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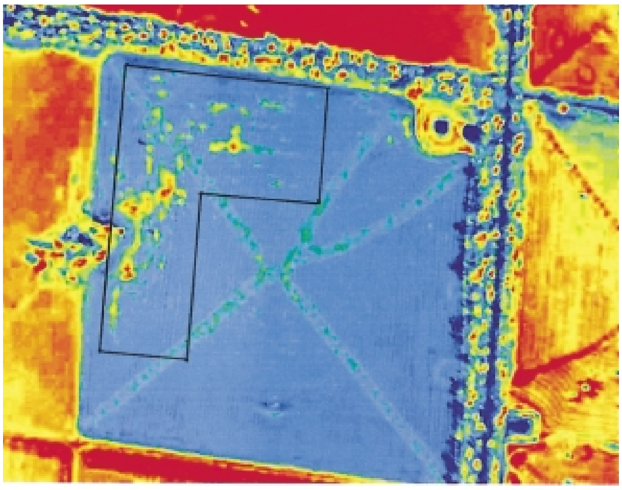

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Genetic and environmental influences on beef tenderness

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Abstract. Mechanical tenderness measurements of *M. longissimus* (LM) and *M. semitendinosus* (ST) were analysed from 1392 tropically adapted (Brahman, Belmont Red and Santa Gertrudis) cattle grown out and finished in both tropical and temperate environments, and 2408 temperate breed (Angus, Hereford, Murray Grey and Shorthorn) cattle grown out and finished in a temperate environment. Groups of cattle from both environments were managed under 2 finishing systems (pasture and feedlot) to market liveweights of 400, 520 (steers and heifers) and 600 kg (steers only). Carcasses were electrically stimulated and care was taken to minimise stress before slaughter.

Estimated genetic variation (GV) of compression of unaged LM and ST muscles was 0.006 and 0.018 kg^2 respectively in tropically adapted and 0.004 and 0.009 kg^2 in temperate breeds (phenotypic means 1.7, 2.1, 1.6, 2.1 kg; heritabilities, h^2 = 0.16, 0.24, 0.10, 0.16). Estimated GV for LM and ST shear force was 0.24 and 0.12 kg^2 in tropically adapted and 0.06 and 0.02 kg^2 in temperate breeds (means 4.3, 4.6, 4.0 and 4.7 kg; h^2 = 0.38, 0.40, 0.11, 0.06). Genetic correlations among shear and compression forces of the ST and LM ranged from 0.28 to 0.95 in tropically adapted and –0.20 to 0.60 in temperate breeds. The fixed effects model (market, finish, breed, birth herd, management group and interactions) explained about half the variation in compression measurements, but only 16% and 27% of the variation of LM shear force in tropically adapted and temperate breeds.

The relatively low genetic variation and inconsistent genetic correlations in temperate breeds suggest genetic improvement in tenderness may be less important than effective pre- and post-slaughter management protocols. The higher additive genetic variances and moderate heritabilities in tropically adapted breeds suggest genetic improvement is possible but this will be most effective if combined with effective control of slaughter protocols.

Additional keywords: heritability, genetic parameters.

Introduction

The production of highly palatable meat is a challenge for the Australian beef industry. Many factors are involved in meeting this challenge, including the identification and use of superior genotypes, minimising any adverse effects of the production environment and ensuring the application of best practice pre- and post-slaughter management. Consumers have consistently rated tenderness as the most important contributor to beef palatability in all markets, including Australia (Hearnshaw and Shorthose 1995), the US (Huffman *et al.* 1996) and Japan (SMART 1993). Where genetic improvement is feasible, it provides permanent benefits for the beef industry.

For genetic parameter estimation and identification of superior genotypes, it is important to control or quantify potential interactions between genotypes and their environment. For example, tenderness can be affected by cold shortening if the temperature decline in muscle during chilling is rapid compared with the fall in pH (Bendall 1973). Under these conditions, genetic variation in fatness may cause variation in chilling rates, leading to variation in myofibrillar shortening, thus confounding the 'true' genetic variation in tenderness.

It is also important to understand the effects of the production environment on tenderness. In Australia, cattle are weaned, backgrounded and finished in a diverse range of production systems ranging from extensive pasture to intensive feedlot systems. Although a number of studies in other countries have reported genetic variation in meat quality traits (e.g. Koch *et al.* 1982; Gregory *et al.* 1995), there are few estimates of genetic parameters for grass or grain finished cattle in Australian domestic or export markets. This paper presents estimates of genetic variances and covariances for 2 objective measurements of tenderness made on 2 muscles from more than 3700 cattle from a range of temperate and tropically adapted breeds, slaughtered under a protocol that included electrical stimulation and attempting to minimise stress before slaughter. We also

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Table 1. Numbers of animals, means, total variances (TV), genetic variances (GV), heritabilities (h^2), phenotypic variation (PV) from the VCE analysis and PV as %TV for shear force (SF) and compression (C) measurements of *M. longissimus* (LM) and *M. semitendinosus* (ST)

Trait	No. of animals	Mean	TV	GV (σ^2_a)	h^2 (%)	PV	PV/TV (%)
Tropically adapted breeds							
LM-SF (kg)	1390	4.31	0.75	0.24	38	0.64	84
LM-C (kg)	1388	1.68	0.06	0.01	16	0.04	67
ST-SF (kg)	1388	4.55	0.41	0.12	40	0.30	74
ST-C (kg)	1386	2.14	0.15	0.02	24	0.08	51
Temperate breeds							
LM-SF (kg)	2390	4.01	0.75	0.06	11	0.54	73
LM-C (kg)	2391	1.65	0.11	0.00	10	0.04	36
ST-SF (kg)	2404	4.74	0.50	0.02	6	0.28	55
ST-C (kg)	2399	2.08	0.11	0.01	16	0.06	49

examine the relative importance of grow-out nutrition, feedlot *v.* pasture finishing and market endpoint [Domestic (D), averaging 220 kg carcass weight; Korean (K), 280 kg; or Japanese (J), >300 kg].

Materials and methods

The straightbreeding program of the Cooperative Research Centre for Cattle and Beef Quality (CRC) was created to obtain information on economically important traits for several breeds of cattle finished on pasture or in feedlots in either temperate or tropical environments. The statistical design of the CRC project, including determination of optimal numbers of sires, linkage arrangements and how progeny were allocated to treatment combinations was described by Robinson (1995). A description of the management of cattle is provided by Upton *et al.* (2001).

Included in this analysis were weaners of 4 temperate breeds, Angus (A), Hereford (H), Murray Grey (MG) and Shorthorn (S) and 3 tropically adapted (henceforth referred to as tropical) breeds, Brahman (B), Belmont Red (BR) and Santa Gertrudis (SG). Temperate breed weaners (average age 8–9 months) were purchased in May 1994, 1995 and 1996 (winter intakes), and January 1995, 1996 and 1997 (summer intakes) while those of tropical breeds (average age 7 months) were acquired between June and September in 1994, 1995 and 1996. A total of 11 Angus, 6 Hereford, 3 Murray Grey, 3 Shorthorn, 4 Brahman, 3 Belmont Red and 4 Santa Gertrudis herds supplied the cattle. For tropically adapted breeds, all progeny were used. For temperate breeds, all male calves from each sire were purchased along with, for certain herds, half the heifers. Calves were produced by single sire mating or AI plus a backup bull. Cases of doubtful paternity were resolved by DNA testing. Numbers of animals used in the analyses are listed in Table 1 for both tropical and temperate breeds. Link sires within each breed enabled year and herd of origin effects to be estimated.

After weaning, all animals were grown out (backgrounded) on pasture, then finished either on pasture or in a feedlot. Weaners from temperate breeds (A, MG, S and H) were grown out on improved pasture at NSW Agriculture's Glen Innes research station in the temperate climate of the New England Tableland of New South Wales, Australia (30°S, 151°E; elevation 1000 m). One-third of each intake of tropical breeds (B, BR and SG) was also grown on the New England Tableland. The remainder were grown out on an improved Buffel grass (*Cenchrus cilicris*)-dominant pasture in the subtropical climate of Central Queensland (24°S, 148°E). These 2 production environments are referred to as the south (New England Tableland) and north (Central Queensland).

Once each contemporary group of steers or heifers reached an average weight of 300 kg, animals destined for the domestic market were transferred from their grow-out pasture to the feedlot or to their finishing pasture. The remaining cattle continued on pasture until the group reached an average weight of 400 kg, when they were transferred to the feedlot or pasture, for finishing to export market weights. Cattle in the north were either finished in a nearby commercial feedlot or on pasture at the same property in Central Queensland where they were grown out. Animals in the south were finished at the University of New England's research feedlot, or on pasture at 1 of 4 properties in New England. Feedlot cattle were fed standard commercial rations; the finishing diet contained a minimum of 75% grain (dry rolled barley in the south; dry rolled and steam flaked sorghum in the north).

Due to abattoir closures and other logistical difficulties, a total of 5 different commercial abattoirs were used to process the cattle. Animals were slaughtered when the mean liveweight of each contemporary group reached the desired market weight [Domestic (D), 400 kg; Korean (K), 520 kg; or (steers only) Japanese (J), 600 kg liveweight]. A final weight was recorded about 1 week before the scheduled slaughter date, to minimise pre-slaughter handling stress. Distances between the finishing properties and abattoirs ranged from 200 to 900 km in the north and 70 to 200 km in the south. Generally, the entire contemporary group was transported to the abattoir the day before slaughter, held overnight and slaughtered the following morning. However, a few large groups (50 or more animals), were subdivided into 2 or, in 1 case, 3 subgroups which were slaughtered over consecutive weeks.

A detailed description of the slaughter protocols and meat quality measurements is provided by Perry *et al.* (2001). Every effort was made to minimise stress before slaughter, particularly during handling, loading, and transport, and in lairage. Water was available at all times in the abattoir holding yards. Animals were stunned using a captive bolt gun and immediately exsanguinated. For all but 3 of the 108 slaughter groups, low voltage electrical stimulation (45 V peak voltage, 36 pulses/s for 40 s) was applied within 5 min of stunning using a nasal rectal probe to prevent cold shortening. For 2 of the remaining 3 groups, high voltage stimulation was applied within 30 min of stunning. One slaughter group was not stimulated. After splitting, carcasses were hung by the achilles tendon and chilled for 20–24 h. On the day following slaughter the *M. semitendinosus* (ST) and a 15 cm section of *M. longissimus* (LM) (between the 13th rib and 2nd lumbar vertebra) were removed from the left side of the carcass, trimmed to a fat depth of 3 mm and frozen at –20°C for later meat quality measurements. The LM was chosen for its high value and low connective tissue content and to provide a comparison with other studies; the ST was chosen as a high connective tissue muscle which is stretched in an achilles hung carcass and so restricted from shortening (Bouton *et al.* 1973).

Objective measurement of tenderness

Frozen ST and LM muscle samples were thawed at 5°C for 48 h before cooking. Rectangular 250 g portions of both muscles were placed in individual plastic bags and cooked in a water bath at 70°C for 1 h. After overnight refrigeration, shear force (SF) and compression (C) were measured on 6 subsamples using a Lloyd LRX (Lloyd Instruments Ltd, Hampshire, UK) according to procedures described by Bouton and Harris (1972). All further unqualified references to meat tenderness should be understood to mean these mechanical measurements of tenderness of the LM and ST.

Statistical analyses

Initial screening of the data revealed 2 slaughter groups of northern feedlot domestic market heifers and steers, with mean ± s.d. LM-SF

Table 2. Description of factors fitted in the fixed and random effects model

Factor	Definition
Finish	Finishing system (feedlot or pasture for temperate breeds; northern feedlot, southern feedlot, northern pasture and southern pasture for tropically adapted breeds).
Market	Market category (domestic, Korean or Japanese).
Herd	Herd from which the animal was purchased after weaning.
Intake group	For tropical breeds, intake group was defined by sex and year of purchase (1994, 1995 or 1996). For temperate breeds, it was defined by sex, year and season of purchase (winter 1994, 1995, 1996; summer 1995, 1996, 1997). Except during grow-out nutrition treatments at Glen Innes, and for tropical breeds transferred south for grow-out and finishing, intake groups were managed together until transferred to their allocated finishing system.
Contemporary group	The common environmental factor experienced by animals run together as a group from intake to slaughter, a combination of intake group, market, finish and sex.
Slaughter group	The subset of a contemporary group slaughtered on a single day (often the entire contemporary group).
Grow-out nutrition	Nutrition treatment of steers grown out at Glen Innes (see Dicker *et al.* 2001). This was fitted within year and season (i.e. treatments of the same type but applied in different years or seasons were not considered to be the same).
Breed	Breed of the animal (tropically adapted breeds were: Brahman, Belmont Red, and Santa Gertrudis; temperate breeds were: Angus, Hereford, Murray Grey, and Shorthorn).

measurements of 8.4 ± 3.0 and 7.4 ± 2.4, but lower ST-SF measurements of 5.2 ± 0.5 and 5.0 ± 0.6. LM-SF values (mean ± s.d.) for the 2 groups were therefore almost twice as high as the average of 4.3 ± 0.9 for the remaining 1390 LM-SF measurements of tropical breeds. The slaughter of these 2 groups coincided with a change over at the abattoir from a low to a high voltage stimulation system. Due to operational difficulties, stimulation was not applied to 1 group whilst, in the other, high voltage stimulation was applied, but it was clearly ineffective. Tenderness measurements of these 2 atypical slaughter groups were therefore deleted from subsequent analyses. In a few other slaughter groups (4 out of 57 for temperate breeds; 7 out of 51 for tropical breeds) 9–21% of animals had relatively high LM-SF values (above 6.0 and at least 0.5 kg higher than ST-SF). These groups, however, were considered to have only a relatively small impact on the overall results and so were retained.

Genetic parameters (heritabilities and correlations) were estimated separately for temperate and tropically adapted breeds, fitting a full animal model by REML using VCE4 (Groeneveld and García-Cortés 1998) in combined analyses including all 4 tenderness traits. Satisfactory convergence (status 1) was achieved. Altogether, there were 2408 and 1392 temperate and tropical breed cattle with tenderness measurements. The cattle were progeny of 179 and 108 temperate and tropical breed sires. Sires were from stud herds and so had extensive pedigree information. The additive genetic relationship matrix was constructed using all available pedigree information on sires, their parents, grandparents and great grandparents. Dams, some of which were used in more than 1 year, were from commercial herds and had very little pedigree information, so only the dam identifier was used in the construction of the relationship matrix.

Fixed effects were modelled as:

Slaughter group + herd × intake × market × finish (temperate breeds, all traits except LM-SF)

Slaughter group + herd × intake + herd × market + herd × finish (LM-SF, temperate breeds)

Slaughter group + herd × intake (all traits, tropically adapted breeds)

The above fixed effects are defined in Table 2. Market, finish and contemporary group were part of the definition of slaughter group, so there was no need to fit separate main effects for these terms. Main effects of herd were fitted as part of the interaction terms. The fixed effects models listed above were derived by fitting all factors with the potential to affect tenderness in a logical sequence (contemporary group, slaughter group, herd, grow-out nutrition treatment × intake group, herd × intake group, herd × market, herd × finish, herd × market × finish, herd × intake group × market, herd × intake group × finish, herd × intake group × market × finish, age of the animal, age × market, age × finish, age × market × finish) then dropping terms (such as age and grow-out nutrition within season) which had no significant effect.

Analyses with fixed effects models, such as those used to estimate genetic parameters, are not always able to determine which of the effects fitted as fixed contribute most to the variation of a trait, for example to distinguish slaughter group or contemporary group effects from market or finish, or the effects of herd from breed (the different breeds were sourced from different sets of herds). Additional analyses were therefore performed to examine the relative importance of the effects fitted in the fixed effects models, but now fitting all effects as random (see Robinson 1987). The model fitted included terms for sire, market, finish, market × finish, breed, market × breed, finish × breed, market × finish × breed, grow-out nutrition × intake group, herd, herd × intake group, market × herd, finish × herd, market × finish × herd, contemporary group and slaughter group. Results were used to determine which factors had the most influence on the 4 measures of tenderness and to compute BLUP solutions and standard errors for market and finish.

Results and discussion

Variances and heritabilities

The proportion of total variation in tenderness explained by fixed effects in the VCE analysis was generally small, especially for LM shear force, where fixed effects accounted for 16 and 27% of total variation in tropical and temperate breeds, respectively (Table 1). Indeed, including all breed effects, all genetic and environmental variances as well as the variation due to year, market, finish, contemporary group and all other fixed effects, total variation in LM shear force of temperate and tropical breeds was only 0.75 kg^2. This contrasts with other studies, for example Wheeler *et al.*

(1996), in which phenotypic variation of LM shear force, even after subtracting breed and other fixed effects, was 2.1 kg^2. This was 3–4 times greater than the phenotypic variation observed in this study. However, it must be noted that, while there are similarities, the technique of measuring shear force was not the same as used here. For example, different cooking methods were used (broiling to an internal temperature of 70°C) and there may have been other differences in protocols and measurement instruments. Therefore, some caution must be exercised when making comparisons between studies.

For the 3 tropically adapted breeds, genetic variation in shear force of LM and ST muscles was 0.24 and 0.12 kg^2. This may represent potentially useful genetic variation, but only if other sources of variation relating to the pre- and post-slaughter environment have been controlled. Including the 2 outlier slaughter groups in the analysis, for example, had very little effect on the genetic variation, σ^2_a of LM-SF, which increased from 0.24 to 0.27. Phenotypic variation, however, nearly doubled from 0.64 to 1.17, so the heritability estimate was almost halved. This change, caused by only 121 LM-SF measurements out of the total of 1511, demonstrates the magnitude by which an increase in environmental variation can reduce accuracy of selection (see also Johnston *et al.* 2001).

Note also that tenderness under optimal slaughter management protocols may not relate closely to tenderness when these factors are not controlled. Thompson (1999) reported an experiment on tenderness of crossbred cattle with 0–100% Brahman content. Correlations between tenderness, assessed by a large consumer panel, of the left and right sides of the LM from the same carcass were close to zero (r = 0.13), when one side was subjected to an effective post-slaughter management procedure (electrical stimulation + ageing), but not the other. This implies that differences due to breeding or feeding may be inconsistent and relatively unimportant, compared with potential variation from inadequate control of the post-slaughter environment.

Genetic correlations

The genetic correlations shown in Table 3 reveal some interesting trends. Within muscle, the correlation between the 2 measures of tenderness (shear force and compression) was high in the case of the ST for both breed groups (0.60 and 0.95 for temperate and tropical breeds, respectively) and also for the LM in tropical breeds (0.66). The exception was the LM in temperate breeds for which the estimated genetic correlation was zero. The 2 measurements have been shown to account for different components of tenderness/toughness (Bouton and Harris 1972). Shear force tends to better describe the myofibrillar component of tenderness, whereas compression measurements are more sensitive to connective tissue effects.

Table 3. Genetic (above diagonal) and residual (below) correlations (%) for the four mechanical measures of tenderness for tropically adapted and temperate breeds

	LM-SF	LM-C	ST-SF	ST-C
		Tropically adapted breeds		
LM-SF	—	66	29	28
LM-C	11	—	60	73
ST-SF	10	–6	—	95
ST-C	0	–1	13	—
		Temperate breeds		
LM-SF	—	0	38	–20
LM-C	22	—	–14	24
ST-SF	9	16	—	60
ST-C	8	18	23	—

The ST has a higher proportion of connective tissue than the LM (McKeith et *al.* 1995). Myofibrillar variation in this muscle from post-slaughter environmental factors should have been minimal, given the use of electrical stimulation and because the ST is stretched when the side is suspended by the achilles tendon (Bouton et *al.* 1973). Consequently, the variation in ST-SF is more likely to be a reflection of the connective tissue contribution, and hence the high genetic correlation between ST-SF and ST-C due to the common influence of connective tissue on both measurements. The relatively high genetic correlation between LM-SF and LM-C in tropical breeds but estimate of zero for temperate breeds is more difficult to explain. Heritabilities in temperate breeds were lower (11 *v.* 38% for LM-SF in temperate *v.* tropical breeds; Table 1), and it is possible that the relative contribution of myofibrillar and connective tissue toughness to overall tenderness/toughness differs between temperate and tropical breeds.

Apart from the estimated genetic correlation of 0.6 between ST shear force and compression, other genetic and environmental correlations between tenderness traits in temperate breeds were relatively low (Table 3). Selection for improved tenderness of the LM in temperate breeds is therefore unlikely to lead to worthwhile improvements of the ST. This was also highlighted in the study by Shackelford *et al.* (1995). Together with the low heritabilities for tenderness, our results suggest there is little overall benefit to be gained from selection for tenderness in temperate breeds.

In tropical breeds, LM-SF had estimated genetic correlations of 0.66, 0.29 and 0.28 with LM-C, ST-SF and ST-C. Genetic correlations of LM-C with ST-SF and ST-C were 0.60 and 0.73, respectively, indicating that compression measurements of the LM and ST are genetically related. However, the low to moderate heritabilities (0.16 and 0.24) and low genetic variation of compression measurements (0.006 and 0.018 kg^2 for LM and ST compression) may reduce the importance of this relationship.

Table 4. Relative importance of market, finish, breed and other effects

Variance of largest 3 effects and variance due to breed are reported as percentage of residual variation (RV)
cgrp, contemporary group; sgrp, slaughter group; mark.fin, market × finish

Trait	Residual variation	Largest three effects and variance as percentage of residual variation					
		%RV	Effect	%RV	Effect	%RV	Effect
Tropically adapted breeds							
LM-SF (kg)	0.58	11	cgrp	10	breed	10	sire
LM-C (kg)	0.04	35	finish	8	breed	6	cgrp
ST-SF (kg)	0.28	24	finish	18	cgrp	9	sire
ST-C (kg)	0.07	80	finish	26	cgrp	8	market
Temperate breeds							
LM-SF (kg)	0.53	21	finish	20	cgrp	8	mark.fin
LM-C (kg)	0.04	140	cgrp	33	finish	24	sgrp
ST-SF (kg)	0.29	49	cgrp	22	sgrp	19	finish
ST-C (kg)	0.05	76	cgrp	53	finish	42	sgrp

Residual environmental correlations

Environmental correlations among tenderness traits were all relatively low, but generally positive, ranging from –0.06 to 0.23 (Table 3). In temperate breeds, phenotypic tenderness of the 2 muscles was therefore not closely related, because of the low genetic and environmental correlations. In tropical breeds, apart from a phenotypic correlation of 0.38 between the 2 tenderness measurements of the ST, (shear force and compression), phenotypic correlations among tenderness traits ranged from 0.09 to 0.24, indicating that overall tenderness of the LM was not closely linked to tenderness of the ST. As stated earlier, Shackleford *et al.* (1995) confirmed the lack of phenotypic relationship between muscles on a larger range of muscles, stating: "… systems that accurately predict the tenderness of the LM of a carcass will do little to predict the tenderness of other muscles."

For our samples of unaged meat, 90% (temperate breeds) and 83% (tropical breeds) of LM shear force measurements were less than 5 kg; overall means were 4.0 for temperate breeds and 4.3 for tropical breeds. Further improvements would be expected with ageing, resulting in a highly acceptable product. We are of the view that the uniformity of product was largely due to control of the environmental variation that can occur during the critical pre- and post-slaughter period. The results from the consumer taste

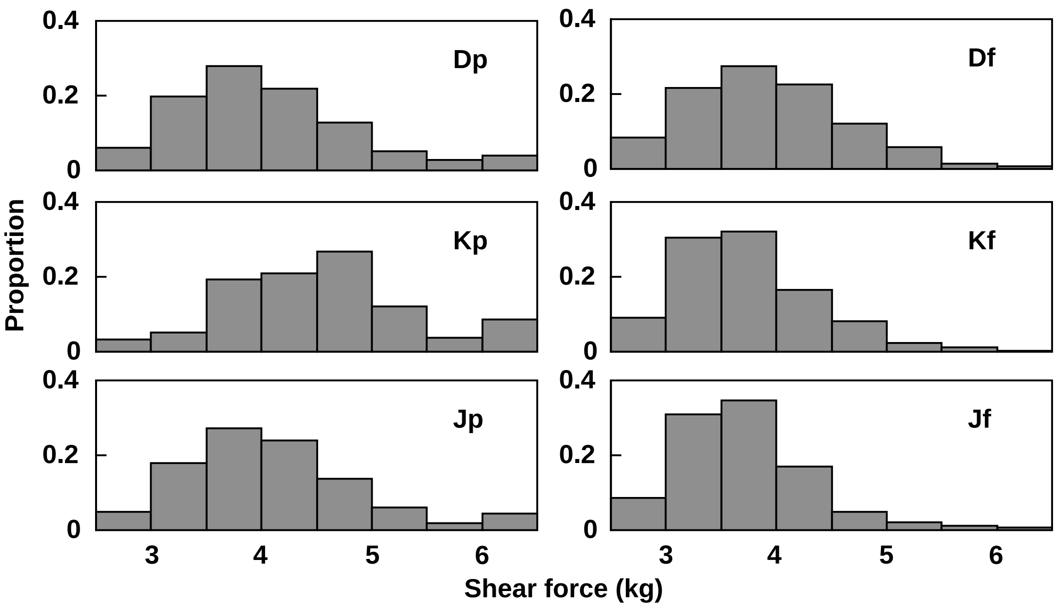

Figure 1. Histograms of LD shear force by market (D, Domestic; K, Korean; J, Japanese) and finish (f, feedlot; p, pasture) in temperate breeds.

panel assessments, currently in progress, will shed more light on the precise relationships between mechanical measurements and consumer ratings for tenderness.

Sources and size of variation for tenderness

Fitting all factors including sire, market, finish, breed and birth herd as random terms in the model showed that, for temperate breeds, contemporary group (i.e. intake group within market and finish) was the largest source of variation in ST-SF, ST-C and LM-C and second largest in LM-SF. (Table 4). Slaughter group and finish were the other main sources of variation in temperate breeds. The relatively large proportion of variation due to slaughter group, as large as that due to whether cattle were finished on pasture or in the feedlot, is rather interesting since every attempt was made to ensure the conditions that prevail in the pre- and post-slaughter management of cattle and their carcasses were kept constant. In fact, the relatively low residual and total variation demonstrate that control of this variation was generally successful. However, further improvements are desirable and have potential benefits as large as the effect of feedlot *v.* pasture finishing.

In tropically adapted breeds, sire was the third most important source of variation in LM shear force, after contemporary group and breed. In contrast, LM-C, ST-SF and ST-C had much lower residual variation (0.04, 0.07 and 0.28, compared with 0.58 for LM-SF; Table 4) and finish (tropical or temperate environment, feedlot or pasture) was the largest source of variation. Second largest was contemporary group for ST-SF and ST-C and breed for LM-C (Table 4).

Estimated breed effects from the variance components analysis were inconsistent over the 4 tenderness measurements. For example, in temperate breeds, Shorthorns had the highest estimated shear force measurements for LM, but lowest for ST. In tropical breeds, no breed differences were evident for ST shear force. However, Brahmans had marginally higher average LM shear force (4.6 kg *v.* 4.2 kg) and compression (1.75 kg *v.* 1.66 kg) values, but their ST tenderness was the same as the other 2 tropical breeds. In fact, despite the much harsher environmental conditions experienced on average, mean ST shear force of the tropical breeds (4.55 kg), was less than the mean of 4.74 kg for the temperate breeds (Table 1), though compression forces were slightly higher (2.14 kg *v.* 2.08 kg). Sherbeck *et al.* (1995) found increasing LM shear force with increasing Brahman percentage, though with somewhat higher residual variation than that observed here for tropically adapted breeds.

Thus, apart from the 2 slaughter groups omitted because of problems with electrical stimulation, it would appear that the pre- and post-slaughter management protocols were reasonably successful in controlling much of the variation normally found in tenderness measurements, with the result that there was little variation left to be explained either by genotype, breed, or production history of the animal. There was, however, some remaining variation due to contemporary and slaughter group, suggesting that further improvements in slaughter management protocols may be desirable. The frequency distribution of LM-SF measurements by market and finish is shown in Figure 1. Some small effects are apparent, mainly relating to outlying observations associated with a small number of slaughter groups. However, in general, for temperate breeds, knowing the production history (i.e. market category or finishing system) of an individual steak conveyed little information about its tenderness.

Table 5 shows the estimated effects of market and finish on the tenderness traits. Finishing had an effect on all measures of tenderness, particularly compression in tropical breeds, for which variation due to finish (tropical or

Table 5. Number of animals, and estimated market (D, domestic; K, Korean; J, Japanese) and finish (F, feedlot; P, pasture; n, north, s, south) effects

Market	Temperate breeds		Tropically adapted breeds			
	Ps	Fs	Ps[A]	Fs	Pn	Fn
	Numbers of animals with LM-SF data					
D	402	567	24	151	193	196
K	344	421	23	239	166	199
J	313	343	23	69	29	78
	Average age of animals (days)					
D	497	471	543	560	772	598
K	725	615	696	775	953	778
J	802	674	845	830	1202	821
	LM-SF (kg; average s.e.d.s are 0.16 and 0.13)[B]					
D	4.1	3.8	4.4	4.3	4.5	4.3[C]
K	4.5	3.8	4.4	4.3	4.5	4.3
J	4.2	3.7	4.2	4.1	4.4	4.2
	LM-C (kg; average s.e.d.s are 0.09 and 0.04)					
D	1.63	1.50	1.69	1.61	1.86	1.60
K	1.72	1.59	1.68	1.62	1.86	1.65
J	1.63	1.49	1.66	1.58	1.86	1.65
	ST-SF (kg; average s.e.d.s are 0.14 and 0.12)					
D	4.7	4.4	4.7	4.5	4.8	4.3
K	4.8	4.5	4.7	4.5	4.8	4.3
J	4.8	4.5	4.7	4.5	4.9	4.3
	ST-C (kg; average s.e.d.s are 0.07 and 0.09)					
D	2.12	1.90	2.16	1.94	2.50	2.10
K	2.18	1.95	2.14	1.94	2.47	2.11
J	2.11	1.88	2.06	1.84	2.38	1.99

[A]Limited number of animals from first intake only; means may be unreliable.
[B]Average standard errors of differences between means for temperate and tropical cattle respectively.
[C]If the 2 outlier kills are included, estimated LM-SF increases to 4.6 and all estimates for pasture north become similar but slightly lower than the estimates for feedlot north at the same market.

temperate environment, feedlot or pasture) was 35% (LM-C) and 80% (ST-C) the size of the residual variation (Table 4). Thus, though variation between animals was greater than the effects of finishing system, pasture finished cattle in the north were, on average, less tender than feedlot finished cattle. This effect probably reflects differences in age (Table 5) and growth rate and/or pattern, with more variable rates observed on pasture compared with feedlot finishing. For example, Robinson and Perry (1998) reported a correlation of –0.74 between contemporary group means for lifetime growth rate and ST-SF. Further, there is evidence (see review by Oddy *et al.* 2001) to suggest that variations in growth will significantly influence the connective tissue contribution to toughness and this is better shown in compression than shear force measurements (Bouton and Harris 1972).

Conclusion

The relatively low genetic variation and low genetic correlations among objective tenderness traits in temperate breeds suggests genetic improvement in tenderness may be difficult in these breeds. Total variation in tenderness measurements was generally lower than reported in other studies, suggesting that when the pre- and post-slaughter environment was controlled, gains from genetic selection for tenderness may be small and possibly of little commercial value. The significance of slaughter group effects suggests further research to improve pre-slaughter management may be desirable. Research into growth path effects, compared with other factors affecting tenderness, may also be worthwhile. If results from such future research were adopted widely, the variation in tenderness currently encountered by consumers might be reduced substantially, leading to a tender product, irrespective of breed, market or finish, and general satisfaction in this, the most important of all meat quality traits.

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