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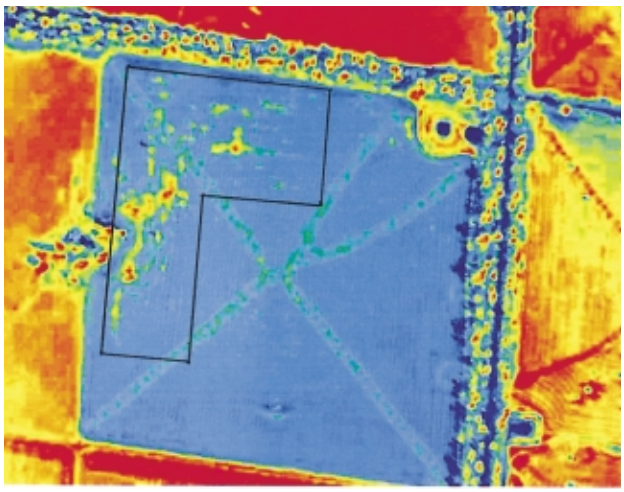

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Review

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Quantitative and molecular genetic influences on properties of beef: a review

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Abstract. The scientific literature is reviewed to identify quantitative and molecular genetic influences on quantity and quality of beef. Genetic variation between breeds is of similar magnitude to genetic variation within breeds for many economically important traits. Differences between breeds are significant and large for most carcass and beef quality attributes, including beef tenderness, although differences for sensory juiciness and flavour are of little practical importance. For traits such as beef tenderness, between-breed differences may be more easily exploited than within-breed differences, because exceptional breeds are easier to identify than exceptional animals. Effects of heterosis on carcass and beef quality attributes are relatively small (3% or less), with most effects mediated through heterotic effects on weight. Carcass composition traits (e.g. carcass weight, fat thickness and marbling) are moderately to highly heritable. Most estimates of retail beef yield percentage are highly heritable, offering good potential for within-breed selection for the trait, although a moderate to strong antagonistic relationship exists between yield and marbling. This relationship needs to be considered in within-breed selection programs for yield percentage. Early estimates of heritability of objective measures of beef tenderness (Warner Bratzler shear force values) indicated tenderness was moderately to highly heritable. Recent estimates using larger numbers of carcasses and more discriminatory methods of analysis indicate that beef tenderness is lowly heritable in *Bos taurus* breeds and moderately heritable in *Bos indicus* and *Bos indicus*-derived breeds. Within breeds, measures of 24-h calpastatin activity are genetically strongly correlated with shear force values but are more heritable. However, phenotypic correlations between shear force values and 24-h calpastatin activities are low. There are also inconsistencies in relationships between these measurements across breeds. Low correlations between tenderness in different muscles, low to moderate heritabilities and inconsistent variation within- and between-breeds for traits such as 24-h calpastatin activity suggest that genetic improvement in beef tenderness may be difficult. The possibility exists that significant mitochondrial genetic effects occur for some carcass and beef quality attributes. A major gene for muscular hypertrophy in cattle significantly affects carcass and beef quality characteristics. Genome-wide screening of DNA markers indicates a number of putative Quantitative Trait Loci (QTL) associated with carcass and meat quality characteristics. Published data for these QTL are summarised. Strategies to combine quantitative and molecular genetic information to maximise genetic progress are discussed.

Additional keywords: carcass and beef quality, crossbreeding, within-breed selection, genetic markers.

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Introduction

Australia is the world's largest beef exporter. To maintain or increase share of the world beef trade, it must continue to produce high quality, contaminant-free beef. Recent reviews (Dikeman 1990; Marshall 1994; Koots *et al.* 1994*a*, 1994*b*) indicate that many traits associated with body composition of cattle, including meat yield, are under direct genetic control. Such control provides an ability to manipulate beef quantity through genetic means. However, the Australian cattle industry is coming under increasing pressure to also improve the eating quality of beef, particularly with respect to consistency of tenderness and palatability. There are substantially fewer reports relating to the genetic influences on eating quality of beef.

Genetic variation in both quantity and quality of beef is evident through differences between breeds and crossbreeds and between sires within a breed. Within-breed variation includes additive genetic effects and also the correlated impacts of additive genetic effects on other economically important productive and adaptive traits that affect beef production. Over the past decade there has been an increasing emphasis on development of molecular genetic tools such as genetic markers, to improve beef production and quality through marker-assisted selection.

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. To do this, they need knowledge of genetic and non-genetic influences on beef production and quality. The purpose of this paper is to review the recent scientific literature to identify the quantitative and molecular genetic influences on beef quantity and quality, and to provide recommendations to Australian beef producers about the best methods of genetically manipulating traits that affect properties of beef.

Measurement of carcass and beef quality attributes

Probably the major difficulty faced by scientists studying carcass and beef quality attributes is the lack of consistency between studies in the definition of these attributes and the use of different measurements for the same trait. This means that, in many cases, it is almost impossible to validly compare results from one experiment with those from other, very similar experiments. By way of example, in Australian abattoirs that use the AUS-MEAT scheme, carcasses are weighed with all internal fat sources removed and with some subcutaneous fat trimming allowed. Consequently, yield or dressing percentages based on data using a different definition of carcass weight (e.g. early Australian data or data from overseas studies) will have systematic errors. Similar problems of definition and measurement across studies extend to most carcass and beef quality attributes. Definitions and measurements of carcass and beef quality attributes reported in this review are summarised in Table 1.

Between-breed variation

Breed and breed-type effects

No single cattle breed has all attributes that are needed to produce beef efficiently in all environments and to meet the requirements of all markets. Great variation exists between breeds in performance for both productive and adaptive traits. Hence, appropriate use of systematic crossbreeding programs provides significant benefits to beef producers, particularly through improved growth and female fertility, in both temperate (e.g. Cundiff and Gregory 1999) and tropical (e.g. Frisch 1997) environments. Numerous reports are available on the effects of crossbreeding on carcass and beef quality attributes in *Bos taurus* breeds of cattle reared in temperate environments. Many of these reports also include tropically adapted breeds in their comparisons. However, there are relatively few reports of breed and heterotic effects on carcass and beef quality attributes of tropically adapted cattle grazed at pasture in the tropics and subtropics.

Possibly the largest experimental crossbreeding program ever undertaken in temperate environments has been ongoing at the US Meat Animal Research Centre (MARC) in Nebraska since 1970. Results from the Germplasm Evaluation Program (GPE) at MARC provide evidence that genetic variation between breeds is similar in magnitude to genetic variation within breeds for many bioeconomic traits (Cundiff and Gregory 1999).

Breed differences in body composition traits have been evaluated in numerous studies and were reviewed by Marshall (1994). Franke (1997) also reviewed carcass composition of subtropically adapted breeds in the USA. A schematic representation of breed differences in body composition and related traits from Cundiff and Gregory (1999) is presented as Table 2.

Results for growth, carcass and beef quality attributes for steers produced in the Germplasm Utilisation Program (GPU) at MARC, as reported by Cundiff and Gregory (1999) are shown in Table 3. These data are for purebred steers produced contemporaneously over 4 calf crops between 1988 and 1991. Differences between breeds were significant and large for carcass and beef quality attributes. As expected, differences between pure breeds in the GPU program were about twice as great as differences between crosses in the GPE project that differ only in sire breed. Breed means for marbling were associated with breed means for tenderness, although this does not necessarily imply a cause and effect relationship. European breed steers excelled in retail product yield but had difficulty grading USDA Choice because of lower levels of marbling. British breeds excelled in USDA carcass quality grade but had excessive fat thickness and percentage fat trim and reduced retail product yields.

Table 4 has been adapted from Cundiff and Gregory (1999) and Cundiff *et al*. (1999) and summarises results for sire breeds for crossbred progeny from cycle 5 of the GPE project. Sire breed differences were large for final weight,

carcass weight, fat thickness, marbling and beef yield traits (Tables 3 and 4). British breeds had significantly lower retail beef yield percentages than did the European breeds. Even though Limousin progeny had lower liveweights than the average of Charolais, Simmental and Gelbvieh progeny, they did not differ from them in retail beef yield percentage because of their higher dressing percentage and lower carcass fat and bone percentages. Preliminary results indicate that Belgian Blue and Piedmontese had from 5 to 9% higher retail yields than other sire breeds, with meat palatability similar to Angus and Hereford sire breeds (Table 4). However, <33% graded USDA Choice, due to their significantly reduced fat cover and marbling. Breed groups differed greatly in fat thickness and marbling score. British breeds were similar in marbling score and intramuscular fat percentage. Preliminary results indicate that tropically adapted Tuli cattle produce progeny with carcass and beef quality attributes more similar to progeny sired by British breeds (i.e. Hereford and Angus) than to progeny sired by *Bos indicus* breeds (i.e. Brahman and Boran). However, Tuli crosses had relatively low average daily weight gains. These results were subsequently confirmed in a separate experiment based in a southern USA environment (Herring *et al*. 1996).

There were also significant differences between sire breeds for percentage of carcasses grading USDA Choice and for objective measures of tenderness (Warner Bratzler shear force) and sensory panel tenderness (Tables 3 and 4).

Table 1. Definition and measurement of carcass and beef quality attributes used in this review

Attribute	Definition and measurement
	Carcass measures
Carcass weight	Hot standard carcass weight (kg)
Dressing percentage	Dressing percentage (ratio of carcass weight to pre-slaughter liveweight)
Retail beef yield	Yield of saleable meat expressed either as a weight (kg) or as a proportion of carcass weight (%). The measurement depends on the amount of fat trim e.g. in Australia, carcasses are generally trimmed to 3 mm of subcutaneous fat, whereas in many USA studies, carcasses are trimmed to 0 mm of fat. Variations of this trait are sometimes referred to in the literature as 'cutability' or 'retail product yield'
Fat thickness	Subcutaneous fat thickness measured at the P8 rump site or the 12th/13th rib site (mm; the more usual site in Australian abattoirs is the rump; the more usual site in the USA is the rib)
Marbling score	Visual assessment of the amount of intramuscular fat in the *M. longissimus dorsi*. Scoring systems vary markedly (e.g. in Australia, AUS-MEAT scores range from 1 to 7 and are scored at a site between the 12th and 13th ribs; the USA system has 11 grades of marbling scored at a site between the 12th and 13th ribs, with each grade scored over a 100 point scale; the Japanese system uses 12 marbling scores scored between the 6th and 7th ribs — these scores are then condensed into 5 marbling grades)
Intramuscular fat percentage	Chemically extracted fat percentage from a sample of the *M. longissimus dorsi* between the 12th and 13th ribs, using either near infra-red spectroscopy or Soxhlet extraction
pH	Ultimate pH of meat sample, within Australia calculated as the mean of 4 measurements using a probe-type combined electrode, with normal values in the range of 5.5–5.7
	Objective measures of beef tenderness
Warner Bratzler initial yield	Initial yield (kg), an index of the myofibrillar contribution to meat toughness
Warner Bratzler peak force	Peak force, also known as shear force (kg), which represents the total meat toughness
Peak force — initial yield	Difference between peak force and initial yield (kg), which is an index of the contribution of connective tissue to meat toughness
Compression	Compression (kg) , measured to determine differences in connective tissue content between muscles (Harris and Shorthose 1988)
Cooking loss	Cooking loss (%), determined from weights taken before and after cooking at 80°C for 1 h in a thermostatically controlled waterbath
Tenderness index	Index of meat tenderness that relates to consumer scoring of meat tenderness on a scale of 0 = extremely tender to 15 = extremely tough using the equation: Index = (1.4 × compression) + (0.6 × peak force) + (0.12 × cooking loss) – 2.6 (Harris and Shorthose 1988)
Myofibrillar fragmentation index	A biochemical measure of beef tenderness predicted by absorbance (Barkhouse *et al*. 1996), with low values indicating tough meat and high values indicating tender meat
Calpastatin activity	Amount of calpastatin activity measured in *M. longissimus dorsi* at 24 h post-slaughter, according to the method of Shackelford *et al*. (1994*a*)
	Subjective sensory panel tests
Tenderness/juiciness/flavour/overall acceptability	Sensory taste panel tests use subjective scores of individual components of beef eating quality (tenderness, juiciness and flavour) and also an overall eating quality score, combining tenderness, juiciness and flavour. Panellists may be either trained or untrained, and the scoring scale varies considerably across experiments

In all cycles of the GPE project, breed differences for sensory juiciness and flavour were of little practical importance, but there were significant differences between breed types for tenderness. Cattle of high *Bos indicus* content had lower marbling scores at a given age and produced less tender and more variable steaks than *Bos taurus* breeds (Koch *et al*. 1982; Crouse *et al*. 1989; DeRouen *et al*. 1992; Van Vleck *et al*. 1992; Wheeler *et al*. 1994; Barkhouse *et al*. 1996.) Some early breed comparison studies have been criticised on the basis of failure to control processing factors that may lead to cold shortening, which results in tougher meat, particularly in leaner and lighter breeds. However, studies where processing factors were tightly controlled (e.g. Johnson *et al*. 1990) also reported tougher meat from carcasses with a high *Bos indicus* content than from *Bos taurus* and low *Bos indicus* content carcasses, indicating that genuine breed differences exist with respect to beef toughness. Increased calpastatin activity in *Bos indicus* accounted for some of the increased toughness (Johnson *et al*. 1990; Wheeler *et al*. 1990; Whipple *et al*. 1990; Shackelford *et al*. 1991; O'Connor *et al*. 1997; Pringle *et al*. 1997). In tenderness evaluated by shear force, British breeds had slightly more favourable (lower) values than the European breeds, with the exception of Pinzgauer, which was equal to Angus. Breed group differences in sensory panel tenderness were smaller than differences in shear force values.

A strong antagonism was evident between carcass quality grade and beef yield percentage between the breed groups. However, breed and biological type rankings developed for growth, carcass and beef quality attributes from the crossbreeding experiments at MARC generally apply to other results based on similar breed types of cattle reared in other temperate environments. Small differences occur in sire breed rankings, depending on the end point of production. Wheeler *et al*. (1996, 1997) reported that adjustment of traits to age, weight, marbling, fat thickness and fat trim end points resulted in some changes in sire breed differences, depending on the end point and the trait being considered, but had little effect on palatability traits.

Results from tropical and subtropical environments are less precise, partly due to the paucity of experimental evidence from these environments and from some breed types, but also because resistance of individuals to environmental stressors has a significant impact on growth rate and hence body composition, beef quantity and, possibly,

Table 2. Breeds grouped into biological types for relative growth rate and mature size, lean to fat ratio, age at puberty and milk production (Cundiff and Gregory 1999)

Increasing number of +s indicate relatively higher values

Breed group	Growth rate and mature size	Lean : fat ratio	Age at puberty	Milk production
Jersey	+	+	+	+++++
Longhorn	+	+++	+++	++
Hereford-Angus (HA_x)[A]	+++	++	+++	++
Red Poll	++	++	++	+++
Devon	++	++	+++	++
Shorthorn	+++	++	+++	+++
Galloway	++	+++	+++	++
South Devon	+++	+++	++	+++
Tarentaise	+++	+++	++	+++
Pinzgauer	+++	+++	++	+++
Brangus	+++	++	++++	++
Santa Gertrudis	+++	++	++++	++
Sahiwal	++	+++	+++++	+++
Brahman	++++	+++	+++++	+++
Nellore	++++	+++	+++++	+++
Braunvieh	++++	++++	++	++++
Gelbvieh	++++	++++	++	++++
Holstein	++++	++++	++	+++++
Simmental	+++++	++++	+++	++++
Maine Anjou	+++++	++++	+++	+++
Salers	+++++	++++	+++	+++
Piedmontese	+++	++++++	++	+
Limousin	+++	+++++	++++	+
Charolais	+++++	+++++	++++	+
Chianina	+++++	+++++	++++	+

[A]HA_o denotes Hereford-Angus reciprocal crosses by original reference sires, HA_c denotes Hereford-Angus reciprocal crosses by more current sires.

Table 3. Means for weight, carcass and beef quality traits for steers of nine pure-breed populations at the Meat Animal Research Centre, adjusted to average age of slaughter of 438 days (adapted from Cundiff and Gregory 1999)

Breed	No. of steers	Final wt (kg)	Carcass wt (kg)	Fat thickness (mm)	Trimmed to 0 mm fat			Marbling score[A]	USDA choice (%)	Shear force (kg)	Sensory panel scores[B]		
					Retail yield (%)	Fat trim (%)	Bone (%)				Tenderness	Juiciness	Flavour
Red Poll	114	525	315	7.62	62.6	22.4	14.9	530	71	4.72	5.15	5.25	4.96
Hereford	146	507	306	11.68	60.1	25.5	14.4	521	60	5.08	5.10	5.25	4.80
Angus	118	515	316	11.68	61.5	24.4	14.1	541	77	4.49	5.55	5.38	4.92
Limousin	142	519	330	4.32	72.3	13.4	14.3	443	14	5.62	4.88	5.01	4.82
Braunvieh	139	567	339	4.57	67.3	16.1	16.5	484	42	5.08	5.06	5.12	4.90
Pinzgauer	118	557	331	4.32	66.8	17.0	16.1	516	55	4.49	5.43	5.20	4.96
Gelbvieh	150	567	340	3.56	70.0	14.2	15.8	453	15	5.76	4.63	5.04	4.75
Simmental	127	581	348	4.06	68.4	15.5	16.1	480	34	5.49	4.80	5.14	4.83
Charolais	126	573	348	3.56	68.7	15.0	16.2	471	24	5.17	4.95	5.12	4.88

[A]Slight = 400–499, small = 500–599 etc.
[B]Score: 1 = extremely tough, dry or bland to 8 = extremely tender, juicy or intense.

beef quality. Genotype × environment (G × E) interactions are very important in tropical and subtropical environments, and have a major impact on breed and breed type rankings for some traits (e.g. see Frisch and Vercoe 1984).

For most purposes in the tropics and subtropics, breeds can be categorised into several general groupings, as has been done for breeds in temperate areas. Even though in temperate areas there may be substantial differences in performance between breeds within the general groupings, in tropical and subtropical areas differences in performance tend to be masked, due to the effects of environmental stressors. The broad breed groupings are outlined in detail in MRC (1997) and performance attributes for the breed groupings, adapted from Frisch (1997) and MRC (1997), are shown here as Table 5. Representative breeds from the various breed groupings shown in Table 5 include Hereford, Angus and Shorthorn (British); Charolais, Simmental and Limousin (European); Africander, Tuli and Mashona (Sanga); Brahman, Sahiwal, Nellore (Indian zebu); and Boran (African zebu). In Table 5, relative performance for growth and fertility traits is compared within temperate and tropical environments.

British and European breed groups have the best growth and fertility rates of the pure breeds in temperate environments. In tropical environments though, they are unable to express the same levels of performance, due to

Table 4. Sire breed averages for final weight and carcass and beef quality attributes of steers representing Hereford, Angus and tropically adapted sire breeds in Cycle V of the germplasm evaluation at the Meat Animal Research Centre, adjusted to average age at slaughter of 447 days (adapted from Cundiff and Gregory 1999 and Cundiff *et al.* 1999)

Sire breed	No. of steers	Final wt (kg)	Carcass wt (kg)	Fat thickness (mm)	Dressing (%)	Marbling score[A]	USDA choice (%)	Number	Shear force (kg)	Sensory panel scores[B]		
										Tenderness	Juiciness	Flavour
Hereford	115	576	348	11.68	60.4	520	70.3	106	5.72	5.13	4.94	5.19
Angus	126	580	351	12.45	60.5	556	84.6	101	5.13	5.38	4.89	5.36
Average	241	578	350	11.94	60.4	538	77.4	207	5.40	5.25	4.92	5.28
Brahman												
(Original)	43	533	326	9.65	61.2	485	29.4	43	7.76	3.77	4.85	4.77
(Current)	76	544	337	10.41	61.9	466	30.4	76	6.80	4.22	4.81	4.79
Average	119	538	331	10.16	61.6	476	29.9	119	7.30	4.00	4.83	4.78
Boran	151	506	310	11.18	61.3	504	47.2	138	6.58	4.48	4.77	5.04
Tuli	162	503	309	10.16	61.3	525	63.8	158	5.72	5.00	4.86	5.17
Piedmontese	35	534	332	5.84	62.3	472	31.8	35	5.40	5.04	4.84	5.02
Belgian Blue	144	566	353	6.60	62.2	464	23.8	143	5.90	4.93	4.85	5.02

[A]Slight = 400–499, small = 500–599 etc.
[B]Score: 1 = extremely tough, dry or bland to 8 = extremely tender, juicy or intense.

Table 5. Comparative rankings of different breed groups for productive traits in temperate and tropical environments and for adaptation to stressors of tropical environments (adapted from Frisch 1997 and MRC 1997)

The higher the number of +s, the higher the value for the trait

Breed group	Temperate area[A]		Tropical area[A]		Mature	Meat	Resistance to environmental stressors				
	Growth	Fertility	Growth	Fertility	size	quality[B]	Cattle ticks[C]	Worms[D]	Eye diseases	Heat	Drought
Bos taurus											
British	++++	+++++	++	++	++++	+++++	+	+++	++	++	++
European[E]	+++++	++++	++	++	+++++	+++++	+	+++	+++	++	+
Sanga	+++	++++	+++	++++	+++	+++++	++++	+++	+++	+++++	+++++
Bos indicus											
Indian zebu	+++	+++	++++	+++	++++	+++	+++++	+++++	+++++	+++++	+++++
African zebu	++	++++	++	++++	+++	++++	+++++	++++	++++	+++++	+++++
F_1 Brahman × British	++++	+++++	++++	+++++	++++	++++	++++	++++	++++	+++++	++++

[A]Temperate area environment is assumed to be an environment free of environmental stressors, whereas rankings shown for tropical environment apply to an environment where all environmental stressors are operating. Hence, while a score of +++++ for e.g. fertility in a tropical environment indicates that breed group would be expected to have the highest fertility in that environment, the actual level of fertility may be less than the actual level of fertility for breeds reared in a temperate area, due to the effect of environmental stressors that reduce performance.
[B]Principally meat tenderness. [C]*Boophilus microplus*. [D]Specifically, *Oesophagostomum, Haemonchus, Trichostrongylus* and *Cooperia* spp.
[E]Data from purebred European breeds not available in tropical environments and responses predicted from the Tropical Beef Centre model.

their poor resistance to ticks, worms, disease, heat and drought (Table 5). Poor levels of adaptation to environmental stressors are also believed to be responsible for changes in breed rankings for meat tenderness in extreme environments, as reported by Pratchett *et al*. (1988). In that study, based on relatively small numbers of animals, beef tenderness of electrically stimulated carcasses from steers of 4 breed types (Shorthorn, Brahman, Brahman × Shorthorn and Africander × Shorthorn) raised in the Kimberley pastoral region of Western Australia were studied. Taste panel and Warner Bratzler shear force tests showed that Shorthorn cattle had less tender, and Africander × Shorthorn the most tender (P<0.05) meat of the breeds studied. Shear force values for Shorthorn, Brahman, Brahman × Shorthorn and Africander × Shorthorn were 5.29, 6.39, 5.26 and 4.51 kg, respectively. Comparable taste panel values on a scale of 1 = very tough to 6 = very tender were 2.94, 3.05, 3.21 and 3.60, respectively, indicating that taste panellists rated Shorthorn beef as tougher. Because Shorthorn cattle were poorly adapted to the harsh dry tropical climate of the Kimberley region, their growth rates were substantially lower than those of the remaining breeds. Hence, it is likely that G × E interactions for growth rate, although unable to be tested by the experimental design, may have had a significant impact on meat quality. The results have serious implications for beef producers in northern Australia as they very clearly demonstrate that, to achieve eating quality specifications, cattle breeds in these areas must not only be genetically able to meet market requirements but also need to be well adapted to environmental stressors.

In most environments, the most productive breed group is the F_1 hybrid between *Bos indicus* and *Bos taurus*, indicating that significant production benefits accrue from crossbreeding. Data from research stations and commercial herds have been used to develop models that demonstrate significant improvements in profitability and sustainability of beef enterprises through combined use of crossbreeding and within-breed selection (Clark *et al*. 1992).

Reports of significant amounts of genetic variation both within- and between-breeds for carcass and beef quality attributes confirm these economic reports. Wheeler *et al*. (1996) reported the mean estimated purebred difference in meat tenderness, measured by shear force, between the most and least tender breeds in the MARC experiments (i.e. Pinzgauer and Nellore) corresponded to 4.76 genetic standard deviations, whereas the total range within a breed was about 6 genetic standard deviations. For retail beef yield percentage, the between-breed variation was larger than the within-breed variation (7.87 *v.* 6 genetic standard deviations, respectively; Wheeler *et al*. 1997).

Van Vleck *et al*. (1992) reported that sires within a breed or crossbred group ranked similarly due to large differences between breed effects (e.g. in their experiments, 6 Sahiwal sires ranked in the highest 6 places for shear force). Those results illustrate that for traits with large breed differences, selection of the proper breed should be done before selection within the breed. Breed effects were important in ranking for breeding value for most of the carcass and beef quality traits. Separate evaluations for breed or breed type, followed by within-breed selection may be an effective approach for genetic improvement in systematic crossbreeding programs. For many traits such as beef tenderness and palatability, between-breed differences may be more easily exploited than within-breed differences because exceptional breeds are

Table 6. Heterosis effects in crosses of *Bos taurus* × *Bos taurus* breeds and in crosses of *Bos indicus* × *Bos taurus* breeds from diallel crossing experiments [adapted from Cundiff and Gregory 1999; estimates are from experiments contributing to North Central Region Project NC-1 (Iowa, Indiana, Missouri, Ohio, USDA-ARS and Nebraska), Southern Regional Project S-10 (Virginia, Florida, Louisiana, Texas, USDA-ARS and Louisiana, USDA-ARS and Florida)]

Trait	*Bos taurus* × *Bos taurus*			*Bos indicus* × *Bos taurus*		
	n^A	Units[B]	%[C]	n^A	Units[B]	%[C]
	Crossbred calves (individual heterosis)					
Calving rate (%)	11	3.2	4.4			
Survival to weaning (%)	16	1.4	1.9			
Birth weight (kg)	16	0.78	2.4	4	3.3	11.1
Weaning weight (kg)	16	7.4	3.9	10	21.7	12.6
Post-weaning ADG (kg/day)	19	0.003	2.6	6	0.116	16.2
Yearling weight (kg)	27	13.2	3.8			
Retail beef yield (%)	24	–0.3	–0.6			
	Crossbred cows (maternal heterosis)					
Calving rate (%)	13	3.5	3.7	7	9.9	13.4
Survival to weaning (%)	13	0.8	1.5	7	4.7	5.1
Birth weight (kg)	13	0.7	1.8	6	1.9	5.8
Weaning weight (kg)	13	8.2	3.9	12	31.1	16.0
Longevity (years)	3	1.36	16.2			

[A]Number of estimates.
[B]Amount of heterosis expressed in units of the trait relative to mid-parent mean value (e.g. kg of weight; percentage of calving rate etc.).
[C]Amount of heterosis expressed as a percentage difference relative to mid-parent mean value.

easier to identify than exceptional animals. However, the effects of environmental factors on these traits must not be overlooked in any genetic improvement programs targeting beef quality.

Estimates of heterosis

Complete expression of heterosis is measured by the difference between the average performance of reciprocal F_1 crosses and the average of the parental breeds joined to produce the reciprocal crosses. Heterosis is caused by non-additive effects of genes such as dominance and epistasis and can be seen through individual animal and maternal effects on the trait. Complete dominance exists when 1 copy of an allele at a single location on paired chromosomes has a similar effect on performance as 2 copies. Epistasis results from similar interactions involving combinations of genes at 2 or more locations in the genome.

Estimates of heterosis averaged over diallel crossing experiments for a number of traits and from many studies throughout the USA were summarised by Cundiff and Gregory (1999) and are reported here as Table 6. They are shown separately for *Bos taurus* × *Bos taurus* and *Bos indicus* × *Bos taurus* crossbreds. Heterosis effects were greatest for traits such as longevity, reproduction rate and lifetime production. Effects of heterosis on carcass and beef quality characteristics in all studies were relatively small (3% or less). In general, heterosis observed for carcass attributes was through heterotic effects on weight. When data were adjusted for differences in carcass weight, heterotic effects on carcass composition were not observed (Cundiff and Gregory 1999). Under subtropical conditions in the USA, and possibly under temperate conditions, *Bos indicus* × *Bos taurus* crosses had higher levels of heterosis than those reported for corresponding traits between *Bos taurus* crosses (see Table 6). Maternal effects were generally not important for carcass and beef quality attributes (Gregory *et al*. 1978; Johnston *et al*. 1992*b*; Cundiff and Gregory 1999).

Estimates of individual and maternal heterosis for specific carcass and beef quality attributes were summarised by Marshall (1994) and are shown here as Table 7. The estimates were expressed as percentages of purebred means and were averaged across specific crosses within a study and then averaged across studies for a particular trait. Therefore, several of the values shown in Table 7 represent mean heterosis levels across many different breed crosses. The estimates were from studies where days fed or calf age was a slaughter end point or statistical covariate, meaning that the estimates retain some effects of carcass weight. Individual heterosis estimates for carcass weight were consistently positive in all studies. Individual heterosis estimates were relatively large (average 10.1%) for fat thickness but tended to be relatively small in magnitude for most other carcass traits. Maternal heterosis estimates were generally positive and relatively large for fatness traits but tended to be small to moderate for other carcass traits (Marshall 1994).

Table 7. Individual and maternal heterosis estimates (% of straightbred mean) for carcass traits, averaged across breed-crosses and studies from crosses of *Bos taurus* × *Bos taurus* and *Bos taurus* × *Bos indicus* (age- or time-in-feedlot-constant basis; adapted from Marshall 1994; values are simple numerical unweighted averages)

Trait	No. of studies[A]	Individual heterosis (%)	Maternal heterosis (%)
Carcass weight	12 (4)	6.5	3.6
Marbling	7 (2)	3.8	–1.1
Fat depth	11 (4)	10.1	8.9
M. longissimus muscle area	9 (3)	4.1	3.3
Retail product weight	2 (1)	6.6	2.2
Estimated retail product (%)	7 (1)	–0.6	–2.5
Fat trim (%)	1 (1)	6.3	12.7
Shear force	2 (1)	–6.7	0
Dressing percentage	3	–0.2	

[A]First number is the number of studies on which the value given for individual heterosis is based. Number in parentheses is for maternal heterosis.

Estimates of heterosis for fatness and other carcass attributes on a weight-constant basis tended to be much smaller than estimates of heterosis for the same characteristics on an age-constant basis (Gregory *et al*. 1978; Drewry *et al*. 1979; Johnston *et al*. 1992*b*), reflecting a faster maturing rate for crossbred animals. If cattle are marketed on a weight end point, then the contribution of individual heterosis to increased fatness or retail beef yield percentage is likely to be small.

There are relatively few studies that have examined the effects of heterosis on beef tenderness measurements and sensory traits of beef. Results from those studies suggest that heterosis for Warner Bratzler shear force values ranges from moderately favourable to slightly unfavourable (about –10 to 5%, Winer *et al.* 1981; Peacock *et al*. 1982; Anderson *et al*. 1986; Marshall *et al*. 1987; Gregory *et al*. 1994*a,* 1994*b*), although some *Bos indicus* × *Bos taurus* crosses may have higher levels of favourable heterosis (DeRouen *et al*. 1992). There were no observed effects of heterosis on sensory evaluation of juiciness, tenderness and flavour (Winer *et al*. 1981; Gregory *et al*. 1994*b*) or for cooked meat colour and overall acceptability (Winer *et al*. 1981).

There is only a single known study that estimated the effects of heterosis on carcass attributes in tropically adapted cattle reared in tropical environments. No studies have estimated these effects for meat quality attributes in cattle reared in the tropics. Thorpe *et al*. (1980) compared Africander, Angoni, Barotse and Boran breeds and reciprocal crosses of the latter 3 breeds in Zambia. For all carcass characters except those related to size, the Sanga breeds (Africander and Barotse) were very similar, as were the 2 zebu breeds (Angoni and Boran). Maternal effects were not important for carcass characters and the Angoni × Barotse and Angoni × Boran crosses showed no heterosis for any carcass attribute. Heterosis estimates in the Barotse × Boran crosses for slaughter and carcass weights and eye muscle area were between 8 and 9.5%, and for linear carcass measurements between 2 and 3%. These results indicate that heterosis for carcass attributes in tropically adapted cattle reared in the tropics may also be generally limited to carcass characters associated with weight, as is the case for cattle reared in temperate environments.

Although heterosis effects do not significantly improve carcass composition or beef quality, crossbreeding can potentially benefit these traits through increased growth rates and also through complementary blending of breed characteristics to reduce problems associated with genetic antagonisms between traits such as retail beef yield and marbling.

Within-breed variation

Heritability of carcass composition traits

There are numerous reports outlining the magnitude of within-breed variation for carcass and beef quality attributes in *Bos taurus* breeds of cattle reared in temperate environments. There are, however, relatively few reports on variances and covariances for these attributes in tropically adapted cattle reared in tropical environments.

Koots *et al*. (1994*a*) and Marshall (1994) reviewed genetic parameters for carcass and beef quality attributes from published reports to 1991 and 1993, respectively. Traits measured at, or adjusted to, different weight, age or finish (fat depth) end points are biologically different, and hence may need to be considered as separate traits. Both Koots *et al*. (1994*a*) and Marshall (1994) reviewed heritabilities at these different end points. Koots *et al*. (1994*a*) concluded there were no consistent differences between unadjusted heritabilities or heritabilities adjusted to a constant age or weight. Estimates adjusted to a constant finish (fat depth) were higher than estimates adjusted to a constant age or weight, but there were too few estimates adjusted to a constant finish to conclude that this was a consistent effect. Table 8 shows estimates of heritability for carcass composition traits (e.g. weight, fatness and marbling) derived from the 2 previously published reviews and includes additional estimates derived since their publication. These additional estimates have been weighted by the number of animals contributing to their estimation and averaged across all recent studies. Heritabilities shown in Table 8 indicate that carcass composition traits are at least moderately heritable and should respond well to genetic selection. Most estimates of retail beef yield percentage are highly heritable. Under a value-based trading system, retail beef yield will be economically valuable to the Australian beef industry and hence beef producers have an opportunity to exploit the

genetic variation that exists to make rapid genetic gains for yield, with the proviso that undesirable consequences for such selection do not occur in their herds. Likely consequences of such selection are discussed in a later section of this paper.

Heritability of beef tenderness and palatability

There are relatively fewer reports relating to within-breed genetic variation for eating quality attributes such as beef tenderness, flavour and juiciness. It is possible that beef tenderness and palatability characteristics measured in different muscles, or from carcasses that have or have not been processed to overcome problems with meat toughness (e.g. through use of electrical stimulation, tenderstretching or ageing of the meat for a minimum period), should be regarded as different traits.

Harris and Shorthose (1988) and Shackelford *et al*. (1995) reported that Warner Bratzler shear force measurement in 1 muscle was not an accurate indication of shear force measurement in other muscles. As well, shear force was not correlated well with trained sensory panel tenderness ratings within most muscles except the striploin (*M. longissimus dorsi*; Shackelford *et al*. 1995). The variance of tenderness between animals was substantially less for the rump (*M. biceps femoris*) and the eye round (*M. semitendinosus*) than the striploin. Location of sample site accounted for a higher percentage of the total variance of tenderness rating and Warner Bratzler shear force value for the eye round than did animal. Neither shear force values nor taste panel ratings were highly repeatable for the rump or the eye round, because there was little between-animal variation in tenderness for these muscles (Shackelford *et al*. 1995). Hence, measurement of one muscle is unlikely to accurately predict tenderness of other muscles. With only 2 exceptions, estimates of heritability of meat tenderness have been based on measurements from a single muscle (*M. longissimus dorsi*).

Meat tenderness can be affected by cold shortening under conditions of rapid chilling relative to the rate of decline in muscle pH post-slaughter (Harris and Shorthose 1988). Under rapid chilling conditions, differences in subcutaneous fat thickness between carcasses may cause variation in chilling rates, resulting in variation in meat toughness and eating quality. This is particularly true for leaner and lighter carcasses. Application of processing techniques such as electrical stimulation, tenderstretching and correct aging of meat can be used to overcome the effects of cold shortening (Harris and Shorthose 1988). It is therefore possible that beef tenderness measured either with or without correct application of processing techniques to overcome cold

Table 8. Published estimates of heritability for some carcass composition traits adjusted to different end points

Trait (adjustment factor)	Koots *et al*. (1994*a*)		Marshall (1994)		Recent studies[A]			
	No. of studies	Weighted heritability[B]	No. of studies	Average heritability	No. of studies	Average no. of animals/study	Range	Average heritability
Fat thickness (age)	26	0.44	6	0.44	6	3949	0.20–0.66	0.39
Fat thickness (finish)	1	0.43						
Fat thickness (unadjusted)	4	0.23						
Fat thickness (weight)	14	0.46						
Retail yield % (age)	12	0.47	5	0.36	5	1796	0.39–0.66	0.54
Retail yield % (unadjusted)	1	0.28						
Retail yield % (weight)	7	0.48						
Carcass weight (age)	19	0.23	9	0.41	5	4419	0.15–0.50	0.39
Carcass weight (finish)	4	0.36			1	1444	0.09	0.09
Carcass weight (unadjusted)	6	0.20			1	392	0.10	0.10
Carcass weight (weight)	4	0.24						
Dressing % (age)	13	0.39			2	1241	0.06–0.19	0.14
Dressing % (unadjusted)	3	0.53			1	392	0.21	0.21
Dressing % (weight)	8	0.38						
Marbling (age)	12	0.38	9	0.35	9	2833	0.26–0.93	0.47
Marbling (finish)	2	0.65			2	1010	0.26–0.52	0.33
Marbling (unadjusted)	4	0.27			1	392	0.16	0.16
Marbling (weight)	3	0.36						
Market weight (age)	52	0.41			2	1241	0.21–0.28	0.25
Market weight (finish)	1	0.56						
Market weight (unadjusted)	4	0.46						
Market weight (weight)	1	0.48			1	392	0.15	0.15

[A]Sources: Barkhouse *et al*. (1996); Crews and Franke (1998); Gregory *et al*. (1994*b*); Gregory *et al*. (1995); Hirooka *et al*. (1996); Johnston *et al*. (1992*a*); O'Connor *et al*. (1997); Shackelford *et al*.(1994*a*); Splan *et al*. (1998); Van Vleck *et al*. (1992); Wheeler *et al*. (1996); Wulf *et al*. (1996).
[B]Individual estimates of heritability were weighted by the relative amount of information (inverse of their estimated sampling variance).

shortening may be measurement for different attributes. Other factors that affect meat tenderness include age of animal at slaughter (effect of increased collagen content as animals age), *Bos indicus* content and effects of abattoir and slaughter group or date of slaughter that can explain significant amounts of variation for beef tenderness (see e.g. Keele *et al.* 1999).

Table 9 summarises published estimates of heritability of objective measures of beef tenderness within and across breed groupings. The objective measures include Warner Bratzler shear force, a physical measure of tenderness; myofibrillar fragmentation index, a biochemical measure of tenderness; and 24-h calpastatin activity, a measure of calpastatin activity at 24 h post-slaughter. Calpastatin is an inhibitor of the calcium-dependent proteases that are involved in the enzymatic degradation of myofibrillar proteins during post mortem aging, and high levels of calpastatin activity are associated with tough meat. Table 10 summarises published estimates of heritability of subjective taste panel assessments of beef tenderness and palatability within and across breed groupings.

Several reviews of the literature concluded that beef tenderness, based on objective measures, was moderately to highly heritable (e.g. Renand 1988, average computed mean heritability of 0.33; Dikeman 1990, heritability from 0.09 to 0.70, with most estimates in the upper range; Koots *et al*. 1994*a*, unweighted mean of 0.43 and weighted mean of 0.29; Marshall 1994, average heritability of 0.37). These reviews were all based on very few studies conducted before 1993. Estimates of heritability from these early studies were generally based on paternal half-sib intraclass correlations using small numbers of animals. More recent studies, based on a substantially greater number of carcasses and using more discriminatory methods of analysis, indicate that meat tenderness and palatability attributes are, at best, only moderately heritable (Tables 9 and 10). REML analyses of Warner Bratzler shear force measurements in *Bos taurus* groups indicate estimates of heritability of ≤0.12 (Table 9), although recent estimates derived using other methods are marginally higher, as are estimates derived in *Bos indicus*-derived cattle, regardless of method of analysis (Table 9). For Warner Bratzler shear values, the weighted average heritability for *Bos taurus* groups was 0.21, and this estimate included 3 early studies where heritability was estimated to be greater than 0.60 (Table 9). The weighted average heritability for combined groups of *Bos indicus* and *Bos taurus* for Warner Bratzler shear values was 0.26 (Table 9), indicating that selection for beef tenderness in tropically adapted genotypes may be more effective than in *Bos taurus* breeds, depending on the amount of variation that exists for the trait.

Consideration needs to be given to the effects of post mortem treatments such as aging on estimates of heritability of beef tenderness. Wulf *et al*. (1996) reported within-breed heritabilities of shear force values at between days 1 and 35 post mortem (Table 9). In their study, shear force differences between sires remained about the same throughout the post mortem aging from 1 to 35 days, and the ranking of sires from least tender to most tender was also similar at all times, suggesting that genetic differences in beef tenderness are not a result of biological differences in mechanisms by which beef tenderness improves through aging. They concluded that genetic differences in tenderness were related to: (i) structural changes in the myofibril and/or proteolytic activity before 1 day post mortem; and/or (ii) genetic differences in tenderness that were established at slaughter (e.g. differences in connective tissue, fibre type, marbling). They suggested that selection for shear force values at any period post mortem would result in similar genetic responses. However, these results may not be consistent across breed types. O'Connor *et al*. (1997) reported significant interactions between biological type and length of aging that affected shear force values, with beef from *Bos taurus* breeds having a much faster rate of post mortem tenderisation than *Bos indicus* types. The difference in shear force between *Bos taurus* and *Bos indicus* types, although significant, became less pronounced over longer aging periods (O'Connor *et al*. 1997). Hence, selection for beef tenderness based on shear force values across breed types, assuming such selection was feasible, would need to consider the period of post mortem aging.

As well, selection for beef tenderness based on shear force values would need to consider the processing conditions that were applied at the time of slaughter. Johnston *et al*. (2001) reported that method of electrical stimulation had a large effect on the mean and variance of shear force values, particularly in the striploin (*M. longissimus dorsi*), in carcasses that had been hung by the Achilles tendon. Non-stimulated slaughter groups were more variable than slaughter groups electrically stimulated with high voltage, which were in turn more variable than slaughter groups stimulated with extra low voltage. It is possible that alternative methods of hanging of carcasses (e.g. tenderstretch; see Bouton *et al*. 1973) may reduce the amount of variation in shear force values even further.

There is only a single study known to have estimated the heritability of myofibrillar fragmentation index (see Table 9). Estimates of heritability from that study indicate similar heritabilities to Warner Bratzler shear values.

Estimates of heritability of 24-h calpastatin activity were higher than for other measures of beef tenderness (Tables 9 and 10). Wulf *et al*. (1996) reported that 24-h calpastatin activity was genetically highly correlated (r_g>1.00 for shear force measures between 1 and 35 days post mortem), but phenotypically, only moderately correlated with Warner Bratzler shear force values (r_p≤0.31). Shackelford *et al*. (1994*a*) reported lower genetic correlations ($r_g = 0.50 \pm 0.22$) and similar phenotypic correlations ($r_p = 0.27 \pm 0.04$)

between 24-h calpastatin activity and Warner Bratzler shear force values. Both studies were based on relatively small numbers of animals (392 and 555 respectively) and the average number of progeny per sire in the Shackelford *et al*. (1994*a*) study was <2.4, meaning that results from both studies should be regarded as preliminary. However, based on the relatively high heritabilities found in these studies (h^2>0.50, Shackelford *et al*. 1994*a*; Wulf *et al*. 1996) and high genetic correlations with shear force values, it appears that beef tenderness could be genetically improved by selection for decreased 24-h calpastatin activity. However, because of the low phenotypic correlations between calpastatin activity and shear force values, level of calpastatin activity is unlikely to be a useful indicator of meat toughness in existing herds in the short to medium term. As well, results reported by O'Connor *et al*. (1997) indicate that the earlier high estimates of heritability based on within-breed studies may be less useful on an across-breed basis. When heritability of calpastatin activity was estimated across biological types, the heritability was similar to that of other measures of meat tenderness (0.15 ± 0.15; O'Connor *et al*. 1997) and the genetic relationships between 24-h calpastatin activity and shear force values were unreliable (r_g ranging from –0.20 ± 0.57 to 0.74 ± 0.47). This is not surprising, because both Shackelford *et al*. (1994*a*) and Wulf *et al*. (1996) reported that while 24-h calpastatin activity was genetically highly correlated with Warner Bratzler shear force measures within breeds, calpastatin activity did not explain the variation in tenderness across *Bos taurus* breeds. Further studies are required to determine phenotypic and genetic relationships between 24-h calpastatin activity and Warner Bratzler shear force values and to validate the estimates of heritability of 24-h calpastatin activity both within and across breeds and breed types.

In general, objective measures of beef tenderness are more heritable than subjective tenderness evaluated by sensory panellists (Table 10). These results are possibly related to the low sensitivity of sensory evaluations, especially those that do not ensure careful control of background environmental effects (Harris and Shorthose 1988).

The above results indicate that selection to improve beef tenderness may be feasible (assuming such selection was practically possible and cost-effective) in *Bos indicus* and *Bos indicus*-derived breeds using objective measures of tenderness. However, before recommendations can be made that breeders should embark on selection programs for beef tenderness, consideration needs to be given to the issue of whether selection to improve tenderness in one muscle will lead to correlated responses in tenderness in other muscles. To date, there is insufficient information on genetic relationships between tenderness in different muscles to generate firm recommendations, although a recent study by Johnston *et al*. (2000) reported a genetic correlation of only 0.34 between shear force values in the striploin (*M. longissimus dorsi*) and the eye round (*M. semitendinosus*), suggesting that genetic improvement in overall beef tenderness may be difficult.

Most estimates of heritability of meat tenderness in the literature are based on animals slaughtered before 18 months of age. Such young slaughter ages are atypical of most Australian production systems, where animals are generally slaughtered for the premium export meat markets between 2 and 3 years of age. Hence, further data collected under Australian production and processing conditions are required to accurately define heritability of meat tenderness at older ages.

Relationships between carcass composition and beef quality attributes

Knowledge of the magnitude and direction of relationships between different traits is required to design effective breeding programs because selection for 1 trait may yield undesirable responses in other traits. Very few estimates of phenotypic and genetic relationships between carcass composition and beef quality attributes are available, and many of those that have been published have large standard errors associated with them, meaning they may not be reliable for use in breeding programs. Koots *et al*. (1994*b*) summarised published estimates of genetic and phenotypic correlations between a number of traits and concluded that general genetic antagonisms exist between some carcass quality traits and retail beef yield. Of more importance though, Koots *et al*. (1994*b*) suggested that many of the genetic relationships between traits of economic importance, and particularly between carcass and meat quality attributes, were poorly understood.

Relationship between retail beef yield and marbling

Genetic relationships between intramuscular fat percentage or marbling, fat thickness and retail beef yield are of particular interest, because in many markets these attributes determine carcass price. Average genetic correlations reported by Koots *et al*. (1994*b*) indicate that higher marbling scores or intramuscular fat percentages are genetically associated with increased subcutaneous fat and decreased lean yield, both within and between breeds. A moderate to strong genetic antagonism exists between carcass fatness traits and retail beef yield percentage. Estimates of genetic correlations between retail beef yield percentage and marbling scores or intramuscular fat percentages include a weighted mean correlation of –0.25 (Koots *et al*. 1994*b*); –0.57 ± 0.15 (Shackelford *et al*. 1994*a*); –0.56 ± 0.19 (Gregory *et al*. 1994*b*); and –0.60 ± 0.20 (Gregory *et al.* 1995).

Relationship between carcass weight, retail beef yield and tenderness

Published estimates of genetic correlations between beef tenderness and other traits are subject to the same difficulties

Table 9. Published estimates of heritability for objective measures of meat tenderness summarised within breed type (*Bos taurus* only or a combined analysis of *Bos taurus* and *Bos indicus* breeds)

PHSC, paternal half-sib intraclass correlation; HM3, Henderson's Method 3; REML, restricted maximum likelihood methods; S, steer; H, heifer; B, bull; LD, *M. longissimus dorsi*, *M. longissimus thoracis* or *M. longissimus lumborum*; ST, *M. semitendinosus*

Heritability	Method	*n*	Breed	No. sires	Sex	Age/wt at slaughter	Processing[A]	Muscle	Source
				*Warner Bratzler shear force (*Bos taurus *only)*					
0.77	PHSC	298	Shorthorn	?	S	?	?	?	Yao and Hiner (1953)
0.92	PHSC	60	Angus	7	S, H	386 days; 407 kg live	?	?	Kieffer *et al*. (1958)
0.62–0.69	PHSC	176	Angus	24	S, H	386 days; 251 kg carcass	?	LD	Christians *et al*. (1961)
0.00	PHSC	679	Hereford	70	S	454 kg live	Aged 10 days	LD	Dinkel and Busch (1973)
0.17 ± 0.10	PHSC	646	Hereford × (Angus × Friesian)	46	S, H	467 kg (S); 415 kg live (H)	Research abattoir	LD	Wilson *et al*. (1976)
0.30 ± 0.07	HM3	1828	European × Dairy breeds	133	B	515–585 kg live	3 commercial abattoirs	LD	Renand (1985)
0.00	PHSC	218	Friesian	37	S	21–24 months / 612 kg live	Slow cooling to avoid cold shortening	LD	More O'Ferrall *et al*. (1989)
0.12 ± 0.08	REML	1599	3 *Bos taurus* composite breeds	227	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al*. (1994*b*)
0.05 ± 0.09	PHSC	1153	Clay Centre purebred groups	214	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al*. (1995)
0.31 ± 0.17	PHSC	441	Clay Centre *Bos taurus* composite groups	92	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al*. (1995)
0.12 ± 0.10	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 1 day	LD	Wulf *et al*. (1996)
0.28 ± 0.15	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 4 days	LD	Wulf *et al*. (1996)
0.12 ± 0.10	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 7 days	LD	Wulf *et al*. (1996)
0.29 ± 0.15	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 14 days	LD	Wulf *et al*. (1996)
0.36 ± 0.18	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 21 days	LD	Wulf *et al*. (1996)
0.14 ± 0.11	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 35 days	LD	Wulf *et al*. (1996)
0.31 ± 0.16	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 1–35 days[B]	LD	Wulf *et al*. (1996)
				*Warner Bratzler shear force (*Bos taurus *and* Bos indicus*)*					
0.86–1.02[C]	PHSC	38	F_1 B × H and Hereford	9	S	~12 months	Aged 7 days	LD & ST	Cover *et al*. (1957)
0.39 ± 0.26	PHSC	241	6 *B.i*. and *B.t*. sire breeds	34	?	?	?	?	DuBose and Cartwright (1967)
0.31 ± 0.08	PHSC	2453	Clay Centre GPE groups	370	S	~280 kg carcass	Common commercial abattoir	LD	Koch *et al*. (1982)
0.09 ± 0.13	REML	682	Clay Centre GPE groups	59	S	13–15 months	2 research labs	LD	Van Vleck *et al*. (1992)
0.65 ± 0.19	REML	555	Clay Centre GPE groups	235	S	385–450 days	L.v. e.s.	LD	Shackelford *et al*. (1994*a*)
0.12 ± 0.08	PHSC	1594	Clay Centre GPE groups	306	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al*. (1995)
0.02 ± 0.06	REML	1431	Clay Centre GPE groups (Group 1 data)	146	S, H	13–15 months	2 research labs—standardised data[D]	LD	Barkhouse *et al*. (1996)
0.27 ± 0.29	REML	237	Clay Centre GPE groups (Group II data)	84	S, B	13–15 months	2 research labs—standardised data[D]	LD	Barkhouse *et al*. (1996)
0.31 ± 0.29	REML	1668	Clay Centre GPE combined groups	147	S, B, H	13–15 months	2 research labs—standardised data[D]	LD	Barkhouse *et al*. (1996)
0.37 ± 0.12	PHSC	888	Clay Centre GPE groups	258	S	426 days/324 kg carcass	L.v. e.s, aged 7 days	LD	Wheeler *et al*. (1996)
0.20 ± 0.16	REML	575	*B.t*. and *B.i*. breeds & crosses	83	S, H	<15 months	L.v. e.s., aged 1 day	LD	O'Connor *et al*. (1997)
0.17 ± 0.15	REML	575	*B.t*. and *B.i*. breeds & crosses	83	S, H	<15 months	L.v. e.s., aged 4 days	LD	O'Connor *et al*. (1997)
0.47 ± 0.20	REML	575	*B.t*. and *B.i*. breeds & crosses	83	S, H	<15 months	L.v. e.s, aged 7 days	LD	O'Connor *et al*. (1997)

Table 9. (Continued)

Heritability	Method	*n*	Breed	No. sires	Sex	Age/wt at slaughter	Processing[A]	Muscle	Source
0.27 ± 0.17	REML	575	*B.t.* and *B.i.* breeds & crosses	83	S, H	<15 months	L.v. e.s, aged 14 days	LD	O'Connor *et al*. (1997)
0.36 ± 0.18	REML	575	*B.t.* and *B.i.* breeds & crosses	83	S, H	<15 months	L.v. e.s., aged 21 days	LD	O'Connor *et al*. (1997)
0.19 ± 0.10	REML	575	*B.t.* and *B.i.* breeds & crosses	83	S, H	<15 months	L.v. e.s., aged 35 days	LD	O'Connor *et al*. (1997)
0.02	REML	1530	*B.t.* and *B.i.* breeds & crosses (low Brahman)[E]	142	S	260–276 kg carcass	Aged 7 days	LD	Crews and Franke (1998)
0.24	REML	1530	*B.t.* and *B.i.* breeds & crosses (mod. Brahman)[E]	142	S	260–276 kg carcass	Aged 7 days	LD	Crews and Franke (1998)
0.36	REML	1530	*B.t.* and *B.i.* breeds & crosses (high Brahman)[E]	142	S	260–276 kg carcass	Aged 7 days	LD	Crews and Franke (1998)
0.58	REML	486	*B.t.* and *B.i.* breeds & crosses (Angus)	121	S	<18 months	Aged 5 days	LD	Elzo *et al*. (1998)
0.17	REML	486	*B.t.* and *B.i.* breeds & crosses (Brahman)	121	S	<18 months	Aged 5 days	LD	Elzo *et al*. (1998)
0.25	REML	486	*B.t.* and *B.i.* breeds & crosses (Angus × Brahman)	121	S	<18 months	Aged 5 days	LD	Elzo *et al*. (1998)
0.43	REML	486	*B.t.* and *B.i.* breeds & crosses (3/4A, 1/4B)	121	S	<18 months	Aged 5 days	LD	Elzo *et al*. (1998)
0.26 ± 0.06	REML	3704	Clay Centre GPE groups	597	S	438 days/550 kg live	Aged 7 days	LD	Splan *et al*. (1998)
Weighted average (*Bos taurus*)[F] 0.21									
Weighted average *(B. indicus* and *B. taurus*)[F] 0.26									
Weighted average (overall)[F] 0.24									
				Calpastatin activity[G]					
0.53 ± 0.15	REML	555	Clay Centre GPE groups	235	S	385–450 days	L.v. e.s.	LD	Shackelford *et al*. (1994*a*)
0.52 ± 0.21	HM3	392	Crossbred *Bos taurus*	18	S,H	463 days/561 kg live	L.v. e.s., aged 1–35 days	LD	Wulf *et al*. (1996)
0.15 ± 0.15	REML	575	*B.t.* and *B.i* .breeds & crosses	83	S,H	<15 months	L.v. e.s., aged 1–35 days	LD	O'Connor *et al*. (1997)
				Myofibrillar fragmentation index[G]					
0.58 ± 0.35	REML	199	Clay Centre GPE groups (Group 1)	81	H	13–15 months	2 research labs—standardised data[D]	LD	Barkhouse *et al*. (1996)
0.17 ± 0.29	REML	237	Clay Centre GPE groups (Group II)	84	S, B	13–15 months	2 research labs—standardised data[D]	LD	Barkhouse *et al*. (1996)
0.19 ± 0.29	REML	436	Clay Centre GPE combined groups	147	S, B, H	13–15 months	2 research labs—standardised data[D]	LD	Barkhouse *et al*. (1996)

[A]Application of processing techniques known to affect meat tenderness (e.g. high or low voltage electrical stimulation, aging of meat) and number of abattoirs used.
[B]Total shear force, weighted by days of aging = 0.006(d1) + 0.072 (d4) + 0.217(d7) +0.324(d14) + 0.169(d21) + 0.213(d35).
[C]Estimates varied depending on cooking method and muscle.
[D]To minimise differences in meat tenderness procedures and locations, data were standardised by dividing by the phenotypic standard deviation associated with the year the record was taken.
[E]Data were classified as high Brahman (50–100% Brahman), moderate Brahman (25–49% Brahman) or low Brahman (0–25% Brahman).
[F]Heritability estimates weighted by number of records contributing to estimate.
[G]Calpstatin activity at 24 h post-slaughter; myofibrillar fragmentation index, a biochemical measure of meat tenderness predicted by absorbance.

Table 10. Published estimates of heritability for subjective measures of eating quality summarised within breed type (*Bos taurus* only or a combined analysis of *Bos taurus* and *Bos indicus* breeds)

PHSC, paternal half-sib intraclass correlation; HM3, Henderson's Method 3; REML, restricted maximum likelihood methods; S, steer; H, heifer; B, bull; LD, *M. longissimus dorsi*, *M. longissimus thoracis* or *M. longissimus lumborum*; ST, *M. semitendinosus*

Heritability	Method	*n*	Breed	No. sires	Sex	Age/wt at slaughter	Processing[A]	Muscle	Source
				*Taste panel tenderness (*Bos taurus *only)*					
0.30	PHSC	298	Shorthorn	?	S	?	?	?	Yao and Hiner (1953)
0.00	PHSC	100	Shorthorn & crossbred	8	?	?	?	LD	Alsmeyer *et al*. (1958)
0.23 ± 0.11	PHSC	646	Hereford × (Angus × Friesian)	46	S, H	467 kg (S)/415 kg live (H)	Research abattoir	LD	Wilson *et al.* (1976)
0.09 ± 0.19	PHSC	218	Friesian	37	S	21–24 months/612 kg live	Slow cooling to avoid cold shortening	LD	More O'Ferrall *et al.* (1989)
0.21 ± 0.08	REML	1599	3 *Bos taurus* composite breeds	227	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1994*b*)
0.08 ± 0.09	HM3	392	Crossbred *Bos taurus*	18	S,H	463 days/561 kg live	L.v. e.s., aged 1–35 days	LD	Wulf *et al.* (1996)
				*Taste panel tenderness (*Bos taurus *and* Bos indicus*)*					
0.28 to 1.19[D]	PHSC	38	F_1B × H and Hereford	9	S	~12 months	Aged 7 days	LD & ST	Cover *et al.* (1957)
0.51	PHSC	90	Brahman	7	?	?	?	LD	Alsmeyer *et al*. (1958)
1.29	PHSC	190	Combined	15	?	?	?	LD	Alsmeyer *et al*. (1958)
0.10 ± 0.13	REML	682	Clay Centre GPE groups	59	S	13–15 months	2 research labs	LD	Van Vleck *et al*. (1992)
0.22 ± 0.08	PHSC	1594	Clay Centre GPE groups	306	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.12 ± 0.09	PHSC	1153	Clay Centre GPE groups	214	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.51 ± 0.18	PHSC	441	Clay Centre GPE groups	92	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.06 ± 0.07	REML	1431	Clay Centre GPE groups (Group I)	146	S, H	13–15 months	2 research labs—standardised data[B]	LD	Barkhouse *et al*. (1996)
0.03 ± 0.28	REML	237	Clay Centre GPE groups (Group II)	84	S, B	13–15 months	2 research labs—standardised data[B]	LD	Barkhouse *et al*. (1996)
0.02 ± 0.28	REML	1668	Clay Centre GPE combined groups	147	S, B, H	13–15 months	2 research labs—standardised data[B]	LD	Barkhouse *et al*. (1996)
0.50 ± 0.12	PHSC	888	Clay Centre GPE groups	258	S	426 days/324 kg carcass	L.v. e.s., aged 7 days	LD	Wheeler *et al.* (1996)
0.31 ± 0.18	REML	575	*B.t.* and *B.i.* breeds & crosses	83	S, H	<15 months	L.v. e.s., aged 1–35 days	LD	O'Connor *et al*. (1997)
0.31 ± 0.08	REML	2386	Clay Centre GPE groups	577	S	438 days/550 kg live	Aged 7 days	LD	Splan *et al.* (1998)
Weighted average (*Bos taurus*)[C] 0.19									
Weighted average (*B. indicus* and *B. taurus*)[C] 0.23									
Weighted average (overall)[C] 0.22									
				*Taste panel juiciness (*Bos taurus *only)*					
0.26 ± 0.11	PHSC	646	Hereford × (Angus × Friesian)	46	S, H	467 kg (S); 415 kg live (H)	Research abattoir	LD	Wilson *et al.* (1976)
0.06 ± 0.19	PHSC	218	Friesian	37	S	21-24 months/612 kg li ve	Slow cooling to avoid cold shortening	LD	More O'Ferrall *et al.* (1989)
0.24 ± 0.08	REML	1599	3 composite breeds	227	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1994*b*)
				*Taste panel juiciness (*Bos taurus *and* Bos indicus*)*					
0.14 ± 0.13	REML	682	Clay Centre GPE groups	59	S	13–15 months	2 research labs	LD	Van Vleck *et al*. (1992)
0.25 ± 0.08	PHSC	1594	Clay Centre GPE groups	306	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.06 ± 0.09	PHSC	1153	Clay Centre GPE groups	214	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)

Table 10. (Continued)

Heritability	Method	*n*	Breed	No. sires	Sex	Age/wt at slaughter	Processing[A]	Muscle	Source
0.70 ± 0.20	PHSC	441	Clay Centre GPE groups	92	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.00 ± 0.05	REML	2386	Clay Centre GPE groups	577	S	438 days/550 kg live	Aged 7 days	LD	Splan *et al.* (1998)
Weighted average (*Bos taurus*)[C]			0.20						
Weighted average (*B. indicus* and *B. taurus*)[C]			0.12						
Weighted average (overall)[C]			0.14						
			*Taste panel flavour (*Bos taurus *only)*						
–0.06 ± 0.06	PHSC	646	Hereford × (Angus × Friesian)	46	S, H	467 kg (S)/415 kg live (H)	Research abattoir	LD	Wilson *et al.* (1976)
0.01 ± 0.18	PHSC	218	Friesian	37	S	21–24 months/612 kg live	Slow cooling to avoid cold shortening	LD	More O'Ferrall *et al.* (1989)
0.06 ± 0.08	REML	1599	3 composite breeds	227	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1994*b*)
0.03 ± 0.07	HM3	392	Crossbred *Bos taurus*	18	S, H	463 days/561 kg live	L.v. e.s., aged 1–35 days	LD	Wulf *et al.* (1996)
			*Taste panel flavour (*Bos taurus *and* Bos indicus*)*						
0.03 ± 0.13	REML	682	Clay Centre GPE groups	59	S	13–15 months	2 research labs	LD	Van Vleck *et al.* (1992)
0.07 ± 0.08	PHSC	1594	Clay Centre GPE groups	306	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.08 ± 0.09	PHSC	1153	Clay Centre GPE groups	214	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.04 ± 0.15	PHSC	441	Clay Centre GPE groups	92	S	438 days/550 kg live	Aged 9 days	LD	Gregory *et al.* (1995)
0.19 ± 0.11	PHSC	888	Clay Centre GPE groups	258	S	426 days/324 kg carcass	L.v. e.s., aged 7 days	LD	Wheeler *et al.* (1996)
0.04 ± 0.06	REML	2386	Clay Centre GPE groups	577	S	438 days/550 kg live	Aged 7 days	LD	Splan *et al.* (1998)
Weighted average (*Bos taurus*)[C]			0.02						
Weighted average (*B. indicus* and *B. taurus*)[C]			0.07						
Weighted average (overall)[C]			0.06						

[A]Application of processing techniques known to affect meat tenderness (e.g. high or low voltage electrical stimulation, aging of meat) and number of abattoirs used.
[B]To minimise differences in meat tenderness procedures and locations, data were standardised by dividing by the phenotypic standard deviation associated with the year the record was taken.
[C]Heritability estimates weighted by number of records contributing to estimate.
[D]Estimates varied depending on cooking method and muscle.

described above for estimation of genetic variation for the trait. Very few studies attempted to control or describe processing conditions under which meat samples for tenderness measurements were collected. Similarly, very few studies were based on animals that were close to slaughter ages typical of most Australian production systems. Hence, published estimates of genetic correlations between beef tenderness and other traits should be treated conservatively in the design of breeding programs applicable to Australian systems.

Marshall (1994) reviewed the literature and suggested that genetic correlations between Warner Bratzler shear force values and other carcass traits were either favourable or close to zero, suggesting that selection for beef tenderness would be compatible with selection for improvement in most other carcass traits. This conclusion was supported by Wulf *et al*. (1996), who reported that very few antagonistic genetic relationships existed between production/carcass traits and beef palatability traits. Published estimates of genetic correlations between carcass weight and Warner Bratzler shear force values are generally negative (favourable) but most have large standard errors. Some estimates include an average estimate from 2 studies of 0.00 (Marshall 1994); –0.10 ± 0.37 (Gregory *et al*. 1995); –0.47 ± 0.39 (Wheeler *et al*. 1996); and estimates ranging from –0.09 to +0.06 depending on breed grouping (Elzo *et al*. 1998).

There are even fewer estimates of genetic correlations between retail beef yield percentage and Warner Bratzler shear force values and standard errors of those estimates are also high. Estimates based on the striploin (*M. longissimus dorsi*) include an average estimate from 2 studies of –0.16 (Marshall 1994); 0.22 ± 0.26 (Gregory *et al*. 1994*b*); and 0 ± 0.28 (Gregory *et al*. 1995).

Relationship between marbling and tenderness

Marbling scores are regularly included in beef grading schemes as putative indicators of beef tenderness. The putative relationship between marbling and beef tenderness is reinforced by crossbreeding studies that clearly show that *Bos indicus* breeds, which have low marbling scores relative to British breeds, also tend to have tougher meat. However, Dikeman (1987) reviewed the literature to examine this relationship and reported that marbling accounted for only 5–10% of the variability in beef palatability. Since then, numerous studies have examined the relationships between marbling and tenderness, at both the genetic and phenotypic level, as part of an ongoing debate about the role of marbling in meat grading schemes.

At the phenotypic level, Jones *et al*. (1991) reported that degree of marbling had no effect on initial or overall tenderness, flavour intensity or desirability, but steaks with slight or greater marbling levels were juicier ($P<0.05$) than those with traces of marbling. The percentage of unacceptable ratings for steaks, based on overall palatability, declined from 38.5% for traces of marbling to 23.7% for modest marbling levels.

Shackelford *et al*. (1994*b*) conducted one of the largest studies on the relationship between marbling score and beef tenderness, based on 1602 carcasses from 9 pure breeds and 3 composite populations finished on medium- and high-energy diets. Although their report indicated statistically significant effects of marbling on objective and sensory tenderness scores, marbling score accounted for less than 10% of the variation in shear force value and sensory tenderness, juiciness and beef flavour intensity scores (simple correlation coefficients between these attributes being –0.32, 0.26, 0.26 and 0.10 respectively). It was concluded that, although degree of marbling accounted for only a low percentage of the variation in tenderness, it did provide a slight assurance of tenderness, juiciness and flavour.

Wheeler *et al*. (1994) reported small, positive associations between marbling score and palatability in beef from both *Bos taurus* and *Bos indicus* breeds. Shear force, taste panel tenderness rating and taste panel juiciness rating improved slightly and variation in shear force values decreased slightly as marbling increased in beef from both *Bos taurus* and *Bos indicus*. However, marbling explained, at most, 5% of the variation in palatability traits. There was a large range in tenderness within each marbling score, indicating there could be a large amount of both tough and tender beef within each score.

Estimates of genetic correlations between marbling (or intramuscular fat percentage) and Warner Bratzler shear force values of the striploin (*M. longissimus dorsi*) include an average of –0.25 from 2 studies (Marshall 1994); –1.00 ± 0.45 in crossbred populations (Gregory *et al*. 1994*b*); –0.57 ± 0.16 (Shackelford *et al*. 1994*a*); –1.00 ± 0.48 in crossbred populations (Gregory *et al*. 1995); estimates ranging from –0.16 ± 0.58 to –1.09 ± 0.58, depending on length of post mortem aging (Wulf *et al*. 1996); –0.55 ± 0.22 (Wheeler *et al*. 1996); estimates ranging from –0.12 ± 0.45 to +0.63 ± 0.53, depending on length of post mortem aging (O'Connor *et al*. 1997); and estimates ranging from –0.06 to –0.24, depending on the breed grouping (Elzo *et al*. 1998). In general, phenotypic correlations were closer to zero than genetic correlations in most studies.

Genetic relationships between marbling and beef tenderness for most cattle breeds may not apply in the case of Japanese Black (Wagyu) cattle. Nishimura *et al*. (1999) reported that the development of adipose tissues in *M. longissimus dorsi* disorganised the structure of the intramuscular connective tissue and contributed to tenderisation of highly marbled beef from Japanese Black cattle during the late fattening period. The authors concluded this tenderisation effect would apply only to breeds of cattle capable of depositing large amounts of intramuscular fat (at least 8%, which corresponds to a beef marbling score of ≥2 in Japanese quality grades).

Mitochondrial inheritance of production traits

Most genes are found in the nucleus of an animal's cell. However, a small number of genes are located in the cell mitochondria. Mitochondrial DNA is transmitted exclusively through dam lines and mitochondrial inheritance has been proposed as a possible source of additional genetic variation, in several reports in the literature. Mitochondrial maternal effect, defined as an effect of dam on offspring performance, additional to the direct additive, maternal and permanent environmental contributions and the nuclear maternal effect, may have both a genetic and environmental origin. Nuclear and cytoplasmic sources have been proposed as genetic causes and it is desirable that these causes are separated or properly accounted for in genetic evaluation procedures, because even small contributions of mitochondrial inheritance to total genetic variation may confer substantial differences in performance between maternal lines. A positive mitochondrial effect is desirable for dams of cows, but not relevant for dams of sires, because such effects are not passed on by male progeny.

In literature reports, 2 approaches have been taken to identify the magnitude of mitochondrial effects on production of beef and dairy cattle. The first method uses a statistical approach to analyse performance data, with cytoplasmic and nuclear effects included in the statistical model. The second approach identifies mitochondrial displacement loop variations using molecular techniques, then statistically relates these variations to phenotypic data.

Several early reports supported the hypothesis that cytoplasmic genetic effects exist and impact on production traits. These studies used similar statistical techniques, but as indicated by Tess *et al*. (1987), the methods did not account for all nuclear additive effects and confounding of nuclear and cytoplasmic genetic effects could not be eliminated as a source of error in these analyses. Simulation studies by Kennedy (1986) showed that unaccounted additive genetic effects produced spurious cytoplasmic genetic effects.

Gibson *et al*. (1997) reviewed published estimates of the mitochondrial contribution to genetic variation of production traits in dairy and beef cattle. They reported that analyses which used appropriate statistical models indicated significant effects on milk fat concentration in 2 studies in Holstein cows but not in 2 other studies, and no significant effect was found for growth and lactation traits in 2 beef cattle studies. They concluded that the evidence is broadly consistent with 0–5% of variation in performance being due to cytoplasmic effects, with the weight of evidence pointing to the low end of this range. The authors suggested that at the upper end of the range, cytoplasmic effects could be of practical importance to cattle breeding.

Since that review, Raaber and Essl (1996) reported that cytoplasmic lineage accounted for 0–8% of the phenotypic variance of 8 dairy traits, 6 reproductive traits and 22 growth and reproductive traits in Simmental cattle. Effects on dairy and reproductive traits were never statistically significant. Significant effects were detected for lean percentage of the carcass, percentage of valuable cuts and chest depth.

The alternative approach of using mitochondrial displacement loop variations to detect cytoplasmic effects is not designed to provide independent evidence of mitochondrial contributions to genetic variance. Rather, it attempts to identify specific mitochondrial genetic variants with effects on performance that can subsequently be investigated in independent populations.

Mannen *et al*. (1998) used this approach to examine relationships between carcass traits and mitochondrial displacement loop variations in Japanese Black fattening steers. Carcass weight, *M. longissimus* muscle area, rib thickness, subcutaneous fat thickness, yield estimate and beef marbling score were compared between 5 mitochondrial types using BLUP procedures. Significant differences between mitochondrial types were detected for *M. longissimus* muscle area and beef marbling score. Significant ($P<0.05$) differences were observed between mitochondrial types 2 and 4 for *M. longissimus* muscle area. There was a highly significant ($P<0.01$) difference of 0.97 units in beef marbling score between types 2 and 4 and also a significant ($P<0.05$) difference between types 1 and 4. Given that beef marbling scores ranged from 0 to 5, with an average of 1.59, a difference of 0.97 units was a substantial effect. Type 4 animals were also reported to have better 'beef quality' than the other types, although 'beef quality' was not defined. These results suggest that cytoplasmic genetic effects are important sources of variation for carcass traits in Japanese Black cattle.

Some studies that examined relationships between yield traits and mitochondrial DNA mutations in cattle indicated problems with interpretation of results (e.g. Boettcher *et al*. 1996) because a number of significant results occur by chance alone. The number of significant differences detected in the Mannen *et al*. (1998) study was about equal to the values that were expected by chance. However, the significant differences were restricted to *M. longissimus* muscle area and beef marbling score, and the extent of the differences, measured by the additive genetic standard deviations (0.557 for beef marbling score and 4.23 for *M. longissimus* muscle area), were considerable, suggesting that the haplotype of mitochondria affected only those measurements.

Since publication of these results, an attempt to confirm them using additional carcass data and mixed model methods for variance component estimation was attempted (H. Mannen pers. comm.). More than 20000 individual records were used, but the statistical analysis failed to detect an effect of mitochondrial inheritance on these traits. Suggested reasons for the lack of significance included: (i) the dataset included large numbers of farms with few animals per farm (2–5 individuals/farm) and this may have

introduced imbalance; (ii) in the published study, average slaughter age was 24.1 (s.e. = ± 0.1) months, whilst in the larger dataset, the average age was 31 months (very large standard error) and trait means were substantially different; and (iii) many additional fixed and random effects were included in the statistical model because of complex field data and these factors may have reduced the detection power of the analysis (H. Mannen pers. comm.).

Gibson *et al*. (1997) acknowledged that many studies would have difficulty detecting all but very large mitochondrial effects, and hence the possibility still exists that substantial mitochondrial effects do occur for some traits.

Single gene effects on carcass and beef quality attributes

Although many meat quality traits have generally been assumed to be under the control of multiple genes, there is considerable evidence that single genes account for a relatively large amount of variation for some traits. A gene can be defined as a major gene when the difference in performance between any 2 genotypes for a particular trait is equal or superior to 1 phenotypic standard deviation of the trait of interest.

Major genes that affect carcass and meat quality attributes in pigs and sheep include: (i) the gene for porcine stress syndrome that results in pale, soft exudative meat and affects pork quality and quantity (Rempel *et al*. 1993); (ii) the RN-gene (Le Roy *et al*. 1990) that results in reduced yield, meat protein content and ultimate pH in pork; (iii) a major gene for intramuscular fat in pigs that doubles levels of intramuscular fat in animals with 2 copies of the gene compared with heterozygotes or non-carriers of the gene (Janss *et al*. 1994); (iv) a major gene for androstenone level, a cause of the 'boar taint' problem in meat from entire pigs (Fouilloux *et al*. 1997); and (v) the callipyge gene in sheep (Cockett *et al*. 1993) that has major effects on body composition, including meat yield and fatness traits at multiple fat depots, and a highly significant detrimental effect on meat tenderness (Koohmaraie *et al*. 1995).

In cattle, a double muscle syndrome caused by a single gene also significantly affects most beef production traits, including carcass and beef quality attributes (see review of Arthur 1995). The highest frequency of occurrence of the gene is found in the Piedmontese and Belgian Blue breeds. The syndrome is characterised by a generalised hypertrophy or hyperplasia of muscles, a reduction in adipose tissue and a reduction in weight of the skeleton. Double-muscled cattle therefore have higher dressing percentages and beef yields, less inter- and intramuscular fat and a higher muscle:bone ratio than normal cattle. Shahin and Berg (1985) reported that muscles most affected by the syndrome were the high-priced muscles, with muscular hypertrophy more marked in hindlimbs than in forelimbs. Most recent reports indicate that beef from double-muscled animals is more tender and also leaner and slightly paler than that of normal cattle (Arthur 1995). However, because the syndrome is associated with production problems such as reduced fertility, dystocia, low calf viability and increased stress susceptibility (Ménissier 1982; Arthur *et al*. 1988), use of planned breeding strategies to overcome these problems will be essential if carrier animals are to be used to improve beef yield and tenderness.

Double-muscling in cattle is believed to be under the control of a single autosomal gene with modifier genes affecting its phenotypic expression (Hanset and Michaux 1985). The autosomal recessive *mh* locus causing double-muscling in Belgian Blue and Piedmontese cattle maps to bovine chromosome 2 within the same interval as myostatin, a member of the transforming growth factor β (TGF-β) family of genes (Charlier *et al.* 1995). The bovine myostatin gene has recently been mapped to the same interval as the *mh* locus by genetic linkage (Smith *et al*. 1997), strongly suggesting that it is the gene causing double-muscling in cattle. Further studies have shown that the *mh* allele involves mutation within the myostatin gene and that myostatin is a negative regulator of muscle growth in both cattle and mice (Grobet *et al*. 1997; Kambadur *et al.* 1997). Use of mice as models for identification of genes that affect performance in cattle demonstrates the value of comparative mapping across species. Identification of myostatin as the gene causing the double-muscle phenotype will encourage development of diagnostic tests to facilitate selection either for or against double-muscling in cattle. As well, identification of the myostatin gene as a key regulator of muscle development will allow study of upstream and downstream factors (such as the myostatin receptor) that might lead to the identification of other genes underlying genetic variation for muscle development in livestock (Grobet *et al*. 1997).

Single genes that affect carcass and meat quality attributes provide opportunities for livestock breeders to increase meat quantity and, in some cases, improve meat quality. With appropriate breeding programs, animals that carry major genes which affect carcass and meat quality attributes also provide opportunities to decrease product variability and to exploit differentiation required for specific markets.

Screening populations for major gene segregation

Phenotypic data derived from pedigreed herds can be analysed to detect segregation of major genes. This approach is useful for screening populations to identify potential family material for further studies aimed at more accurate detection and location of genetic markers (see following section). Maximum likelihood methods were used by Hoeschele (1988), Knott *et al.* (1991*a,* 1991*b*) and Hofer and Kennedy (1993) to calculate genotype probabilities and estimate polygenic breeding values for simple pedigree

structures. An alternative, iterative approach to calculating genotype probabilities (Van Arendonk *et al*. 1989; Janss *et al*. 1994) can also be used, together with a mixed-model regression procedure, to account for the effects of polygenes under any pedigree structure (Kinghorn *et al*. 1993). This approach was used by Kerr *et al*. (1994) to identify a major gene for resistance to cattle ticks in British breeds of cattle. Both the maximum likelihood methods and the iterative regression method can lead to estimates of genotype effects and gene frequencies for the population, as well as genotype probabilities and estimated breeding values for all individuals (Kinghorn *et al*. 1994). However, results may be somewhat biased if significant selection has occurred for the trait being analysed (Kinghorn *et al*. 1994), and are difficult to interpret in cases where many phenotypes are missing (e.g. carcass attributes or sex-limited traits.)

More recently, Monte Carlo analysis techniques have been used in segregation analysis. For example, a new MCMC method, based upon the linear model widely used for the genetic evaluation of many species of domesticated livestock, has been developed. Janss *et al.* (1994) used this approach to identify a major gene for intramuscular fat in pigs.

The methods described in this section do not make use of genetic markers and seem unlikely to detect genes reliably with an effect of less than about 0.5 of a phenotypic standard deviation, even with favourable combinations of population size, population structure and polygenic variation (Kinghorn *et al*. 1994). However, they are useful tools to identify individuals and families that warrant closer scrutiny via test matings and use of genetic marker technologies.

Quantitative trait loci and marker-assisted selection

Quantitative trait loci (QTL) comprise 1 or more genes whose allelic variation contributes to a proportion of the variation in a quantitative trait in a particular population (family, herd or breed). The position of a QTL is defined relative to unique flanking markers on a specific chromosome. Genetic markers are indicators of the different forms of genes (alleles) responsible for genetic variation in a population. Development of genetic markers requires identification of the genes responsible for individual differences for a particular trait. This has been facilitated in cattle by development of genetic maps (e.g. Barendse *et al*. 1994; Bishop *et al*. 1994). Genetic markers can be used to systematically search the genome for QTL that are segregating in a population.

As suggested by Cunningham (1999), the eventual goal of livestock genome scientists is to produce sufficiently dense genetic linkage maps to assist in the search for both major genes and the QTL that contribute to the variation observed for traits of economic importance. The major weakness in achieving this goal is likely to be the amount of recorded (phenotypic) data available and the appropriateness of the pedigree structure to allow detection and validation of major genes and QTL. Linkage maps and information about marker associations with QTL will be used to develop strategies for marker-assisted selection (MAS) through inclusion of marker information in livestock genetic evaluation schemes. The theoretical framework underlying MAS was first developed during the 1970s and 1980s (Soller and Beckmann 1983). However, MAS only became a possibility during the 1990s with the development of livestock genetic linkage maps based on highly polymorphic microsatellite DNA markers. The current status of the genome maps for a range of species (from Cunningham 1999) is summarised in Table 11.

Genetic markers for carcass and beef quality attributes

Carcass and meat quality attributes are becoming increasingly economically important to livestock breeders. However, genetic evaluation for these attributes in breeding animals is generally difficult and expensive. Use of real-time ultrasound scanning for eye muscle area and fat thickness as a predictor of saleable beef yield is an effective tool for genetic evaluation of carcass quantity in young animals (Perkins *et al*. 1992; Robinson *et al*. 1993; Bergen *et al*. 1996; Moser *et al*. 1998). Ultrasonography is also potentially useful for genetic evaluation of intramuscular fat (marbling) in young animals, particularly in heifers or steer half-sibs (Wilson *et al*. 1998). Other than ultrasonography, the only tool currently available to livestock breeders to genetically evaluate carcass and beef quality attributes is progeny testing, a long-term and expensive option. The development of MAS could potentially allow direct evaluation of breeding animals for these traits and significantly reduce the time needed for evaluation. Preliminary data from genome-wide screening of DNA markers have revealed a number of putative QTL associated with carcass and beef quality characteristics, although few results have been published to date.

A summary of reports presented at a Beef Genomics Workshop in Texas in 1997 (http://www.beef.org/library/research/genomcov.htm) indicated that several studies had been successful in identifying economically important genes and many of the genes were detected in more than 1 study. The chromosomal locations of at least 5 genes influencing beef tenderness and another 4 genes influencing marbling have now been identified, although some caution must be expressed in statements regarding specific genes that have been identified. Due to the statistical effects of fitting many genetic markers, magnitudes of QTL effects can often be overestimated. As well, in general, QTL for easy-to-measure traits have higher levels of statistical significance than the more difficult-to-measure traits, because an accurate measure of the phenotype is essential for accurate identification of associations between performance and genetic markers.

Table 11. Current status of genome maps in various species (adapted from Cunningham 1999)

bp, base pairs; cM, centimorgans

Species	Haploid chromosome number	Approx. size of haploid genome (bp)	Genetic markers mapped	Coverage of genome	Average marker density	Relevant internet resources, links and references	World-wide-web URLs
Human	23	3.1×10^9	>15,000	~95%	~199 kb	The Genome Database	http://bdbwww.gdb.org/
Homo sapiens			~4000 type I	3699 cM	~0.2 cM	MIT Institute for Genome Research	http://www-genome.wi.mit.edu/
Mouse	20	2.3×10^9	>14,000	~100%	~165 kb	Mouse Genome Informatics	http://www.informatics.jax.org/
Mus domesticus			~3500 type I	1361 cM	~0.1 cM	The Genome Database	http://gdbwww.gdb.org/
Cattle	30	$\sim 3.1 \times 10^9$	>870	~90%	~3.1 Mb	Cattle Genome Mapping Project	http://sol.marc.usda.gov/genome/cattle/cattle.html
Bos taurus			~300 type I	2513 cM	~2.9 cM	BovMaP Cattle Gene Mapping	http://www.ri.bbsrc.ac.uk/bovmap/bovmap.html
Bos indicus						Cattle Genome Database	http://spinal.tag.csiro.au/
Sheep	27	$\sim 3 \times 10^9$	>250	~75%	~9 Mb	AgResearch SheepMap Database	http://dirk.invermay.cri.nz/
Ovis aries			~50 type I	2070 cM	~8.3 cM	SheepBASE (USDA)	http://tetra.gig.usda.gov:8400/sheepbase/manager.html
Pig	19	2.8×10^9	>700	~90%	~3.6 Mb	US Pig Gene Mapping	http://www.public.iastate.edu/~pigmap/pigmap.html
Sus scrofa			~125 type I	1997 cM	~2.9 cM	Swine Genome Mapping Project	http://sol.marc.usda.gov/genome/swine/swine.html
Chicken	39	1.2×10^9	>600	~90%	~1.8 Mb	US Poultry Gene Mapping	http://poultry.mph.msu.edu/
Gallus domesticus			~80 type I	2500 cM	~4.2 cM	ChickMAP	http://www.ri.bbsrc.ac.uk/chickmap
Horse	32	$\sim 3 \times 10^9$	>300	~85%	~10.8 Mb	US Davis Horse Genetics	http://www.vgl.ucdavis.edu/~lvmillon
Equus caballus			~50 type I	3000 cM	~10 cM	Horsemap (Roslin Institute)	http://www.ri.bbsrc.ac.uk/horsemap
Salmon	30	$\sim 3 \times 10^9$	>250	~100%	~21.4 Mb	SalMap Norwegian Veterinary	http://www.veths/no/
Salmo salar					~20 cM	College, Oslo	

Specific details from gene marker studies have, in general, not been published in the scientific literature owing to commercial sensitivity. However, summaries of public domain information from a number of large, specifically designed experiments are outlined below.

Hetzel *et al*. (1997) and Hetzel and Davis (1999) reported outcomes from 3 large half-sib families of about 200 progeny per sire that were bred from F_1 Charolais × Brahman bulls mated to unrelated dams derived from a tropically adapted composite breed. Experimental animals were bred at the National Cattle Breeding Station, 'Belmont', near Rockhampton in Queensland and finished at pasture at Brigalow Research Station and 'Duckponds' in Central Queensland. They were slaughtered at about 3 years of age. Details of the family design, measurements and genotyping can be found in Hetzel *et al*. (1997). More than 100 QTL associated with variation in growth, carcass and beef quality were detected after a complete analysis of data derived from the project (Hetzel and Davis 1999). Each QTL was localised on a chromosome with respect to flanking satellite markers. Table 12, from Hetzel *et al*. (1997) shows the size of effects of some of the QTL and their genetic standard deviations for carcass and beef quality attributes. Main project outcomes (Hetzel and Davis 1999) included:

(i) *Growth.* An average of 4.1 QTL per growth trait were detected, with a range of 3–6. The QTL were located on 8 different chromosomes, with a concentration on 5 chromosomes (5, 6, 14, 19 and 21). Sizes of effect ranged from 0.5 to 1.6 standard deviations with a relatively high frequency of large QTL in excess of 1 standard deviation. The QTL detected allow selection for combinations of early and late growth and thereby bending of the growth curve.

Table 12. Size of effects of quantitative trait loci (QTL) detected for carcass and meat quality traits (source: Hetzel *et al*. 1997)

Carcass and meat traits	Herd mean	Estimated QTL effect	
		Actual units	Genetic standard deviation units
Carcass weight	268 kg	9	1.5
Dressing percentage	50.5%	1.5	1.0
Predicted saleable beef yield	196 kg	8	1.1
Eye muscle area	69.8 cm^2	6.5	0.9
Marbling score	1.2 units	0.4	1.1
Peak force	5.8 kg	0.4	1.1
Rump fat depth	10.5 mm	2.5	0.8
Subcutaneous fat colour (*M. longissimus dorsi*)	16.0 units	2.5	1.4
Tenderness index (*M. semitendinosus*)[A]	8.4 units	0.6	1.0

[A]Tenderness index values ranged from 0, extremely tender to 15, extremely tough.

(ii) *Retail yield.* On average, 3 QTL per beef yield trait were detected. The effects were generally smaller than for growth, being in the range of 0.5–0.7 standard deviations and accounting for <30% of phenotypic variance within sires. A large QTL of almost 1 standard deviation was found for carcass value.

(iii) *Fatness traits.* These were analysed for sexes separately and also pooled because of differences in both means and variances. Using this approach, an additional QTL was detected in females for rib fat and for marbling in males. Some of the estimated QTL had effects of >1.5 standard deviations. Because the distribution of marbling scores was binary rather than normal, the estimated sizes were likely to be biased upwards. Different QTL were observed in each sex for both rib and rump fat. Similarly the QTL detected for marbling and intramuscular fat percentage were on different chromosomes. By contrast, the intramuscular fat percentage and moisture loss (in *M. longissimus dorsi*) QTL were in the same region.

(iv) *Beef tenderness.* An average of 2.2 QTL were detected per tenderness trait. Sizes of the effect generally ranged from 0.5 to 0.8 standard deviations, accounting for up to 25% of phenotypic variance. QTL for beef tenderness traits in either *M. longissimus dorsi* or *M. semitendinosus* were often in the same chromosomal region. However there was little commonality in QTL location between the 2 muscles.

(v) *Meat and fat colour.* The number of QTL detected for meat and fat colour traits averaged only 1.2, suggesting that variation in these traits was more influenced by non-genetic factors. There were no QTL regions in common between meat and fat colour. Because of the non-normal distribution of some fat colour traits, sizes of effect could not be accurately estimated.

(vi) The effects of different carcass and beef quality traits were distributed throughout the genome, with a concentration on chromosomes 5, 6 and 14.

Several experimental herds have also been established in the USA to detect genetic markers for carcass and beef quality attributes. At the Angleton Research Station in Texas, an experiment was designed in which F_1 Angus × Brahman dams were mated to purebred Angus and Brahman sires using multiple ovulation and embryo transfer to produce full-sib families of 3/4 Angus, 1/4 Brahman or 3/4 Brahman, 1/4 Angus breeding. In total, 32 families with an average of 20 progeny per sire were produced. The breeds were selected on the basis of known differences in marbling and tenderness. Progeny were finished in a feedlot and slaughtered at about 20 months of age (Taylor and Davis 1997). A total of 325 markers were scored in the Angleton families. The markers were located on all 29 autosomes and on the X and Y sex-determining chromosomes. A number of possible QTL were identified for several traits, including 5 genes that appear to affect marbling and an additional 7 genes that influence either tenderness as assessed by Warner Bratzler shear force or sensory taste panel. Additionally, the project identified 5 QTL effects on rib eye area and 5 QTL for dressing percentage. One QTL effect that was detected appeared to influence post-weaning growth independent of birth weight variation. This QTL maps to the same chromosome (bovine chromosome 2) that was identified to contain the myostatin gene, which causes double muscling (Green *et al*. 1999).

At the US Meat Animal Research Centre (MARC) in Nebraska, genomic screens for QTL affecting carcass traits are being conducted on 4 half-sib families. Brahman × Angus, Brahman × Hereford, Piedmontese × Angus or Belgian Blue × MARC III composite sires were mated to MARC III composite cows and slaughter data collected on the offspring (Stone 1997). An initial study analysed the double-muscling locus (*mh*) by evaluating the effect of one copy of the allele in quarter-blood Belgian Blue or Piedmontese (Casas *et al*. 1998). Subsequent studies have provided compelling evidence for a QTL allele of Brahman origin affecting an increase in rib bone and a decrease in dressing percentage on chromosome 5. Putative QTL at, or just below, the threshold for genome-wide significance included an increase in retail product yield and component traits on chromosomes 2 and 13 and an increase in rib eye area on chromosome 14 (Stone *et al*. 1999). A definitive QTL for beef tenderness, based on offspring from a single Brahman × Hereford bull, was positioned on chromosome 15. Animals inheriting alleles in this region had about 1.5 lb (0.69 kg) Warner Bratzler shear force less than those inheriting Brahman alleles in this area in beef that had been aged for 14 days (Keele *et al*. 1999). However, the QTL interacted significantly with slaughter group. The QTL explained 26% of the phenotypic variance for 1 slaughter group but was not significant for 3 others. The authors concluded that the sensitivity of the QTL effect to environmental factors may complicate utilisation of markers for genetic improvement of meat tenderness (Keele *et al*. 1999). Other studies at MARC failed to demonstrate a relationship between markers for calpastatin and beef tenderness (Lonergan *et al*. 1995).

In Canada, the obese gene was hypothesised as a candidate gene for fat characteristics in beef cattle (Fitzsimmons *et al*. 1998). The BM 1500 microsatellite near the obese gene was characterised in 158 purebred beef bulls for which carcass trait information was available. Angus, Charolais, Hereford and Simmental breeds were included in the study. The carcass traits rib fat percentage, rib lean percentage, average fat and grade fat were found to be significantly associated with the different alleles. The presence of the 138-bp allele in the genotype was correlated with higher levels of fat, whereas the 147-bp allele had the opposite effect (Fitzsimmons *et al*. 1998).

Evidence to date clearly shows that genetic markers can be used to identify specific chromosomal regions where genes constituting QTL are located. However, it is likely that the linkage phases identified from 1 particular set of families may not be relevant to other family (or breed) populations. This means that the QTL detected using linkage analysis may be difficult to exploit beyond the research population. Before commercial use, markers must be validated in independent populations and ideally, the genes themselves identified and cloned to provide direct tests for the genes of interest.

MAS has the potential to greatly improve the genetic component of beef carcass merit, but a substantial amount of variation in beef quality is also due to environment, and this component will not respond to DNA technology. Use of genetic markers and MAS will not replace current animal breeding practices, but rather will add to them using program design and genetic evaluation methods that cover both known and unknown QTL.

Use of marker-assisted selection in breeding programs

Both direct and linked markers can be used in MAS programs that also use other pedigree and phenotypic information for the genetic evaluation of animals. A number of simulation studies have compared traditional selection programs to those incorporating some combination of marker and phenotypic information. Davis and DeNise (1998) summarised the factors that influence the rate of genetic change in these simulated studies, as shown in Table 13. Strategies using both marker and phenotypic information were always superior to phenotypic selection alone in early generations. However, the magnitude of superiority was dependent on the number of generations of selection, the population size and structure, the number of markers and the heritability of the trait and magnitude of QTL effect. MAS was most efficient in large populations in early generations of selection and when selection occurred before measurement of the trait (see Table 13). Efficiency of MAS was also related to the degree of difficulty of measuring the trait, with efficiency increasing for more difficult-to-measure traits such as carcass and meat quality attributes, efficiency of feed utilisation and resistance to diseases and parasites that affect production or quality attributes. As heritability increases, the increase in response owing to the incorporation of marker information is reduced relative to selection on breeding value estimated from phenotypic data alone (Davis and DeNise 1998). Gibson (1994) and Garrick (1997) used simulation to predict response to selection in a population in which a QTL and linked markers were segregating. In both studies, response was greater through selection on the marker in the early generations of selection. In the long term though, response was greatest through selection on EBV, ignoring the marker

Table 13. Factors influencing the rate of genetic change in simulated marker-assisted selection programs (source: Davis and DeNise 1998)

QTL, quantitative trait loci

Factor	Effect	Cause	Reference
Population size	Greatest change in large populations	Large population sizes result in accurate estimate of QTL effects	Lande and Thompson (1990); Zhang and Smith (1993); Gimelfarb and Lande (1994); Whittaker *et al*. (1995)
Amount of linkage disequilibrium	Greatest change with maximum disequilibrium	All markers are informative	Lande and Thompson (1990); Zhang and Smith (1992, 1993); Gimelfarb and Lande (1994)
Generations of selection	Most effective in the early generations of selection linkage	Recombination reduces disequilibrium	Zhang and Smith (1992); Gimelfarb and Lande (1994); Whittaker *et al*. (1995)
Heritability	Efficiency decreases with increasing heritability	Phenotypes become better predictors of genotype as heritability increases, thus markers provide little information when heritability is high	Lande and Thompson (1990); Zhang and Smith (1992, 1993); Gimelfarb and Lande (1994); Whittaker *et al*. (1995); Meuwissen and Goddard (1996)
Number of markers	Optimum number required for optimum response	Too few markers and the power to detect an effect is low, too many result in low significance levels for any one marker	Zhang and Smith (1992, 1993); Gimelfarb and Lande (1994)
Size of QTL effects	QTL accounting for a substantial amount of the genetic variation contribution to genetic gain	QTL with large effects improve accuracy of selection	Whittaker *et al*. (1995); Meuwissen and Goddard (1996)
Sex-limited traits	Efficiency of selection is improved	Improved accuracy of selection	Lande and Thompson (1990); Meuwissen and Goddard (1996)
Records available after selection	Efficiency of selection is improved	More information is included in the estimate	Meuwissen and Goddard (1996)
Selection for chromosomal segments	Selection for large segments of chromosomes is more effective than individual markers	It is more effective to select for large segments of chromosomes instead of estimating recombination events	Gimelfarb and Lande (1994); Whittaker *et al*. (1995)

information. Both authors ascribed this to the reduced selection pressure on residual polygenic effects in the animals with the favoured QTL allele. The models used for these simulation studies were simplistic because they assumed a large, single perfect marker effect for a trait that was easily measured before selection. Discrete generations were assumed and both authors examined only a single tier of population structure. Henshall and Goddard (1997) examined response to MAS under a more realistic scenario of overlapping generations and a multi-tiered population structure, estimating the polygenic breeding value and QTL effect simultaneously in an animal model BLUP analysis. They found that MAS gave greater response than breeding value selection alone following 20 years of selection.

Future developments and recommendations

Differences between breeds for carcass and beef quality attributes are well documented in the scientific literature and, in general, there would be little justification for additional research in this area. An exception to this generality is an ongoing need to describe the carcass and beef quality attributes of some tropically adapted indigenous breeds in Africa and South America, to determine their potential role as partial or complete replacements for *Bos indicus* genotypes in harsh production environments where resistance of cattle to environmental stressors is paramount, but where market specifications demand tender and palatable beef.

Based on previous studies, differences between breeds are significant and large for most carcass and beef quality characteristics, including beef tenderness, although between-breed differences for sensory juiciness and flavour are not important. On the other hand, effects of heterosis on carcass and beef quality attributes are relatively small, after effects of heterosis on weight are removed. Commercial beef producers can readily capitalise on the significant benefits that crossbreeding provides with respect to carcass quantity and composition. For characteristics such as beef tenderness and palatability, selection of the appropriate breeds for use in a crossbreeding system should allow exploitation of significant between-breed differences.

Within breeds, reports from the literature suggest that most carcass composition traits are at least moderately heritable, indicating that significant genetic progress could be made through use of within-breed selection. The position with respect to beef tenderness is less clear. Early estimates of heritability of Warner Bratzler shear force values indicated tenderness was moderately to highly heritable. More recent estimates using larger data sets and more discriminatory methods of analysis indicate that beef tenderness is lowly heritable in *Bos taurus* breeds and moderately heritable in *Bos indicus* and *Bos indicus*-derived breeds. Low correlations between tenderness in different muscles, low to moderate heritabilities and inconsistent variation within and between breeds for some tenderness attributes suggest that within-breed selection to improve tenderness may be difficult. In addition, there are currently too few estimates of the nature and magnitude of relationships between different carcass and beef quality attributes, particularly for tropically adapted cattle reared in tropical and subtropical environments. Preliminary estimates of some of these relationships indicate antagonisms exist between some of these traits. Such antagonisms could only be accommodated through use of multiple trait selection indices, which still need to be developed for application in commercial production systems. As well, the nature and magnitude of relationships between carcass and beef quality attributes and other production traits such as female fertility remain very poorly defined.

In the short to medium term, increasingly dense bovine genome maps will facilitate practical application of marker-assisted selection for major genes and QTL for carcass and beef quality characteristics. In the medium to longer term, development of diagnostic tests will be required for more accurate MAS applications, either through within-breed selection or introgression of economically important genes from one breed grouping to another. There are clear potential genetic benefits to beef producers from the ongoing developments in the molecular genetics field, but producers need to recognise that molecular technologies are unlikely to replace traditional genetic evaluations. Rather, the molecular tools, in conjunction with crossbreeding and within-breed selection, will increase the accuracy and rate of genetic progress.

In the medium to longer term, a greatly enhanced biological understanding of the mode of action of major genes is likely to provide considerable extra value to beef producers. Knowledge of the mode of action of genes for particular attributes, and their associated effects on phenotype, could lead to increased efficiency of animal production through both genetic and non-genetic means. For example, knowledge of the mode of action of genes may allow development of alternative management, pharmaceutical or nutritional regimes for animals to optimise production. As well, knowledge of the mode of inheritance of genes will allow better understanding of genetic correlations between traits.

To improve the consistency of eating quality of beef, it is highly likely that multiple genetic and non-genetic strategies will be needed. Selection of breeds and animals within breeds using both quantitative and molecular genetic tools, nutritional strategies that optimise growth pathways, animal handling on farm and pre-slaughter, and post-mortem processing technologies all represent potential methods to improve eating quality of beef. A value-based marketing system that rewards beef producers, processors and retailers for implementation of such strategies will be the economic driver needed to guarantee the quality of Australian beef in future.

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