, because in many markets they are key attributes in determining carcass value. Genetic correlations between IMF and MARB were close to unity, suggesting that both are measurements of the same trait at the genetic level. Estimates of r_p for the same traits were weaker, although positive (0.46 and 0.48 for TEMP and TROP, respectively). For IMF and MARB, h^2 was similar across TEMP and TROP but TROP had about half the additive variance compared with TEMP. Similar early results were reported by Johnston *et al.* (1999b). With the exception of FATC, all fat measurements were positively genetically correlated with each other and negatively correlated with RBY. Estimates of r_g between both subcutaneous fat depths (P8 and RIB) were very high for both TEMP and TROP (0.82 ± 0.04 and 0.79 ± 0.04 for TEMP and TROP, respectively). However, the r_p between the same pair of traits was only moderate (0.48 and 0.49 for TEMP and TROP, respectively). Estimates of r_g between IMF and fat depths

ranged from 0.20 ± 0.05 for the r_g between IMF and RIB for TROP to 0.34 ± 0.08 between IMF and P8 for TEMP. Finally, negative estimates of r_g between fat measurements and RBY ranged from -0.65 ± 0.07 between RBY and RIB for TEMP to -0.28 ± 0.09 between RBY and P8 for TROP. Likewise, the review of Marshall (1994) concluded that, averaged across studies, genetic correlations indicate an antagonism between increased marbling and decreased subcutaneous fat depth. Similarly, working on a variety of breed groups, Gregory *et al.* (1995) concluded that r_g was generally high among all measures of carcass fat, indicating major difficulty in achieving a high percentage of retail product simultaneously with a high intramuscular fat content of the *longissimus* muscle that is required for carcass quality grade under the USA grading system. However, our r_g estimates of -0.38 and -0.43 for TEMP and TROP, respectively, suggest that although the traits are moderately antagonistic, simultaneous improvement in both traits could be achieved using a multiple-trait selection index approach and recording both traits.

For both TEMP and TROP, results indicate that selection for decreased subcutaneous fat depth at a weight-constant basis will increase CWT at an age-constant basis ($r_g = -0.39$). To our knowledge, except for Moser *et al.* (1998), Reverter *et al.* (2000), and Shanks *et al.* (2001) who also reported a negative r_g between subcutaneous fat and CWT, no other previous study has reported a negative genetic relationship between these traits. Estimates at constant age ranged from 0.13 by Gregory *et al.* (1995) to 0.38 by Wilson *et al.* (1993). The review by Koots *et al.* (1994b) reported a weighted mean r_g between age constant back fat and CWT of 0.29.

The estimate of r_g between RBY and MUSC for TEMP was low (0.20) and moderate (0.53) for TROP. At the phenotypic level, these correlations were closer to zero, in agreement with previously discussed results from LSMEANS. The low h^2 of MUSC limits its usefulness as an indicator trait for RBY, particularly if fat and ELW (or LTL area) are routinely measured.

Market weight effect

Bi-variate REML estimates of V_A , h^2 , and r_g between domestic and export (jointly Korean and Japanese) market weight end points for each trait and for TEMP and TROP are given in Table 9. For both TEMP and TROP, greater estimates of V_A were found for CWT, RBY, IMF, P8, RIB, and MARB for animals finished to export weights than to domestic market weights. Most estimates of h^2 were consistent across TEMP and TROP within and across market. Exceptions include MARB with a h^2 estimate 5 times (TROP) and twice (TEMP) as large in the export market compared with the estimate in domestic market weights. However, these vast differences in h^2 between domestic and export market weights were not seen in the

Table 9. Bivariate REML estimates of additive genetic variance (V_A), heritability (h^2), and genetic correlation (r_g) between domestic and export (jointly Korean and Japanese) market weight endpoints for each trait for temperate and tropically adapted breeds
See Table 1 for trait definition and units

	CWT	RBY	IMF	P8	RIB	ELW	FATC	MEATC	MARB	MUSC	DBTEMP
<i>Temperate breeds</i>											
Domestic V_A	159.99	1.87	0.33	1.55	0.77	15.57	0.07	0.01	0.02	0.07	0.29
h^2	0.42	0.64	0.41	0.35	0.24	0.35	0.05	0.05	0.09	0.10	0.10
Export V_A	233.09	2.50	1.28	3.11	1.93	19.95	0.03	0.03	0.09	0.10	0.33
h^2	0.40	0.53	0.47	0.33	0.24	0.25	0.02	0.10	0.20	0.14	0.10
Domestic-export r_g	1.00	1.00	0.92	0.85	1.00	0.98	-1.00^A	1.00	1.00	0.94	0.75
<i>Tropically adapted breeds</i>											
Domestic V_A	112.00	1.95	0.21	3.76	1.89	25.37	0.02	0.03	0.01	0.04	0.28
h^2	0.32	0.54	0.39	0.38	0.41	0.44	0.13	0.13	0.07	0.07	0.13
Export V_A	270.68	2.15	0.47	4.24	3.45	23.61	0.03	0.03	0.12	0.08	0.02
h^2	0.40	0.45	0.38	0.26	0.42	0.27	0.12	0.08	0.35	0.10	0.01
Domestic - Export r_g	0.95	0.73	1.00	1.00	1.00	1.00	0.53	0.75	0.91	1.00	1.00^A

^AEstimates are uninterpretable given the numeric instabilities resulting from negligible variances.

objectively measured IMF. This was attributed to the small phenotypic variance observed for MARB at the domestic market level (0.02 and 0.01 square scored units for TEMP and TROP, respectively). This was expected given the strong right-skewed distribution of MARB in the domestic market weight endpoint (Table 3). A non-linear model for the analysis of MARB may be more appropriate to identify further genetic variance.

Genetic correlations between traits across market weight endpoints were positive and close to unity, with the exception of RBY for TROP and FATC for TEMP. Present literature reporting on market weight effects on carcass traits is limited to phenotypic comparisons and with limited numbers (see for instance Dubeski *et al.* 1997; Mandell *et al.* 1997). To our knowledge, no published research exists reporting genetic parameters for carcass traits across market weight endpoints. Three distinct beef markets (based mainly on weight) exist in Australia. However, delivery of 3 sets of carcass EBV to industry would be unacceptably. The high r_g estimates of traits across market groups (Table 9) support the single basis of reporting carcass EBV adopted by BREEDPLAN Version 4.1 (Johnston *et al.* 1999a).

Genetic correlations deviating from unity include that between domestic and export market weight for FATC (-1.0 for TEMP and 0.53 for TROP) and RBY for TROP (0.73 ± 0.16). The extreme (-1.0) r_g estimated for FATC between market destinations is attributed to numerical instabilities associated with negligible variances, which result in uninterpretable covariances. For RBY, even though TROP animals finished to the domestic market produced RBYs that were 3.05% higher (Table 4) than their relatives finished to the export market, they had a phenotypic variance that was lower (3.62 v. 4.73%). RBY is a percentage measurement, and hence, more variation is expected for values closer to the middle of the parameter space. Similar results were observed in animals from TEMP: 2.93 v. 4.71% for the same pair of values. However, the raw, unadjusted variance of RBY for TROP animals finished to the domestic and export market weight end-points was 5.79 and 8.34% , respectively. These same values for TEMP animals were 7.46 and 11.17% . Lower means with higher variances at the export compared with domestic levels were also reported by Reverter *et al.* (2000) with an Angus and Hereford subset of these data. TROP animals finished to the domestic market weight endpoint required little or no trimming for obtaining RBY, whereas this was not the case in the export. These differences in trimming requirements could be responsible for r_g deviating from unity.

Finishing regime effect

Bi-variate REML estimates of V_A , h^2 , and r_g between feedlot- and pasture-finished animals for TEMP are presented in Table 10. With the exception of RBY and ELW, higher means (Tables 4 and 5) were associated with

higher V_A and h^2 . The low V_A and h^2 of ELW that were estimated in feedlot-finished animals are likely to be due to measurement errors resulting from ELW being computed by multiplying length by width of the LTL muscle. Again, similar to results for the effect of market weight (Table 9), and with the exception of FATC, most estimates of r_g between traits across feedlot v. pasture finishing were high and within 1 standard error of unity and show no evidence of genotype \times finishing interactions. For TEMP breeds, genetic correlations between finishing regimes were close to unity. However, possible $G \times E$ interactions were found for TROP for P8, MEATC, and MARB between North- and South-finished, and between feedlot- and pasture-finished animals for RBY and MEATC.

Tri-variate REML estimates of V_A , h^2 , and r_g between feedlot North and South and pasture North (subtropical) for TROP are given in Table 11. Additive variances and h^2 were similar for feedlot finishing (North v. South) for most of the traits but generally differed with parameters for pasture North. Estimates of V_A and h^2 were negligible for FATC with the exception of those found for North pasture finished animals. Genetic correlations between feedlot and pasture finishing in the North were generally high with the exception of RBY, MEATC, and MARB. Similar to the results for TEMP, little evidence was found for the occurrence of genotype \times finishing regime interactions. The exception for TROP was RBY and is consistent with results in Table 9 from the domestic v. export comparisons observed for RBY in Table 11.

Genetic correlations between geographic regions of feedlot finishing (i.e. North and South) were high for CWT, RBY, IMF, RIB, and FATC suggesting little evidence of a $G \times E$ interaction. The low correlations between finishing regimes for MARB differ with those estimated for IMF. This may be attributed to errors in measurements of the subjective MARB and may not be a true $G \times E$. For the other traits the correlations were less than zero and were likely to be caused by low additive variances and heritabilities for the remaining traits leading to numerical instabilities. The r_g between P8 in feedlot North and South was 0.64 ± 0.21 . From these results, the genes responsible for fat deposition at the rump site in subtropical environments are not exactly the same as those expressed in temperate environments. Animals finished in the North feedlot had 3.56 mm more fat at the P8 site than those finished in feedlot South (Table 6). The estimate of V_A for P8 in animals finished in feedlot North was 3.16 times larger than that for feedlot South animals (5.41 v. 1.71 mm²). This difference was not significant at the RIB level. A possible explanation for this phenomenon is that animals eating high-energy diets tend to deposit more fat. However, the distribution of this fat across the body mass might vary with the environment, favouring the lumbo-sacral region against the thorax under subtropical environments as part of their thermoregulation. Burrow *et al.* (1991) reported

Table 10. Temperate breeds: bivariate REML estimates of additive genetic variance (V_A), heritability (h^2), and genetic correlation (r_g) between feedlot- and pasture-finished animals for each trait

See Table 1 for trait definition and units

	CWT	RBV	IMF	P8	RIB	ELW	FATC	MEATC	MARB	MUSC	DBTEMP
Feedlot V_A	251.73	2.65	1.22	2.38	1.50	7.94	0.00	0.01	0.09	0.08	0.57
h^2	0.45	0.60	0.49	0.28	0.19	0.12	0.00	0.12	0.23	0.13	0.17
Pasture V_A	167.98	1.41	0.46	2.57	1.61	34.31	0.01	0.04	0.03	0.10	0.09
h^2	0.37	0.43	0.30	0.37	0.34	0.47	0.02	0.09	0.09	0.12	0.03
Feedlot–pasture r_g	0.88	0.93	1.00	0.92	0.81	1.00	-1.00^A	1.00	0.91	1.00	1.00^A

^AEstimates are uninterpretable given the numeric instabilities resulting from negligible variances.

Table 11. Tropically adapted breeds: trivariate REML estimates of additive genetic variance (V_A), heritability (h^2), and genetic correlation (r_g) between feedlot and pasture and Northern and Southern finished animals for each trait

See Table 1 for trait definition and units

	CWT	RBV	IMF	P8	RIB	ELW	FATC	MEATC	MARB	MUSC	DBTEMP
Feedlot North (FN) V_A	229.06	2.99	0.47	5.40	3.65	25.12	0.00	0.04	0.11	0.03	0.17
h^2	0.41	0.62	0.46	0.33	0.47	0.31	0.04	0.15	0.35	0.04	0.09
Feedlot South (FS) V_A	246.87	2.05	0.49	1.71	1.92	17.92	0.00	0.01	0.15	0.16	0.49
h^2	0.39	0.48	0.42	0.19	0.32	0.24	0.02	0.04	0.43	0.19	0.15
Pasture North (PN) V_A	173.94	1.84	0.21	8.55	3.91	34.36	0.12	0.06	0.04	0.12	0.02
h^2	0.40	0.52	0.31	0.49	0.53	0.45	0.25	0.16	0.16	0.18	0.01
FN–FS r_g	0.97	0.81	0.94	0.64	0.99	1.00	1.00^A	0.59	0.75	0.63	-0.25^A
FN–PN r_g	0.87	0.60	0.95	0.91	0.91	0.80	1.00^A	0.51	0.37	0.95	0.91^A
FS–PN r_g	0.73	0.55	0.99	0.90	0.93	0.81	1.00^A	0.99	0.78	0.36	0.34^A

^AEstimates are uninterpretable given the numeric instabilities resulting from negligible variances.

evidence of differential fat deposition in lines of cattle selected for high growth and low EBV for rectal temperature. Conversely, the differences may have resulted from different growth paths in North v. South.

Conclusions

Production system can be used to phenotypically alter age at slaughter and carcass traits at market weight constant endpoints. Given the moderate heritabilities, phenotypic variances, and moderate to strong genetic correlations, selection for improved abattoir carcass traits is possible for temperate and tropically adapted breeds. The consistency of the parameters across TEMP and TROP both within and across finishing regimes and market weight end points provides little evidence of genotype by environment interactions. Therefore breeding stock can be selected to maximise performance on either pasture, feedlot, or geographic region (for tropically adapted breeds) and be well suited to a range of market endpoints.

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