

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

1. Animal measures*

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Abstract. A total of 7622 cattle were measured for several weight and body composition traits in temperate and tropically adapted breeds. Traits included: liveweight, hip height, body fat score, muscle score, flight time, ultrasound scanned fatness, and eye muscle area. Measurements were taken at 3 stages during the project: post-weaning, start of finishing, and end of finishing (i.e. pre-slaughter). Animals were finished to 3 target market-weight end-points (220, 280, or 340 kg carcass weight), either on pasture or in a feedlot, and in 2 different geographic regions for tropically adapted breeds. These data were used to estimate genetic parameters for the traits at each stage, and also to estimate the effect of market weight and finishing regimes on the phenotypic and genetic expression of each trait measured at the end of finishing stage. Results showed, for all traits, that the magnitude of the phenotypic expression increased across the stages and market-weight end-points for the end of finishing measures. Feedlot finishing decreased the age at slaughter, and increased fatness and muscling compared with pasture-finished animals. Heritabilities ranged from 0.13 to 0.58, with subjectively scored traits generally being lower than objectively measured traits. Additive genetic variances generally increased with stage of measurement, and with increasing market weight. Genetic correlations of the same measure across stages or market weights were all close to unity. Additive genetic variances of the various traits were similar for feedlot versus pasture finish groups, and the genetic correlation between each measure for feedlot and pasture finish was generally greater than 0.80. The effect of finishing geographic region (i.e. temperate versus subtropical environments) for the tropically adapted breeds had little effect on the size of the additive genetic variances or genetic correlations between traits across geographic regions.

The results imply that changing the production system had a significant impact on the phenotypic expression of growth and body composition traits but little effect on the underlying genetic expression and subsequent ranking of sires (i.e. no evidence of genotype by production environment interactions). Therefore, these live animal measures could be used as selection criteria in genetic evaluation programs and may also be genetically correlated with abattoir carcass and meat quality traits.

Additional keywords: cattle, ultrasound, correlations, G × E interactions.

Introduction

There is increasing interest within the breeding sector of the Australian beef industry to improve carcass and meat quality traits through genetic selection. Primarily our domestic and overseas consumers are driving this focus on meat quality.

However, to improve any of these traits through selection, suitable selection criteria must exist. The selection criterion (i.e. the trait measured) must be heritable, cost-effective to measure, and correlated to traits in the breeding objective. One possible set of selection criteria are live animal traits

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

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that are genetically correlated with, often difficult to measure, carcass and meat quality traits. In the design of an effective genetic evaluation program it is important to examine if the ranking of animals and the expression of traits, both phenotypic and genetic, are altered by management or environment.

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 conditions and production systems, the Cooperative Research Centre for Cattle and Beef Quality (Beef CRC) straightbreeding project was established (Bindon 2001). The objectives of this project were firstly to quantify the effect of different market weight endpoints and finishing regimes on the phenotypic expression of numerous animal, carcass, and meat quality traits for temperate and tropically adapted breeds; secondly, to estimate genetic parameters, including heritabilities and genetic and phenotypic correlations for animal, carcass, and meat quality traits in temperate and tropically adapted breeds; lastly, to determine the existence of genotype by environment interactions for all traits by considering the records on animals in different market weights and finishing regimes as separate traits. Preliminary results from this project have been published by Reverter *et al.* (2000), Robinson *et al.* (2001), and Johnston *et al.* (2001).

The objective of this paper is to present estimates of genetic and phenotypic parameters for several animal traits that are related to carcass, and possibly meat quality traits. Measurements used in this paper were taken at 3 post-weaning stages of production and were used to investigate the change in genetic expression of the traits over time. The study aimed to quantify the effect of finishing regimes on the genetic expression of these animal measures and the genetic correlation of traits across finishing regimes. Results from this study were used in Reverter *et al.* (2003b) to estimate the genetic correlation of animal measures with abattoir carcass and meat quality measures on the same animals. This paper is first in a series of 4 papers that reports on the genetic and phenotypic description of animal, carcass, and meat quality traits from the Beef CRC straightbreeding project. Presented in the remaining 3 papers are genetic and phenotypic characterisation of abattoir carcass traits (Reverter *et al.* 2003a), meat quality traits (Johnston *et al.* 2003), and correlations among animal, carcass, and meat quality traits (Reverter *et al.* 2003b) from temperate and tropically adapted breeds.

Materials and methods

Animals

Animals used in this study were from the straightbreeding project of the Beef CRC. The design management and operations of the project have been reported earlier by Robinson (1995) and 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. Additional 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.

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 1993–98 in 36 cooperator herds (23 for TEMP and 13 for TROP) throughout eastern Australia. Parentage and date of birth were recorded on all animals on the cooperator herds and at weaning the animals were delivered to CRC managed properties in central Queensland and north-eastern NSW (Bindon 2001; Upton *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 progenies were balanced across treatments. Cattle were assigned to 1 of 3 target market carcass weight groups [domestic 220 kg (DOM), Korean 280 kg (KOR), and Japanese 340 kg (JAP)]. Market weight group was cross-classified with finishing regime of pasture (PAST) or feedlot (FLOT). These target weights were selected because they are indicative of the Australian domestic and export Korean and Japanese markets respectively. The TEMP progeny were finished in north-eastern NSW and were denoted as either PAST-SOUTH or FLOT-SOUTH. For TROP progeny, there were 3 finishing regimes. The first 2 levels were animals grown out and finished on pasture (PAST-NORTH) or feedlot (FLOT-NORTH) in a subtropical environment of central Queensland. The third treatment, representing approximately one-third of the tropically adapted animals, was relocated after weaning from central Queensland to temperate environments in north-eastern NSW for grow-out and feedlot finishing (FLOT-SOUTH). The relocation was done to generate a geographic region effect. The original design included a fourth level for pasture south; however, only one cohort ($N = 75$) was allocated to this treatment before low numbers forced this to be dropped from the design. Numbers of animals by breed, market weight, and finishing regimes are presented in Table 1.

Measurements and stages

Traits included in the analyses were taken at 3 stages during the post-weaning to slaughter period. The first set of measurements was taken on an intake group of calves when they were delivered post-weaning at the 2 CRC properties (i.e. all calves from the cooperators' herds, within a year and season). These measurements were termed post-weaning (POSTW). However, up to 3 months difference in time of delivery and measurement were observed within a year. The second set of measurements was recorded at the start of finishing just after completing their grow-out period. For DOM market weight groups this occurred when the mean liveweight of the intake group was 300 kg and at 400 kg mean liveweight for KOR and JAP market weight groups. Measurements at this stage were termed start of finishing (STARTF) and were recorded within 2 weeks of the start of finishing date. Lastly, records were taken at the end of finishing, just prior to slaughter, when the average weight of an intake, market weight, finishing regime subgroup was predicted to achieve target carcass weights for their assigned market (i.e. DOM, KOR, or JAP). Measurements taken at this time were termed end of finishing (ENDF). All ENDF records were taken within 21 days of slaughter, with the average being 8 days prior to slaughter.

Traits chosen for inclusion in this paper were those that were either repeatedly measured at the different stages, or had large numbers of the

Table 1. Numbers 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-NORTH	–	1319
	PAST-NORTH	–	1360

animals measured at a single stage. Traits included: liveweight (LWT), hip height (HH), body condition score (CS), muscle score (MS), flight time (FT), ultrasound-scanned fat depth at P8 site (SP8), scanned fat depth at 12/13th rib site (SRIB), and scanned eye muscle area (SEMA). See Table 2 for a complete description of each measure.

Statistical analyses

Least square means

A series of analyses was run using the GLM procedure of SAS (SAS 1988) to compute least square means (LSMEANS) for traits measured at ENDF stage by each of the design effects. For all analyses, subjectively scored traits were analysed as linear variables where the categorical nature of the trait was not considered. However, for the majority of the scored traits, more than 4 scores were observed.

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 weight group, finishing regime, market weight \times finishing regime, sex, and sex \times market weight group (for TROP only)]. To estimate the LSMEANS for a particular design effect (e.g. market weight 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. Eqn 1 is an example of the fixed effect model used to analyse each of the dependent variables of AGE, MS, SRIB, SP8, SEMA, HH, and LWT (measured at ENDF) to generate LSMEANS for market weight effect for TEMP and TROP separately:

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

where y_{ijkl} is the observation for 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, age_l is the linear effect of age of the animal at ENDF as a deviation from the mean, and e_{ijkl} is random residual error.

Orthogonal contrasts were estimated to assess the magnitude of the effects on each trait. Contrasts for sex were evaluated after removing steers finished to the Japanese market weight endpoint. 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

Table 2. Description of measurements recorded at each stage

Table adapted from Upton *et al.* 2001

Code	Trait	Description
CS	Body condition score	Visual assessment of amount of fat coverage on the body, scored on a 6-point scale, with 0, emaciated; 6, over fat (Lowman <i>et al.</i> 1976). For TEMP a 2–7 scoring scale was used with half scores, and to avoid decimals, all scores were multiplied by 10. For TROP, animals were scored on the 6-point scale but with each category having '+' and '-' subcategories. TROP scores were re-coded to a numeric variable 1–, 1; 5+, 15
MS	Muscle score	Visual assessment for muscling based on thickness and convexity of shape relative to frame size, after allowing for fatness. Scored on an A–E scale, with A, heavily muscled; E, poorly muscled, with each alpha category having '+' and '-' subcategories (Perry <i>et al.</i> 1993). Scores were re-coded to a numeric variable E–, 1; A+, 15
SRIB	Scan rib fat depth (mm)	Real-time ultrasound-scanned ^A subcutaneous fat depth between 12th and 13th ribs
SP8	Scan P8 fat depth (mm)	Real-time ultrasound-scanned ^A subcutaneous fat depth at P8 site (located at the intersection of a line parallel to the spine from the <i>tuber ischium</i> and a line perpendicular to it from the spinous process of the third sacral vertebra)
SEMA	Scan eye muscle area (cm ²)	Real-time ultrasound-scanned ^A area of the eye muscle (<i>M. longissimus thoracis et lumborum</i>) between 12th and 13th ribs
HH	Hip height (cm)	The vertical height at the hook, on an animal standing squarely on a level surface
FT	Flight time (s*100)	Electronically recorded time taken for an animal to cover a fixed distance (1.7 m) after exiting a weighing crush (Burrow <i>et al.</i> 1988)
LWT	Liveweight (kg)	Weight of the animal using electronic weigh scales
AGE	Age at measurement (day)	Age of the animal recorded in days (i.e. weight date minus date of birth)

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

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

All variance components were estimated using an animal model REML 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:

$$y_i = X_i b_i + Z_i u_i + e_i \quad (2)$$

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 age at measurement covariate and contemporary group fixed effects in vector b_i ; 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; I is an identity matrix; σ_A^2 is the additive direct genetic variance; and σ_E^2 is the residual error variance.

Contemporary group for POSTW included the effects of herd of origin, sex, weigh date, geographic region, and age slice. Age slice was included to reduce the spread in age within a group. For TEMP, age slice was 10 days and for TROP it was set to 60 days because of the greater spread in calving compared with TEMP. Contemporary group for STARTF was defined as the effects of herd of origin, sex, weigh date, market weight group, and nutrition treatment group. Nutrition treatment group accounted for differences in grow-out nutrition treatments applied to some of the TEMP intake groups (see Dicker *et al.* 2001) and for growth promotant (HGP) treatments for some of the TROP groups (see Hunter *et al.* 2001). For ENDF, the contemporary group was defined as the combined effect of herd of origin, sex, and slaughter group. Slaughter group accounted for the effects of year, season, market weight group, and finishing regime.

All analyses were performed separately for TEMP and TROP. The first group of analyses estimated genetic parameters simultaneously (up to 8 traits) for all traits measured within a stage. Then a series of multivariate analyses was performed where the same measure at the different stages (i.e. POSTW, STARTF, and ENDF) were considered as different traits. A representation of the bi-variate model used is given in Eqn 3. Finally, to assess the magnitude of genotype by environment interactions, each of the traits measured at ENDF was treated as a different trait in a multivariate model 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 for TROP. However, the original market weight group was still used to define contemporary groups. Only contemporary groups with 3 or more records were used in the estimation analyses. Pasture south finished animals for TROP were dropped from all genetic analyses due to low numbers (see Table 1). For each trait, records from DOM market groups and EXP groups were considered as 2 traits. Then, 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, *viz.* PAST-NORTH, FLOT-NORTH, and FLOT-SOUTH.

The bivariate animal model can be represented as:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \quad (3)$$

with expectation:

$$E \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

and variance:

$$\text{Var} \begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} \sigma_{A_1}^2 A & \sigma_{A_{1,2}} & 0 & 0 \\ \sigma_{A_{2,1}} & \sigma_{A_2}^2 A & 0 & 0 \\ 0 & 0 & \sigma_{E_1}^2 I & \sigma_{E_{1,2}} \\ 0 & 0 & \sigma_{E_{2,1}} & \sigma_{E_2}^2 I \end{bmatrix}$$

where y_1 and y_2 are the observations (traits across stages, market weight group, or finishing regime); X , b , Z , u , e , A , I , σ_A^2 , and σ_E^2 have been defined previously. $\sigma_{A_{1,2}}$ is the additive genetic covariance between y_1 and y_2 , and $\sigma_{E_{1,2}}$ is the residual covariance between y_1 and y_2 only for the analyses of traits measured across stages; however, for the analyses of traits across design effects (e.g. DOM *v.* EXP, PAST *v.* GRAIN), these residual covariances were zero.

Results and discussion

Trait means, standard deviations, and ranges at each stage are presented in Tables 3 and 4 for TEMP and TROP, respectively. The number of records and traits recorded differed slightly across stages and between TEMP and TROP. Flight time was not measured for TEMP and fewer liveweights were recorded at POSTW because a few DOM cohorts at arrival had already reached the target weight to commence finishing. Significant market weight and finishing regime effects ($P < 0.001$) were observed for all traits at ENDF for TEMP. Similarly, TROP, market weight, finishing regime, and sex by market were significant effects for all traits. LSMEANS for each of these effects are presented in Table 5 for TEMP and TROP; orthogonal contrasts and R^2 are presented in Table 6.

Least square means

Age and liveweight

For TEMP, the average LSMEANS for AGE at ENDF were 500, 676, and 746 days for DOM, KOR, and JAP market weights, respectively. On average, TROP animals took longer to reach the target weights (618, 818, 908 days), with the greatest effect being the increased age of PAST-NORTH groups. PAST animals took an average 86 and 217 days longer to reach target weights compared with FLOT for TEMP and

Table 3. Trait means, standard deviations, and ranges at the 3 recording stages for temperate breeds

See Table 2 for a description of traits. POSTW, postweaning; STARTF, start of finishing; ENDF, end of finishing

Stage	<i>N</i>	Mean	s.d.	Min.	Max.
<i>AGE (days)</i>					
POSTW	3613	282.6	35.98	152	416
STARTF	3716	466.5	83.00	259	673
ENDF	3716	624.5	129.90	290	961
<i>LWT (kg)</i>					
POSTW	3613	248.6	44.71	75	397
STARTF	3771	361.5	63.95	145	568
ENDF	3771	511.1	94.89	140	792
<i>CS (units)</i>					
POSTW	3149	42.6	4.13	30	55
STARTF	3352	48.8	5.13	30	65
<i>MS (units)</i>					
POSTW	3054	7.1	0.92	1	11
STARTF	3283	7.3	0.88	2	12
ENDF	3327	7.6	0.91	1	11
<i>HH (cm)</i>					
POSTW	2865	115.4	5.52	93	135
<i>SRIB (mm)</i>					
POSTW	3103	2.1	1.13	1	8
STARTF	3424	3.3	1.93	1	14
ENDF	3427	8.6	4.17	1	27
<i>SP8 (mm)</i>					
POSTW	3301	2.5	1.42	1	10
STARTF	3485	4.4	2.62	1	20
ENDF	3428	11.0	4.93	1	33
<i>SEMA (cm²)</i>					
POSTW	3029	39.5	6.75	19	65
STARTF	3355	49.1	7.76	26	84
ENDF	3190	63.1	11.32	26	114

TROP, respectively. For TROP, the average age at ENDF for FLOT-SOUTH animals was 679 days, compared with 690 days for FLOT-NORTH. Although the performance of the TEMP and TROP are not directly comparable, these results suggest that the difference in age at finishing was predominantly the effect of the different environments.

Liveweights at the ENDF for DOM, KOR, and JAP were 407, 533, and 594 kg for TEMP and 410, 510, and 571 kg for TROP, respectively. Average liveweights were similar, by design, across finishing regimes for TROP, 484, 489, 489 kg for FLOT-NORTH, FLOT-SOUTH, and PAST-NORTH respectively. FLOT animals for TEMP were slightly heavier (515 kg) than PAST animals (499 kg). Heifers were on average 22 kg lighter than steers for TROP. The slight differences observed between the treatments were predominantly the result of management requirements (e.g. feedlot throughput or abattoir availability).

Table 4. Trait means, standard deviations, and ranges at the 3 recording stages for tropically adapted breeds

See Table 2 for a description of traits. POSTW, postweaning; STARTF, start of finishing; ENDF, end of finishing

Stage	<i>N</i>	Mean	s.d.	Min.	Max.
<i>AGE (days)</i>					
POSTW	3851	246.5	39.19	128	392
STARTF	3851	580.5	108.80	303	856
ENDF	3851	759.1	169.30	378	1326
<i>LWT (kg)</i>					
POSTW	3851	196.9	40.80	76	334
STARTF	3851	350.6	60.75	176	620
ENDF	3851	484.5	89.56	248	795
<i>CS (units)</i>					
POSTW	3301	6.3	1.38	3	11
STARTF	1529	7.5	1.32	3	12
<i>MS (units)</i>					
STARTF	1434	6.8	1.02	3	10
ENDF	3701	7.0	1.32	3	12
<i>HH (cm)</i>					
POSTW	3119	115.5	6.87	89	139
STARTF	1398	134.4	7.23	109	162
ENDF	1673	140.8	7.73	121	183
<i>FT (s*100)</i>					
POSTW	3594	123.3	52.66	40	300
<i>SRIB (mm)</i>					
POSTW	3285	1.2	0.50	1	6
STARTF	2629	2.3	1.33	1	13
ENDF	3770	6.6	3.20	1	24
<i>SP8 (mm)</i>					
POSTW	3427	1.4	0.82	1	10
STARTF	2630	3.7	2.39	1	20
ENDF	3767	11.6	5.04	1	41
<i>SEMA (cm²)</i>					
POSTW	3270	36.2	7.00	13	65
STARTF	2629	49.6	8.17	28	79
ENDF	3649	67.8	10.46	38	108

Fatness and muscle traits

LSMEANS for ultrasound traits and muscle score measured at ENDF stage are presented in Table 5. Comparisons between TROP versus TEMP or between TROP NORTH v. SOUTH are not valid due to a confounding of ultrasound scanners and muscle scorers. Operator biases, if they existed, have not been removed in the LSMEANS. For TEMP and TROP, LSMEANS for SEMA followed the differences exhibited in liveweight. However, PAST finished animals, at similar liveweights, had significantly smaller SEMA, 60.5 and 66.1 cm² for TEMP and 65.9 and 70.8 cm² for TROP, compared with FLOT, suggesting that changes to body composition have occurred. Differences in MS between market weight groups were relatively small;

Table 5. Least square means for traits measured at end of finishing (ENDF) for temperate and tropically adapted breeds
See Table 2 for a description of traits; see Table 1 for a description of levels

Treatment	Levels	AGE (days)	MS (units)	SRIB (mm)	SP8 (mm)	SEMA (cm ²)	HH (cm)	LWT (kg)
<i>Temperate breeds</i>								
Market weight (M)	DOM	500.0	7.5	5.1	7.0	54.2	–	407.4
	KOR	675.9	7.6	9.2	12.2	65.8	–	532.6
	JAP	745.7	7.6	11.6	15.0	71.2	–	594.1
Finishing regime (F)	FLOT-SOUTH	591.5	7.6	9.7	12.3	66.1	–	515.1
	PAST-SOUTH	677.0	7.5	6.9	9.7	60.5	–	498.7
M × F	DOM-FLOT	482.3	7.6	6.3	8.3	57.1	–	421.7
	DOM-PAST	516.1	7.3	3.9	5.6	51.7	–	392.3
	KOR-FLOT	625.7	7.6	10.4	13.2	67.6	–	533.5
	KOR-PAST	729.1	7.6	8.0	11.3	64.9	–	532.8
	JAP-FLOT	685.2	7.6	13.3	16.5	76.1	–	603.2
	JAP-PAST	808.9	7.5	9.7	13.5	66.1	–	584.8
<i>Tropically adapted breeds</i>								
Market weight (M)	DOM	618.1	6.9	4.7	8.5	61.0	135.9	409.8
	KOR	818.4	7.2	7.1	13.2	69.7	141.7	510.3
	JAP	908.1	7.0	8.9	15.2	76.6	144.3	570.6
Sex	Heifer	736.2	6.8	6.9	12.8	64.8	136.5	449.8
	Steer	708.3	7.3	5.2	9.3	65.2	141.4	472.0
Sex × M	Heifer-DOM	623.4	6.6	5.5	9.9	60.4	133.0	397.5
	Steer-DOM	609.7	7.2	4.2	7.4	61.7	137.1	421.6
	Heifer-KOR	834.6	7.0	8.3	15.5	70.0	138.8	500.5
	Steer-KOR	796.1	7.3	6.0	10.9	69.2	143.7	519.4
Finishing regime (F)	FLOT-NORTH (FN)	690.4	7.1 ^A	6.7 ^A	12.9 ^A	70.8 ^A	136.5 ^A	484.4
	FLOT-SOUTH (FS)	678.8	7.2 ^A	6.9 ^A	11.0 ^A	64.8 ^A	146.0 ^A	489.2
	PAST-NORTH (PN)	907.7	6.7 ^A	5.5 ^A	10.8 ^A	65.9 ^A	140.9 ^A	488.8
M × F ^A	DOM-FN	565.4	7.1	4.7	9.5	64.0	132.4	396.4
	DOM-FS	534.0	7.3	6.0	9.0	60.3	139.5	415.1
	DOM-PN	763.6	6.4	3.4	7.1	59.6	137.6	415.4
	KOR-FN	756.1	7.1	7.3	14.4	72.7	138.6	509.1
	KOR-FS	753.7	7.6	7.7	12.4	67.4	147.3	510.1
	KOR-PN	951.0	6.8	6.2	13.0	67.9	141.8	505.9
	JAP-FN	804.4	6.8	9.7	16.6	77.2	139.7	563.7
	JAP-FS	787.7	7.4	9.3	14.0	75.5	149.7	559.0
	JAP-PN	1141.5	6.9	7.9	15.2	76.3	144.9	585.3

^AMeans may be influenced by operator differences between geographic regions.

however, KOR animals had higher MS than the other 2 market groups for both TEMP and TROP. For TROP, SEMA was not significantly different across sexes.

LSMEANS for scan fatness traits increased as market weight increased from DOM to KOR and JAP (7.0, 12.2, 15.0 mm for SP8 for TEMP and 8.5, 13.2, 15.2 mm for SP8 for TROP, respectively). FLOT finishing increased fatness traits compared with PAST groups; for example, SRIB was 2.8 mm and 1.2 mm greater in FLOT compared with PAST for TEMP and TROP, respectively. Muir *et al.* (1998) reported increasing fatness with increasing turn-off weights but no difference in fatness between grain versus pasture finishing.

Heifers at the same market were fatter than steers for TROP. The effect of geographic region on fatness showed

that TROP animals finished in the north (FLOT-NORTH) had significantly higher SP8 fat (12.9 mm) but similar SRIB (6.7 mm) compared with SP8 in FLOT-SOUTH (SP8 10.9 mm and SRIB 6.9 mm). These effects may have been due to scanner differences; however, a similar difference was reported for carcass P8 fat (Reverter *et al.* 2003a). Similarly, the significant difference in HH between FLOT-NORTH and FLOT-SOUTH is likely to be an artefact of slightly different measurement techniques used to measure HH at the different geographic regions.

Genetic parameters

Post-weaning

Heritabilities and correlations between measures recorded POSTW are presented in Table 7 for TEMP and

Table 6. Solutions from orthogonal contrasts of treatment effects for each trait measured at the end of finishing for temperate and tropically adapted breedsSee Table 2 for a description of traits; see Table 1 for a description of levels. All contrasts are significantly different from zero (at $P = 0.05$); n.s. non-significant

Treatment	Contrast	AGE (days)	MS (units)	SRIB (mm)	SP8 (mm)	SEMA (cm ²)	HH (cm)	LWT (kg)
<i>Temperate breeds</i>								
Market weight	R^2	0.94	0.36	0.66	0.64	0.65	–	0.81
	DOM v. KOR	–175.9	–0.15	–4.08	–5.14	–11.64	–	–125.2
	DOM v. JAP	–245.6	–0.09	–6.47	–8.00	–16.99	–	–186.6
Finishing regime	JAP v. KOR	69.7	n.s.	2.38	2.86	5.35	–	61.4
	R^2	0.95	0.39	0.67	0.65	0.68	–	0.81
	PAST v. FLOT	85.5	–0.15	–2.77	–2.57	–5.66	–	–16.4
<i>Tropically adapted breeds</i>								
Market weight	R^2	0.92	0.50	0.44	0.47	0.58	0.71	0.77
	DOM v. KOR	–200.4	–0.27	–2.36	–4.71	–8.68	–5.86	–100.6
	DOM v. JAP	–290.0	n.s.	–4.18	–6.65	–15.55	–8.41	–160.8
	JAP v. KOR	89.6	–0.17	1.83	1.95	6.87	2.55	60.4
Sex ^A	R^2	0.96	0.59	0.49	0.53	0.61 ^B	0.67	0.75
	Heifer v. steer	27.9	–0.44	1.69	3.47	–	–4.85	–22.4
Finishing regime	R^2	0.89	0.52	0.47	0.52	0.63	0.73	0.78 ^B
	PAST v. FLOT	217.3	–0.36	–1.17	–2.02	–4.92	4.37	–
	FN v. FS	11.7	n.s.	n.s.	1.86 ^C	5.98 ^C	–9.50 ^C	–

^AFor domestic and Korean markets only.^BMain effect was not significant.^CComparisons may be influenced by operator differences between geographic regions.**Table 7. Heritabilities (diagonals) and genetic (above) and phenotypic (below) correlations for traits measured at post-weaning for temperate breeds and tropically adapted breeds**

See Table 2 for a description of traits; standard errors of heritability and genetic correlation estimates ranged from 0.03 to 0.06 and from 0.03 to 0.15, respectively

	MS	SRIB	SP8	SEMA	CS	HH	LWT	FT
<i>Temperate breeds</i>								
MS	0.13	–0.06	–0.02	0.55	0.30	–0.04	0.34	–
SRIB	0.14	0.28	0.86	0.50	0.27	0.06	0.36	–
SP8	0.15	0.77	0.38	0.40	0.26	0.10	0.36	–
SEMA	0.32	0.22	0.22	0.32	0.33	0.27	0.67	–
CS	0.30	0.27	0.26	0.33	0.20	–0.00	0.61	–
HH	0.06	0.11	0.12	0.28	0.14	0.44	0.60	–
LWT	0.29	0.34	0.32	0.53	0.43	0.64	0.58	–
<i>Tropically adapted breeds</i>								
SEMA	–	–	–	0.23	0.71	0.32	0.65	–0.04
CS	–	–	–	0.29	0.33	0.01	0.44	–0.00
HH	–	–	–	0.26	0.09	0.44	0.72	–0.15
LWT	–	–	–	0.41	0.33	0.67	0.57	–0.10
FT	–	–	–	–0.02	–0.02	0.01	0.02	0.31

TROP. Traits ranged in heritability from low (MS = 0.13 ± 0.03) to high (LWT = 0.58 ± 0.06), with the subjectively scored traits generally having lower heritabilities. This reflected the small variation exhibited in these traits at this stage and possibly the unsuitability of the linear model used. For example, 83% of CS records for TEMP were in only 2 classes. Ultrasound scan traits for TEMP were heritable: 0.28

± 0.05, 0.38 ± 0.05, and 0.32 ± 0.05 for SRIB, SP8, and SEMA, respectively. For TEMP, the scan traits were both phenotypically and genetically positively correlated with LWT. Arnold *et al.* (1991), Robinson *et al.* (1993), and Moser *et al.* (1998) have reported similar results. No genetic estimates for scanned fatness traits were obtained for TROP due to failed convergence because little phenotypic variation

Table 8. Heritabilities (diagonals) and genetic (above) and phenotypic (below) correlations for traits measured at start of finishing for temperate breeds and tropically adapted breeds

See Table 2 for a description of traits; standard errors of heritability and genetic correlation estimates ranged from 0.03 to 0.05 and from 0.02 to 0.13, respectively

	MS	SRIB	SP8	SEMA	CS	HH	LWT
<i>Temperate breeds</i>							
MS	0.13	-0.29	-0.00	0.18	0.43	-	-0.07
SRIB	0.11	0.38	0.87	0.13	0.36	-	0.25
SP8	0.12	0.74	0.38	0.19	0.43	-	0.18
SEMA	0.29	0.20	0.20	0.30	0.54	-	0.51
CS	0.36	0.28	0.30	0.32	0.16	-	0.25
HH	-	-	-	-	-	-	-
LWT	0.30	0.34	0.31	0.50	0.40	-	0.48
<i>Tropically adapted breeds</i>							
MS	0.15	-0.48	-0.46	0.35	0.32	-0.49	0.08
SRIB	0.03	0.25	0.82	-0.05	0.11	-0.20	-0.38
SP8	0.02	0.68	0.19	-0.16	0.33	-0.15	-0.46
SEMA	0.28	0.09	0.10	0.23	0.49	-0.13	0.28
CS	0.42	0.32	0.34	0.25	0.17	0.46	-0.24
HH	-0.16	-0.02	0.01	0.12	-0.10	0.42	0.78
LWT	0.21	0.12	0.16	0.38	0.22	0.59	0.31

existed for these traits at POSTW (e.g. 85% of SRIB records were 1 mm).

Heritability of HH was 0.44 ± 0.05 for both TEMP and TROP, and 0.58 ± 0.06 and 0.57 ± 0.05 for LWT, for TEMP and TROP, respectively. The estimates for weight are higher than in the review by Koots *et al.* (1994a) and are possibly due to inflated additive genetic variances as a result of not being able to partition maternal genetic and environmental effects. Flight time was 0.31 ± 0.03 heritable and is in close agreement with estimates of Burrow *et al.* (1988) and Burrow and Corbet (2000). However, FT was generally not correlated, either phenotypically or genetically, with the other traits measured at this stage.

Start of finishing

Heritabilities and correlations for measures at STARTF are presented in Table 8. Similar trends to POSTW were observed and standard errors associated with estimates were of similar magnitude. Heritabilities for scan traits at this stage are in close agreement with the heritabilities reported by Meyer and Graser (1999) in seedstock Angus and Hereford heifers. Condition score and MS both showed low heritability for TROP and TEMP. However, the score traits were positively genetically correlated with their related objective measures (e.g. TEMP CS and SP8 = 0.43; TROP MS and SEMA = 0.35). Scan fatness traits for TROP showed greater phenotypic expression at this stage compared with POSTW and heritabilities were 0.25, 0.19, and 0.23 for SRIB, SP8, and SEMA, respectively.

Genetic correlations were consistent across TROP and TEMP with the exception of LWT. LWT in TEMP had

positive genetic correlations with fatness measures (scans and CS), whereas in TROP these correlations were negative. Johnson *et al.* (1993) reported a -0.53 genetic correlation between yearling ultrasound fatness and weight in tropically adapted Brangus cattle. In contrast, Moser *et al.* (1998), also working with Brangus, estimated a positive 0.11 genetic correlation between scan rib fat and yearling weight. The discrepancy in the correlation estimates between the studies may be due to the very low additive variances of the fatness traits as a result of the leanest of the cattle (<5 mm) at the time of scanning.

End of finishing

Heritabilities for ENDF measures (Table 9) were generally moderate to high for the scan fatness traits and liveweight for both TROP and TEMP. Standard errors associated with estimates were of similar magnitude to the 2 previous stages. Muscle score and SEMA heritabilities were 20% or less for TROP and TEMP. Muscle score had a positive genetic correlation with SEMA (TROP = 0.52 ± 0.07 ; TEMP = 0.43 ± 0.03). Hip height for TROP was strongly correlated with LWT. As seen at STARTF (Table 8), genetic correlations between LWT and fatness measures were positive for TEMP but negative for TROP.

Across stages

Additive genetic and residual variances for the measures across stages are presented in Table 10, and genetic correlations between stages in Table 11. For all traits, both TEMP and TROP, additive variances increased from POSTW to STARTF to ENDF. The magnitude of the

Table 9. Heritabilities (diagonals) and genetic (above) and phenotypic (below) correlations for traits measured at end of finishing for temperate breeds and tropically adapted breeds

See Table 2 for a description of traits; standard errors of heritability and genetic correlation estimates ranged from 0.03 to 0.05 and from 0.04 to 0.11, respectively

	MS	SRIB	SP8	SEMA	HH	LWT
<i>Temperate breeds</i>						
MS	0.16	-0.08	-0.07	0.43	-	-0.16
SRIB	-0.06	0.38	0.79	0.00	-	0.14
SP8	-0.07	0.71	0.36	0.02	-	0.26
SEMA	0.23	0.12	0.14	0.20	-	0.44
HH	-	-	-	-	-	-
LWT	0.21	0.31	0.29	0.42	-	0.45
<i>Tropically adapted breeds</i>						
MS	0.20	-0.32	-0.22	0.52	-0.07	0.33
SRIB	0.02	0.41	0.75	0.05	-0.26	-0.10
SP8	0.03	0.63	0.44	-0.12	-0.16	-0.01
SEMA	0.26	0.15	0.10	0.19	-0.05	0.23
HH	-0.03	-0.03	-0.00	0.17	0.48	0.76
LWT	0.28	0.21	0.22	0.43	0.57	0.32

variances for TEMP and TROP was similar for all measures at ENDF. The additive variances for scan fatness traits at STARTF for TROP were similar to the magnitude of the variances for those traits at POSTW for TEMP, reflecting the differences in the level of fatness at the initial stages between TEMP and TROP. Variances for CS are not comparable between TEMP and TROP because of different scoring scales used. A relatively higher residual variance for SEMA at ENDF, compared with the 2 earlier stages, resulted in a lower heritability estimate at this stage. This may have been due to increased error in measuring SEMA as animals were at commercial levels of fatness.

Genetic correlations across stages were highest for measures taken at STARTF and ENDF, with all traits having correlations greater than 0.80. Koots *et al.* (1994b) reported mean weighted genetic correlations between weaning weight and yearling weight of 0.81 and yearling weight and market weight of 0.56. Scan P8 fat had 0.93 ± 0.02 and 0.84 ± 0.05 genetic correlations across STARTF and ENDF for TEMP and TROP, respectively. The genetic correlations across the 3 stages for SEMA tended to be slightly lower for TROP (0.87 ± 0.09 , 0.81 ± 0.09 , 0.67 ± 0.09) compared with TEMP (0.90 ± 0.05 , 0.97 ± 0.05 , 0.91 ± 0.07). The 0.67 genetic correlation for SEMA for TROP appears to reflect the relatively low correlation between LWT at the same stages. In general, the greater the time between the stages (i.e. POSTW to ENDF) the lower the correlations. The scored traits generally had lower genetic correlations across stages relative to objectively measured traits.

Table 10. Additive genetic and residual variances for each trait at each stage for temperate and tropically adapted breeds

See Table 2 for a description of traits; Stage 1, post-weaning; Stage 2, start of finishing; Stage 3, end of finishing. i.d., Insufficient data available; i.v., insufficient phenotypic variance

Trait	Variance component	Stage		
		POSTW	STARTF	ENDF
<i>Temperate breeds</i>				
CS	Additive genetic	1.13	1.29	i.d.
	Residual	5.37	6.83	i.d.
MS	Additive genetic	0.06	0.05	0.08
	Residual	0.42	0.42	0.43
SRIB	Additive genetic	0.29	0.53	2.27
	Residual	0.46	0.81	3.44
SP8	Additive genetic	0.43	1.05	3.25
	Residual	0.66	1.48	5.44
SEMA	Additive genetic	4.65	7.22	7.26
	Residual	13.54	15.96	27.39
LWT	Additive genetic	332.94	495.44	835.95
	Residual	272.32	514.87	924.62
<i>Tropically adapted breeds</i>				
CS	Additive genetic	0.32	0.15	i.d.
	Residual	0.69	0.88	i.d.
MS	Additive genetic	i.d.	0.08	0.15
	Residual	i.d.	0.61	0.61
SRIB	Additive genetic	i.v.	0.23	2.55
	Residual	i.v.	0.67	3.35
SP8	Additive genetic	i.v.	0.54	5.74
	Residual	i.v.	1.82	7.43
SEMA	Additive genetic	5.17	4.96	6.43
	Residual	20.72	23.12	32.06
HH	Additive genetic	7.01	6.63	11.18
	Residual	9.06	7.62	7.18
LWT	Additive genetic	303.21	297.41	553.26
	Residual	182.93	501.00	1116.28

Market weight effect

Market weight effects on the additive variances and heritabilities for ENDF measures are presented in Tables 12 and 13. In general, heritabilities were slightly higher for the DOM market weight group, although the additive variances were smaller than for the EXP group. Scan P8 fat for TROP had an additive variance of 7.2 mm² for the EXP group compared with 4.3 mm² in DOM groups. Large differences in additive variances between markets existed for LWT. The genetic correlations were all unity between market weight groups for the same trait with the possible exception of SP8 that had correlations of 0.95 ± 0.09 and 0.91 ± 0.07 for TEMP and TROP, respectively. These results show that the genetic expression of the traits was increased with increasing market weight, possibly reflecting increases in scale. The high correlation between the same trait measured at the different market weights suggests that the effect of genotype by market weight interaction is small, and hence the pooling

Table 11. Genetic correlations between stages for traits for temperate and tropically adapted breeds

See Table 2 for a description of traits; Stage 1, post-weaning; Stage 2, start of finishing; Stage 3, end of finishing; standard errors of genetic correlation estimates ranged from 0.02 to 0.16

Trait	Stage 1 and 2	Stage 2 and 3	Stage 1 and 3
<i>Temperate breeds</i>			
CS	0.74	n.d.	n.d.
MS	0.39	0.89	0.75
SRIB	0.88	0.92	0.76
SP8	0.87	0.93	0.82
SEMA	0.90	0.97	0.91
LWT	0.91	0.96	0.79
<i>Tropically adapted breeds</i>			
CS	0.83	n.d.	n.d.
MS	n.d.	0.99	n.d.
SRIB	n.d.	0.82	n.d.
SP8	n.d.	0.84	n.d.
SEMA	0.87	0.81	0.67
HH	0.88	1.00	0.91
LWT	0.83	0.85	0.62

n.d., No data available to estimate this correlation.

of measures across markets for the ENDF stage was reasonable.

Finishing regime effect

Finishing regime effects on the additive variance and heritability of the ENDF measures are presented in Tables 12 and 13. The magnitude of variances and heritabilities was inconsistent across the finishing regimes. For both TEMP and TROP, the additive variances for SP8 were higher in PAST-SOUTH and PAST-NORTH relative to FLOT-SOUTH and FLOT-NORTH. However, the reverse was observed for SRIB. Scan P8 fat for TEMP had a correlation between FLOT

and PAST of 0.73 ± 0.11 but SRIB was 1.0. This result seems unusual given the high correlation between the 2 measures but may be caused by the changes in additive genetic variances. A large difference existed for TEMP for the additive variance and heritability of SEMA between FLOT (11.2 cm^4 and 0.29) and PAST (3.8 cm^4 and 0.13). However, this difference was not observed for TROP. Genetic correlations were generally high but several were less than unity including MS with correlations of 0.60 ± 0.30 and 0.85 ± 0.24 for TEMP and TROP respectively. However, the 0.60 genetic correlation estimate for TEMP should be taken with caution given the very small genetic variance for MS at pasture finish (0.04 unit^2) and large standard error. Scan eye muscle area, despite different variances, had correlations of 1.0 and 0.91 for TEMP and TROP, respectively.

For TROP, finishing geographic region had little effect on the magnitude of the genetic variance of the measures. Slightly higher additive variances were observed for FLOT-SOUTH compared with FLOT-NORTH traits. The genetic correlations were all close to unity, indicating no evidence for genotype by geographic region interactions for the traits studied.

Conclusions

Stage of production, market weight, and finishing system altered the magnitude of the genetic, and certainly the phenotypic, expression of live animal measures. Market weight increased the age of turn-off, the fatness, and measures of size, whereas feedlot finishing decreased the age of turn-off, and increased fatness and muscling. However, the genetic ranking of animals is expected to be on average quite similar across the market weights and finishing regimes. For TROP, geographic region of finishing resulted in only small differences in age of turn-off and similar genetic expression for the majority of traits studied.

Table 12. Additive genetic variances (V_a), heritabilities (h^2), and genetic correlations (r_g) for each trait by market weight and finishing regime for end of finishing measures for temperate breeds

See Table 2 for a description of traits; see Table 1 for a description of levels

Treatment	Level	Variable	MS	SRIB	SP8	SEMA	LWT
Market weight ^A	DOM	V_a	0.09	1.2	2.2	6.9	695.6
		h^2	0.18	0.45	0.58	0.25	0.48
	EXP	V_a	0.08	3.0	4.1	8.0	879.4
		h^2	0.15	0.39	0.37	0.21	0.46
Finishing regime ^B	FLOT-SOUTH	r_g	1.00	1.00	0.95	1.00	1.00
		V_a	0.17	2.4	3.0	11.2	885.6
		h^2	0.30	0.36	0.34	0.29	0.46
		r_g	0.60	1.00	0.73	1.00	0.85
	PAST-SOUTH	V_a	0.04	2.0	4.6	3.8	820.4
		h^2	0.09	0.41	0.52	0.13	0.53
		r_g	0.60	1.00	0.73	1.00	0.85
		r_g	0.60	1.00	0.73	1.00	0.85

^AStandard errors were not computable as a result of the unity correlations; s.e. of the SP8 correlation was 0.09.

^BStandard errors of heritability and genetic correlation estimates ranged from 0.04 to 0.07 and from 0.08 to 0.30, respectively.

Table 13. Additive genetic variances (V_a), heritabilities (h^2), and genetic correlations (r_g) for each trait by market weight, finishing regime, and geographic region for end of finishing measures for tropically adapted breeds

See Table 2 for a description of traits; see Table 1 for a description of levels

Treatment	Level	Variable	MS	SRIB	SP8	SEMA	LWT
Market weight ^A	DOM	V_a	0.11	1.6	4.3	8.4	377.2
		h^2	0.14	0.52	0.54	0.27	0.34
	EXP	V_a	0.18	3.3	7.2	6.1	695.4
		h^2	0.23	0.43	0.43	0.14	0.34
Finishing regime ^B	FLOT-NORTH	r_g	1.00	1.00	0.91	1.00	1.00
		V_a	0.22	3.5	4.6	5.6	539.8
		h^2	0.27	0.60	0.34	0.15	0.33
	PAST-NORTH	V_a	0.10	1.7	8.5	6.1	652.3
		h^2	0.14	0.36	0.60	0.17	0.45
		r_g	0.85	0.80	0.94	0.91	0.92
Geographic region ^C	FLOT-SOUTH	V_a	0.14	2.6	5.1	10.6	603.6
		h^2	0.19	0.36	0.41	0.24	0.30
		r_g	0.86	0.92	1.00	0.99	0.99
	FLOT-NORTH	V_a	0.22	3.5	4.6	5.6	539.8
		h^2	0.27	0.60	0.34	0.15	0.33
		r_g	0.86	0.92	1.00	0.99	0.99

^AStandard errors were not computable as a result of the unity correlations; s.e. of the SP8 correlation was 0.07.^BStandard errors of heritability and genetic correlation estimates ranged from 0.04 to 0.05 and from 0.10 to 0.24, respectively.^CStandard errors of heritability and genetic correlation estimates ranged from 0.04 to 0.08 and from 0.01 to 0.18, respectively.

Weights and hip height were highly heritable and correlated. Ultrasound scanning produced consistent, heritable, correlated results for both TEMP and TROP and suggests that these measurements taken at either stage could be used in a genetic evaluation, provided adequate levels of fatness are being expressed. Subjectively scored traits generally had low heritability and lower correlations across stages; however, their moderate correlations with scan traits may provide a cheaper, but less accurate, method of including body composition measures in a genetic evaluation scheme. Some or all of these traits studied could be used in a genetic evaluation scheme to genetically improve growth and carcass traits. The stage of measurement or production system is not critical but differences in variances would need to be considered in a genetic analysis. Finally, these traits may have added value in a genetic improvement program as early life stage indicators of carcass and meat quality; this is reported in the companion papers (Johnston *et al.* 2003; Reverter *et al.* 2003a, 2003b).

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