Genetics of Meat Quality

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Introduction

Historically, cattle production systems and breeding programmes have often been dictated by cow herd constraints (e.g. dairy production, climate, availability of production resources) rather than consumer preferences for beef product quality. Meat traits were not routinely included in industry genetic evaluation programmes, because of the difficulty in obtaining measurements and the assumption that meat traits were of less importance to economic efficiency than growth or reproduction. More recently, the cattle industries of many countries are under increasing pressure to improve consumer qualities of beef products with regard to meat palatability, diet/health concerns and product convenience. At the same time, increasing competition from the pork and poultry industries have forced cattle producers to seek new methods of improving the cost efficiency of meat production. Consequently, there is currently much interest in the potential for genetic manipulation of such traits and the associated impact on other production parameters.

In this chapter, meat quality is broadly defined to include body composition traits, technological (chemical and physical) attributes and sensory characteristics (visual appeal and eating quality). Cattle breeders have long assumed that body composition traits are generally quite heritable, whereas genetic control of technological and sensory attributes of beef has not been thoroughly studied until recently. In order to design appropriate breeding programmes to produce desirable beef products at a competitive cost, cattle breeders need genetic information, such as heritability, genetic correlations and breed differences. The aim of this chapter is to summarize current knowledge of genetic aspects of meat quality and to discuss potential implications of genetic change for the cattle industry.

Genetic Parameters and Selection Implications

Heritability of meat traits

A survey of the research literature indicated that scientists, like the cattle industry, have recently placed increased emphasis on eating qualities of beef. Previous reviews of genetic parameters in cattle meat traits (Renand, 1988; Koots *et al.*, 1994a, b; Marshall, 1994) included many estimates for carcass composition traits, but relatively few estimates for technological or sensory quality traits. Several very recent studies have included genetic parameters for traits more directly related to the physical appearance and eating quality of beef.

Carcass composition is often measured at or adjusted to constant age, weight or fatness, and each trait–end-point combination could be considered a separate trait. Heritability estimates for commonly measured composition traits are presented in Table 21.1 separately for different end-points when end-point could be determined from the research publication. Included are values averaged across studies from the review of Koots *et al.* (1994a) and from studies reported after that review. Heritability estimates for objective measures of technological quality and for subjective evaluations of sensory traits are shown in Tables 21.2 and 21.3, respectively.

Carcass composition traits are sufficiently heritable for improvement through genetic selection to be relatively effective in many cattle populations.

Table 21.1. Heritability (h^2) estimates of cattle carcass composition traits.

Trait*	Review estimates† (mean h^2)	Recent estimates‡		
		Mean h^2	(n)§	Range
Lean yield (A)	0.47	0.50	(11)	0.26–0.76
Lean yield (W)	0.48			
Lean yield (F)		0.76	(1)	
Carcass weight (A)	0.23	0.35	(11)	0.15–0.59
Carcass weight (F)	0.36	0.10	(1)	
Dressing % (A)	0.39	0.26	(6)	0.06–0.40
Dressing % (W)	0.38			
Dressing % (F)		0.21	(1)	
Fat thickness (A)	0.44	0.39	(11)	0.25–0.56
Fat thickness (W)	0.46			
Kidney or kidney, pelvic and heart (KPH) fat (A)		0.34	(5)	0.28–0.43
Lean %	0.55	0.71	(1)	
Longissimus muscle area (A)	0.42	0.37	(12)	0.06–0.65
Longissimus muscle area (W)	0.41			
Longissimus muscle area (F)		0.45	(2)	0.38–0.52
Fat trim weight (A)		0.32	(1)	
Fat trim % (A)		0.49	(3)	0.35–0.59
Veal carcass fleshiness		0.31	(1)	
Retail product weight (A)		0.41	(3)	0.28–0.50
Bone weight (A)		0.39	(1)	
Bone % (A)		0.37	(3)	0.21–0.47
Rib thickness (A)		0.32	(3)	0.26–0.41
Lean/bone ratio (A)	0.63			
Marbling score (A)	0.38	0.49	(15)	0.19–0.79
Marbling score (F)	0.65	0.32	(3)	0.18–0.52
Marbling score (W)	0.36			

*Letter in parentheses indicates that the trait was evaluated at a constant age or days in feedlot (A), animal or carcass weight (W) or fat thickness (F).
†Source: review of Koots *et al.*, 1994a.
‡Sources: Van Veldhuizen *et al.*, 1991; Johnston *et al.*, 1992a; Mukai *et al.*, 1993; Robinson *et al.*, 1993; Gregory *et al.*, 1994b, 1995; Renand *et al.*, 1994; Shackelford *et al.*, 1994b; Mukai *et al.*, 1995; Aass, 1996; Hirooka *et al.*, 1996; Wheeler *et al.*, 1996, 1997; Wulf *et al.*, 1996; AAA, 1997; Anderson, 1997; ASA, 1997; O'Connor *et al.*, 1997; Kim *et al.*, 1998; Lee *et al.*, 1998; Splan *et al.*, 1998.
§Number of estimates included in the mean.

Intramuscular fat content (usually evaluated in the longissimus dorsi muscle) is often subjectively evaluated by visual inspection of a cross-section of the muscle (i.e. marbling score, Table 21.1), and in some studies has been measured objectively by chemical analysis (i.e. intramuscular lipid percentage, Table 21.2). Both measures indicate that intramuscular fat content is highly heritable. Shear force and myofibrillar fragmentation index are physical and biochemical measures of tenderness, respectively, whereas calpastatin is an inhibitor of the calcium-dependent proteases involved in the enzymatic degradation of myofibrillar proteins during post-mortem storage (ageing). Each of these

Table 21.2. Heritability (h^2) estimates of technological quality traits of beef.

Trait	Review estimates* (mean h^2)	Recent estimates† Mean h^2	(n)‡	Range
Intramuscular lipid %	0.26	0.54	(6)	0.26–0.93
Shear force	0.30	0.25	(10)	0.02–0.53
Calpastatin activity		0.43	(4)	0.15–0.65
Myofibrillar fragmentation		0.39	(3)	0.17–0.58
Lean colour reflectance	0.26			
L*a*b lightness		0.29	(1)	0.27–0.30
L*a*b redness		0.17	(1)	0.16–0.17
L*a*b yellowness		0.11	(1)	0.08–0.13
Ultimate pH	0.26	0.15	(3)	0.10–0.19
Water loss	0.24			

*Adapted from the reviews of Renand, 1988; Koots *et al.*, 1994a.
†Sources: Gregory *et al.*, 1994b, 1995; Renand *et al.*, 1994; Shackelford *et al.*, 1994b; Aass, 1996; Barkhouse *et al.*, 1996; Wheeler *et al.*, 1996; Wulf *et al.*, 1996; O'Connor *et al.*, 1997.
‡Number of studies. In studies reporting more than one estimate from the same animals, all estimates were used in the range, but only the within-study mean was used to calculate the across-study mean.

Table 21.3. Heritability (h^2) estimates of subjective sensory traits.*

Trait	Mean h^2	(n)†	Range
Lean firmness	0.30	(2)	0.29–0.30
Lean texture	0.14	(1)	
Lean texture and firmness	0.28	(1)	
Lean colour	0.16	(2)	0.12–0.19
Lean colour and gloss	0.24	(1)	
Veal colour	0.16	(1)	
Fat colour	0.00	(1)	
Fat colour, gloss, and quality	0.16	(1)	
Tenderness	0.22	(12)	0.03–0.50
Juiciness	0.14	(7)	0.00–0.26
Flavour intensity	0.10	(9)	0.00–0.43
Flavour desirability	0.01	(1)	
Overall acceptability	0.04	(1)	

*Sources: Dinkel and Busch, 1973; Wilson *et al.*, 1976; Oikawa and Kyan, 1986; More O'Ferrall *et al.*, 1989; Dijkstra *et al.*, 1990; Van Veldhuizen *et al.*, 1991; Van Vleck *et al.*, 1992; Gregory *et al.*, 1994b, 1995; Shackelford *et al.*, 1994b; Barkhouse *et al.*, 1996; Wheeler *et al.*, 1996; Wulf *et al.*, 1996; O'Connor *et al.*, 1997; Kim *et al.*, 1998; Splan *et al.*, 1998.
†Number of studies.

objective indicators of tenderness, based on a limited number of studies, seems to be more heritable than subjective tenderness evaluated by sensory panellists. Other technological quality traits (water-binding capacity, pH and lean colour) appear to be slightly to moderately heritable. Subjective sensory traits appear to be considerably less heritable than carcass composition traits.

Genetic correlations with meat traits

Genetic correlations are important to consider in multiple-trait selection and in the design of breeding systems, because selection for one trait can cause a response in other traits. Genetic antagonisms tend to slow the rate of improvement or even cause undesirable change in some traits. When genetic antagonisms exist between dam traits and market calf traits, then terminal breeding systems offer a potential advantage. On an industry-wide basis, terminal systems could allow seedstock breeders to focus on fewer traits within a given breed, increasing the rate of change per trait.

Body composition

Genetic correlations among body composition traits are presented in Table 21.4. The genetic relationships of marbling score with fat thickness and lean yield are of particular interest, because in many markets these variables are important criteria in the determination of carcass price. Traditionally, it has been assumed that higher marbling scores were genetically associated with increased external fat and decreased lean yield, both within and between breeds, and the average genetic correlations found by Koots *et al.* (1994b) agree with that view. Recent estimates have generally ranged from moderately antagonistic to slightly favourable, suggesting that external fatness and

Table 21.4. Average values of genetic correlations (r_g) among carcass weight and composition traits.

Trait 1	Trait 2	Review estimates* (mean r_g)	Recent estimates† Mean r_g	(n)‡	Range
Carcass weight§	Lean yield	0.00	–0.06	(6)	–0.19 to 0.19
	Dressing percentage	0.04			
	Fat thickness	0.29	0.23	(7)	–0.01 to 0.39
	Longissimus muscle area	0.48	0.41	(7)	0.23 to 0.66
	Marbling score	0.25	0.09	(8)	–0.05 to 0.36
Dressing percentage	Longissimus muscle area	0.36	0.18	(1)	
	Marbling score	0.25	0.24	(2)	–0.20 to 0.68
Lean yield	Fat thickness	–0.56	–0.77	(6)	–0.86 to –0.62
	Longissimus muscle area	0.45	0.63	(5)	0.32 to 0.79
	Marbling score	–0.25	–0.19	(8)	–0.60 to 0.12
Fat thickness	Longissimus muscle area	0.01	–0.17	(7)	–0.43 to 0.01
	Marbling score	0.35	0.09	(9)	–0.12 to 0.44
Longissimus muscle area	Marbling score	–0.21	0.01	(10)	–0.40 to 0.49

*Source: Koots *et al.*, 1994b.

†Sources: Johnston *et al.*, 1992a; Van Vleck *et al.*, 1992; Gregory *et al.*, 1994b, 1995; Mukai *et al.*, 1995; Aass, 1996; Hirooka *et al.*, 1996; Moriya *et al.*, 1996; Wheeler *et al.*, 1996, 1997; Wulf *et al.*, 1996; AAA, 1997; Anderson, 1997; ASA, 1997; Kim *et al.*, 1998.

‡Number of estimates.

§Carcass weight adjusted to a common age or number of days in feedlot.

marbling are almost genetically independent in some populations. In a study involving a variety of breeds, Koch *et al.* (1982b) predicted that single-trait selection for reduced subcutaneous fat thickness would decrease marbling. Gwartney *et al.* (1996) demonstrated that selection based on expected progeny difference values of Angus bulls could decrease fat thickness while maintaining marbling.

Technological quality

The use of a subjective marbling score as an indicator of intramuscular fat percentage is confirmed by a high genetic correlation (Table 21.5). Fat thickness and lean yield appear to be more closely correlated with actual intramuscular fat percentage (Table 21.5) than with subjective marbling (Table 21.4), based on across-study averages. However, it should be noted that most of the estimates with intramuscular fat percentage were from studies reporting relatively high correlations with marbling, whereas most of the studies reporting low correlations with marbling did not measure intramuscular fat percentage.

Based on average genetic correlation estimates, improvement in shear force would be associated with increased intramuscular fat and decreased calpastatin activity and would have relatively little effect on muscling, ultimate pH or water-holding capacity (Table 21.5). Genetic correlation estimates of shear force with subcutaneous fatness or lean yield have varied considerably across studies, with the mean values indicating slight antagonisms.

Phenotypically, low pH in meat is often associated with pale colour, softness and low water-binding capacity. However, few estimates of genetic correlations for such traits in cattle are available. In contrast to the expected relationship between colour and firmness of lean, Shackelford *et al.* (1994a) reported a slight genetic tendency for darker meat to be softer and a moderate tendency for darker meat to be more coarsely textured. Renand (1985) reported genetic correlations of near zero among shear force, pH and water loss. Based on Hunter-L*a*b colour values, Aass (1996) reported that lower ultimate pH of meat was moderately genetically associated with increased degree of redness and yellowness, but was relatively unrelated to degree of lightness. Dinkel and Busch (1973) reported that increased desirability of lean colour score (pink = desirable versus dark red = undesirable) was slightly genetically associated with increased marbling and lower firmness scores and that increased marbling was moderately associated with increased firmness. Oikawa and Kyan (1986) found that higher (more desirable) scores for lean colour quality (Japanese system) were genetically associated with improved scores for marbling, quality of lean texture and firmness and quality and colour of fat. Several relatively large genetic correlations of carcass composition traits with meat colour have been reported (Dinkel and Busch, 1973; Oikawa and Kyan, 1986; Aass, 1996), although the numbers of estimates have been too small to make generalizations. The review of Renand (1988) reported relatively weak negative genetic correlations of carcass fatness with colour (reflectance), ultimate pH and water loss.

Table 21.5. Average values of genetic correlations (r_g) with technological quality traits.*

Trait 1	Trait 2	Mean r_g	No. estimates	Range
Intramuscular fat %	Carcass weight	0.32	2	0.26 to 0.38
	Lean yield	–0.47	5	–0.90 to –0.11
	Fat thickness	0.26	3	–0.06 to 0.71
	Longissimus muscle area	–0.10	3	–0.41 to 0.20
	Marbling score	0.81	2	0.65 to 0.96
	Shear force	–0.64	4	–0.93 to –0.05
	Calpastatin activity	–0.34	1	
	Meat colour – lightness†	0.05	1	
	Meat colour – redness†	–0.09	1	
	Meat colour – yellowness†	0.12	1	
	Ultimate meat pH	0.37	1	
Shear force	Carcass weight	–0.19	3	–0.47 to 0.00
	Lean yield	0.18	6	–0.19 to 0.70
	Fat thickness	–0.16	4	–0.40 to 0.33
	Longissimus muscle area	–0.26	5	–0.63 to 0.14
	Marbling score	–0.47	10	–1.00 to 0.28
	Calpastatin activity	0.63	4	0.35 to > 1
	Ultimate meat pH	–0.03	1	
	Water loss	–0.06	1	
Calpastatin activity	Lean yield	0.10	2	–0.25 to 0.44
	Longissimus muscle area	–0.30	1	
	Marbling score	–0.27	3	–0.75 to 0.61
Meat colour – reflectance	Carcass fatness	–0.15	3	
Meat colour – lightness†	Longissimus muscle area	0.92	1	
	Ultimate meat pH	–0.02	1	
	Meat colour – redness†	–0.36	1	
	Meat colour – yellowness†	0.39	1	
Meat colour – redness†	Longissimus muscle area	< –1	1	
	Ultimate meat pH	–0.37	1	
	Meat colour – yellowness†	0.77	1	
Meat colour – yellowness†	Longissimus muscle area	–0.44	1	
	Ultimate meat pH	–0.31	1	
Meat colour desirability‡	Marbling score	0.52	2	0.22 to 0.82
	Firmness of lean ‡	–0.19	1	
	Texture and firmness of lean ‡	0.86	1	
	Colour and quality of fat ‡	0.51	1	
Meat colour darkness§	Softness of lean§	0.19	1	
	Coarseness of lean§	0.60	1	
Colour and quality of fat ‡	Carcass weight	–0.20	1	
	Longissimus muscle area	–0.07	1	
	Marbling score	0.25	1	
	Texture and firmness of lean‡	0.48	1	
Ultimate pH	Dressing percentage	0.65	1	
	Longissimus muscle area	–0.62	1	
	Carcass fatness	–0.23	3	
	Water loss	–0.13	1	
Water loss	Carcass fat percentage	–0.35	1	
	Carcass fatness	–0.16	3	
Increased firmness of lean	Lean yield	0.60	1	
	Longissimus muscle area	0.61	1	
	Fat thickness	–0.34	1	
	Marbling score	0.47	1	
Decreased firmness of lean	Texture of lean	0.52	1	

*Sources: Dinkel and Busch, 1973; Koch *et al.*, 1982b; Renand, 1985, 1988; Oikawa and Kyan, 1986; Van Vleck *et al.*, 1992; Gregory *et al.*, 1994b, 1995; Shackelford *et al.*, 1994b; Aass, 1996; Barkhouse *et al.* 1996; Wheeler *et al.*, 1996, 1997; Wulf *et al.* 1996; O'Connor *et al.* 1997; Kim *et al.*, 1998.

†Colour evaluated by machine (Hunter-L*a*b).

‡Higher subjective scores assigned for increased desirability.

§Higher subjective scores for increased softness (less firm), darker colour or coarser (less fine) texture.

In summary, genetic correlations with technological quality attributes have not been widely studied. Limited evidence suggests that selection for leanness could be slightly antagonistic to water-binding capacity. Effects of selection for leanness on intramuscular fat content could range from negligible to moderately antagonistic. Effects of selection for increased intramuscular fat content or improved shear force on technological quality could range from slightly antagonistic to moderately favourable.

Sensory quality

Flavour intensity, juiciness and tenderness are the most commonly studied sensory traits of beef, and are highly genetically correlated to one another (Table 21.6). The bulk of evidence from sensory-panel evaluation indicates that selection for leanness could be slightly antagonistic to tenderness and juiciness. However, in a study of Charolais bulls, Renand *et al.* (1994) suggested

Table 21.6. Average values of genetic correlations (r_g) with sensory panel traits.*

Trait 1	Trait 2	Mean r_g	No. estimates	Range
Flavour intensity	Carcass weight	0.01	2	–0.12 to 0.13
	Lean yield	–0.06	4	–0.25 to 0.16
	Fat thickness	–0.07	3	–0.62 to 0.31
	Fat trim %	0.04	2	–0.11 to 0.19
	Longissimus muscle area	0.04	3	–0.25 to 0.22
	Marbling score	0.43	6	–0.19 to 1.00
	Intramuscular fat %	0.29	3	–0.14 to 0.48
	Intramuscular fat % (cooked)	0.35	1	
	Shear force	–0.71	5	–1.00 to 0.27
	Calpastatin activity	0.21	1	
Juiciness	Carcass weight	0.03	1	
	Lean yield	–0.26	2	–0.31 to –0.20
	Fat thickness	0.40	2	0.34 to 0.45
	Fat trim %	0.15	1	
	Longissimus muscle area	0.12	2	–0.01 to 0.24
	Marbling score	0.42	4	0.23 to 0.60
	Intramuscular fat %	0.33	3	0.29 to 0.41
	Shear force	–0.78	4	–0.96 to –0.23
	Flavour intensity	0.86	3	0.78 to 1.00
Tenderness	Carcass weight	0.24	2	0.15 to 0.32
	Lean yield	–0.19	4	–0.48 to 0.03
	Fat thickness	0.10	4	–0.14 to 0.30
	Fat trim %	0.20	2	–0.07 to 0.46
	Longissimus muscle area	0.21	4	–0.25 to 0.56
	Marbling score	0.38	9	0.00 to 0.90
	Intramuscular fat %	0.30	3	0.06 to 0.50
	Intramuscular fat % (cooked)	0.36	1	
	Shear force	–0.86	9	–1.00 to –0.64
	Calpastatin activity	–0.70	3	< –1.00 to 0.00
	Flavour intensity	0.86	5	0.63 to 1.00
	Juiciness	0.79	4	0.43 to 0.95

*Sources: Renand, 1988; Van Vleck *et al.*, 1992; Gregory *et al.*, 1994b, 1995; Barkhouse *et al.*, 1996; Wheeler *et al.*, 1996, 1997; Wulf *et al.*, 1996; O'Connor *et al.*, 1997; Kim *et al.*, 1998.

that selection for leanness would favourably affect tenderness, because of increased collagen solubility and proportion of white-type muscle fibres, even though intramuscular lipid content would be reduced. The genetic association between subcutaneous fat thickness and flavour intensity has been somewhat variable across studies, with the average estimate approximating zero. Longissimus muscle area is apparently not closely associated with flavour intensity or juiciness, although its genetic correlations with sensory tenderness have ranged from slightly negative to moderately positive. Genetic correlations of intramuscular fatness with flavour intensity and tenderness have ranged from slightly negative to moderately or highly positive. Recent estimates of the genetic correlation between intramuscular fatness and juiciness have been moderately positive, although Wilson *et al.* (1976) reported a value of −0.81 for marbling with juiciness (phenotypic correlation was 0.21). Myofibrillar fragmentation index and calpastatin activity might be genetically correlated to sensory tenderness, but have not been widely studied. Shear force appears to be highly genetically correlated to sensory quality, and seems to be the best indicator of genetic potential for sensory quality among all carcass composition or technological quality traits of beef that have been evaluated to date.

Reproduction and growth

The ease with which a cow maintains body condition may be important for her to begin cycling early after calving, at least in some environments. Therefore, there is concern among producers that selection for leanness could be antagonistic to cow rebreeding performance. Very little information exists regarding within-population genetic correlations between reproductive traits in the cow herd and carcass traits of market calves. The study of MacNeil *et al.* (1984) suggested that selection for reduced external fatness in steers could be associated with delayed puberty and reduced fertility in female relatives. In the study of Splan *et al.* (1998), heifer age at puberty was not genetically associated with subcutaneous fat depth or marbling score in steer relatives. Heifer calving rate was favourably associated with increased marbling, but unfavourably associated with increased leanness of steers. The impact on reproductive traits from genetic changes in body composition could be reduced through the use of terminal matings (Bennett and Williams, 1994).

Carcass external fat thickness is positively genetically correlated with live animal growth during pre- and postweaning (Koots *et al.*, 1994b; Marshall, 1994) and with age-adjusted carcass weight (Table 21.4). However, age-adjusted carcass weight appears to be unrelated to lean yield (Table 21.4). Thus, within-population selection for growth could be expected to increase carcass weight at a given age, with a corresponding increase in weight of both fat and lean. Renand *et al.* (1994) found that index selection for growth and improved feed efficiency in Charolais bulls resulted in progeny carcasses with increased lean percentage and decreased fat percentage.

Average genetic correlations with age-adjusted carcass weight were positive for marbling score, percentage intramuscular fat and longissimus muscle area (Tables 21.4 and 21.5). Recent studies indicate that age-adjusted carcass weight is poorly correlated with shear force (Table 21.5) and sensory tenderness (Table 21.6), although Renand (1988) reported moderately antagonistic genetic relationships of growth rate (daily gain or final live weight) with shear force ($r = 0.34$ from three estimates) and sensory tenderness ($r = -0.31$ from two estimates). Shackelford *et al.* (1994b) reported a favourable genetic relationship between postweaning gain and shear force ($r = -0.40$). Genetic correlations of carcass weight with other technological and sensory attributes appear to be quite low, although few estimates are available (Tables 21.5 and 21.6). The review of Renand (1988) reported low genetic correlations for growth rate with lean colour, ultimate pH and water loss. Selection for growth and improved feed efficiency in Charolais resulted in decreased intramuscular lipid content, but had little effect on several other technological measures of meat quality in the longissimus dorsi muscle (Renand *et al.*, 1994). In general, there seems to be little basis for concern regarding genetic antagonisms between growth rate and meat quality within most populations.

Live-animal ultrasound evaluation

Historically, most cattle breeders considered carcass merit to be of lower economic importance than growth or reproductive traits, and assumed that the value of genetic improvement would be relatively low compared with the associated cost. More recently, meat quality has become more of a focal point for the industry, because of the realization that consumers were increasingly choosing alternative foods instead of beef. However, the development of genetic evaluation programmes for carcass traits has been slowed by the difficulty of measuring carcass traits in breeding animals and by the costly nature of progeny testing. Consequently, there has been much interest in the use of ultrasound technology to evaluate meat traits in the live animal, both to facilitate direct measurement on breeding animals and to expand data availability on non-breeding relatives.

In studies in which the average measurement age ranged from about 1 year to 470 days, heritability estimates of ultrasonic measurements have averaged approximately 0.30 (ranged from 0.04 to 0.56) for fat depth and 0.25 (ranged from 0.11 to 0.40) for longissimus muscle area (de Rose *et al.*, 1988; Turner *et al.*, 1990; Arnold *et al.*, 1991; Johnson *et al.*, 1993; Robinson *et al.*, 1993; Nagamine *et al.*, 1996; Shepard *et al.*, 1996; Crump *et al.*, 1998; Graser *et al.*, 1998). Average heritability estimates of live-animal ultrasonic measures of subcutaneous fat depth and longissimus muscle area have been somewhat lower than those based on post-mortem carcass measurement, but sufficiently large to provide for effective genetic evaluation. Although ultrasound technology for evaluation of intramuscular fat is at a more preliminary stage of development, results have been reasonably promising (Izquierdo *et al.*, 1997; Graser *et al.*, 1998; Wilson *et al.*, 1998).

Breeding animals typically are measured at a younger age, are leaner and have less intramuscular fat as compared with non-breeding cohorts. Thus, concern exists regarding whether actual differences in subcutaneous and intramuscular fatness of market progeny can be accurately predicted from estimated breeding values that are based on ultrasonic measurements of breeding animals. Although few estimates of genetic correlations between ultrasonic measures and actual carcass measures are available, a growing body of evidence suggests that ultrasound evaluation of seedstock should be encouraged (Bertrand *et al.*, 1997; Robinson *et al.*, 1998; Wilson *et al.*, 1998). Future comprehensive genetic evaluation programmes for carcass traits will probably be based on a combination of ultrasonic measurements of seedstock and non-breeding animals and post-mortem carcass measurements of market animals.

Heterosis Effects in Breed Crosses

Body composition

Direct heterosis for body composition traits is related to an increased rate of maturing for crossbred animals (Marshall, 1994). At a given age, crossbred animals are generally heavier with increased marbling, fat cover and muscle, whereas overall lean yield is little affected by heterosis (Table 21.7). On a weight-constant basis, heterosis estimates for carcass composition traits tend to be relatively small (Gregory *et al.*, 1978; Drewry *et al.*, 1979; Johnston *et al.*, 1992b).

Technological and sensory quality

Heterosis effects on technological quality or sensory traits of beef have not been widely studied with the exception of shear force. The majority of heterosis estimates for shear force have ranged from moderately favourable to slightly unfavourable (i.e. approximately –10 to 5%) (Winer *et al.*, 1981; Peacock *et al.* 1982; Anderson *et al.*, 1986; Marshall *et al.*, 1987; Gregory *et al.*, 1994a, b), although certain crosses between *Bos taurus* and *Bos indicus* may result in higher levels of favourable heterosis (DeRouen *et al.*, 1992).

Table 21.7. Direct heterosis effects on carcass composition traits (age-constant or time-in-feedlot-constant basis).*

Trait	Heterosis (%)	No. studies
Fat cover	10.1	11
Longissimus muscle area	4.1	9
Lean yield or retail product %	–0.6	7
Marbling	3.8	7

*Values given are from the review of Marshall (1994). Heterosis estimates were averaged across specific crosses within study and across studies, and expressed as a percentage of the straightbred mean.

Non-significant heterosis estimates were reported by Winer *et al.* (1981) and Gregory *et al.* (1994b) for sensory evaluation of juiciness, tenderness and flavour and by Winer *et al.* (1981) for cooked colour and overall desirability.

Major Genes and Quantitative Trait Loci

Although quantitative traits have generally been assumed to be controlled by multiple genes, individual genes may account for a relatively large amount of variation for some traits. The muscle hypertrophy condition known as double muscling has for some time been thought to probably be controlled by a single major gene (Arthur, 1995). This condition has been observed in several breeds, and is predominant in some (e.g. Belgian Blue and Piedmontese). Recent evidence suggests that double muscling in these two breeds is caused by mutation of a gene located on bovine chromosome 2 that produces the protein myostatin (Grobet *et al.*, 1997; Kambadur *et al.*, 1997; Smith *et al.*, 1997). Normally, myostatin serves to repress skeletal muscle growth, but the mutation apparently blocks this effect and permits extra muscle growth. Compared with normal cattle, double-muscled animals generally have an increased proportion of muscle relative to fat and bone, and have reduced organ weights at a given body weight (Hanset, 1981). Carcasses from double-muscled cattle tend to have a higher proportion of 'valuable' meat cuts, and, although results have varied across studies, the tenderness of meat from double-muscled cattle tends to be acceptable and often preferred compared with that of other breeds (Arthur, 1995). A recent study found that animals inheriting a single copy of the muscle hypertrophy (*mh*) allele from a crossbred Belgian Blue or crossbred Piedmontese sire had increased longissimus muscle area and retail yield and reduced external and intramuscular fatness compared to animals receiving no copies of the *mh* allele (Casas *et al.*, 1998).

Currently, breeding animals can be evaluated for carcass composition by ultrasound or progeny testing, whereas sensory trait evaluation is limited to progeny testing only. The development of molecular marker-assisted methods of genetic evaluation could potentially allow direct evaluation of breeding animals and significantly reduce the time needed for evaluation. Preliminary data from genome-wide screening of DNA markers have revealed a number of putative quantitative trait loci (QTLs) associated with meat traits, although few results have been published to date (Hetzel and Davis, 1997; Stone, 1997; Sugimoto, 1997; Taylor and Davis, 1997). Beever *et al.* (1990) reported significant associations of genetic markers with carcass composition traits in a half-sib Angus family. Kim and Marshall (1998) reported a small association of lean yield with a polymorphism in the growth hormone gene. The calpastatin gene (Killefer and Koohmaraie, 1994) has been proposed as a candidate locus for marker-assisted selection, because of the role calpastatin plays in post-mortem tenderness as an inhibitory regulator of the calpain system (Koohmaraie, 1992). Significant associations between beef tenderness and calpastatin genotype, based on restriction fragment length polymorphisms, were detected by Green *et al.* (1996a, b), but not by Lonergan *et al.* (1995).

Breed Variation

Substantial between-breed variation exists for many carcass composition and meat quality characteristics. Thus, it would seem that beef producers could, with relative ease, identify an appropriate breed or blend of breeds to fit their particular market needs. However, the choice of breeds for beef production is often complicated by constraints in the cow herd. For example, much of the beef is produced in dairy herds in some countries. In many non-dairy situations, the breed type of the cow herd must be matched to available resources and environmental constraints of the individual production unit. In either case, the genetic type best suited for cow herd production efficiency might not be optimal for postweaning production or meat traits.

Body composition

Breed differences for body composition traits have been evaluated in numerous studies, and have been reviewed by Renand (1985) and Marshall (1994). Franke (1997) has reviewed carcass composition of subtropically adapted breeds in the USA. A general summary of approximate breed differences in body composition is presented in Table 21.8. It is important to recognize that breed differences and rankings can vary due to such factors as sampling effects, environmental effects and production system (including end-point criteria). Also, the performance of a given breed in crossbreeding can vary due to differences in heterosis, depending on which other breeds are used in the cross.

Several *B. taurus* breeds that rank high for marbling tend to rank low for lean-to-fat ratio and vice versa. In general, *B. indicus* breeds tend to have moderate lean-to-fat ratios and below average marbling, although Boran may be comparable to many *B. taurus* breeds for marbling.

Dairy breeds tend to be quite variable in carcass composition. Holsteins or Friesians are similar to many beef breeds in lean-to-fat ratio and marbling, although they tend to have more bone and thus less muscle per unit of carcass weight as compared with many beef and dual-purpose breeds (El-Hakim *et al.*, 1986; Knapp *et al.*, 1989). Jerseys tend to have lower lean-to-fat ratios and more marbling than most beef breeds. Terminal matings of dairy cows to bulls of breeds with high lean-to-fat ratios have been frequently used as a way to increase the value of meat from dairy herds.

Several of the beef breeds of British origin tend to have low lean-to-fat ratios and relatively high marbling scores. Among breeds originating in central Europe, the dual-purpose breeds tend to rank at or somewhat above average in lean-to-fat ratio, and about average for marbling, whereas several other

Table 21.8. Breed characterization for body composition.*†

Category/breed	Lean-to-fat ratio (age-constant)	Longissimus muscle area/carcass wt	Marbling (age-constant)
British beef			
Angus	– –	–	+ +
Devon	–	=	=
Galloway	=	+	+
Hereford	– –	–	=
Red Angus	– –	–	+ +
Red Poll	– –	=	+
Shorthorn	– –	–	+ +
South Devon	–	=	+
Continental beef			
Belgian Blue	+ + +	+ + +	– –
Blonde d'Aquitaine	+ + +	+ + +	– – –
Charolais	+ +	+ +	–
Chianina	+ + +	+ +	– – –
Limousin	+ +	+ +	– –
Piedmontese	+ + +	+ + +	–
Continental dual-purpose			
Salers	+	+	=/–
Maine Anjou	+	+	=/–
Gelbvieh	+	+	=/–
Pinzgauer	=	=	+
Simmental	+	+	=/–
Tarentaise	=	=	=
Braunvieh	+	+	=
Zebu			
Boran	=	=	–
Brahman	=	–	– –
Nellore	=	–	–
Sahiwal	=	=	– –
Brahman derivative			
Brangus	– –	– –	=
Santa Gertrudis	– –	– –	=
Non-zebu subtropical			
Tuli	=	=	=
Dairy			
Brown Swiss	+	+	=
Holstein	=	–	=
Jersey	– –	–	+ + +
Other			
Texas Longhorn	=	=	=

*Adapted from Renand, 1988; Cundiff, 1992; Marshall, 1994; Wheeler *et al.*, 1996; Franke, 1997; Cundiff *et al.*, 1997.

†Minus signs, equal signs and plus signs, respectively, indicate relatively lower levels, moderate levels and higher levels.

breeds (e.g. Belgian Blue, Piedmontese, Chianina) tend to have very high lean-to-fat ratios and relatively little marbling. Japanese Black, Japanese Brown and Wagyu have relatively high genetic potential for marbling, but a relatively low growth rate.

Technological quality

Homer *et al.* (1997) reported no significant sire breed differences among Limousin, Charolais, Belgian Blue, Piedmontese, Angus and Hereford in pH at 3 or 24 h. In that same study, meat (uncooked) from Angus crosses tended to be darker (colour reflectance) than meat from other breeds. Drip loss from uncooked sirloin steaks tended be slightly less for British crosses, but not significantly so.

Renand (1985) found no sire breed differences between carcasses of young bull progeny of Charolais, Blonde d'Aquitaine, Limousin, Coopelso 93 synthetic (Blonde d'Aquitaine × Charolais × Limousin) and Inra 95 double-muscled synthetic (Blonde d'Aquitaine × Charolais) in ultimate pH or water loss of longissimus dorsi muscle. Liboriussen *et al.* (1977) reported that colour (reflectance) of uncooked muscle was lighter for carcasses of crossbred bull calves from Limousin, Romagnola, Charolais and Blonde d'Aquitaine as compared with Simmental, Hereford, Danish Red and White and Chianina. More O'Ferrall *et al.* (1989) reported that drip loss from longissimus dorsi muscle was greater for carcasses of Charolais-sired progeny as compared with progeny of Friesian, Hereford or Simmental sires (dams were Friesian). Muscle pH was greater for Simmental than for Hereford at 48 h post-mortem, although there were no significant differences in pH at 3 h.

Shear force and sensory quality

Sire breed comparisons from the US Meat Animal Research Center germplasm evaluation (GPE) project for shear force and sensory quality traits are presented in Tables 21.9, 21.10 and 21.11. Different sire breeds have been compared over time in the GPE project, with Angus and Hereford sires used in each 'cycle' as a control. In cycles I, II and III, tenderness differences were quite small among *B. taurus* breeds (Table 21.9). Meat tenderness was slightly reduced for Brahman-sired cattle and significantly reduced for Sahiwal compared with most *B. taurus* breeds. In cycle IV, steaks from calves of Pinzgauer and Piedmontese sires were slightly more tender, whereas steaks from Nellore-sired calves were significantly less tender than average at age (Table 21.10), weight and fat end-points. In cycle V, steaks from the progeny of Belgian Blue, Piedmontese, Angus, Hereford and Tuli were more tender than steaks from progeny of Boran or Brahman (Table 21.11). In all cycles of the GPE project, breed differences for sensory juiciness and flavour were of little practical importance.

Table 21.9. Sire breed comparisons for shear force and sensory quality from cycles I, II and III of the MARC GPE study*.

Category/breed	Shear force (kg)	Tenderness†	Flavour†	Juiciness†
Hereford, Angus	3.3	7.3	7.3	7.3
Red Poll	3.4	7.3	7.4	7.1
South Devon	3.1	7.4	7.3	7.4
Charolais	3.3	7.3	7.4	7.3
Chianina	3.6	6.9	7.3	7.2
Limousin	3.5	6.9	7.4	7.3
Maine Anjou	3.4	7.1	7.3	7.2
Gelbvieh	3.5	6.9	7.4	7.2
Pinzgauer	3.4	7.1	7.4	7.2
Simmental	3.5	6.8	7.3	7.3
Tarentaise	3.7	6.7	7.3	7.0
Brahman	3.8	6.5	7.2	6.9
Sahiwal	4.1	5.8	7.1	7.0
Brown Swiss	3.5	7.2	7.4	7.2
Jersey	3.1	7.4	7.5	7.5

*Age-constant (457, 473 and 445 days for cycles I, II and III, respectively) values. Dam breeds were Angus and Hereford. Sources: Koch *et al.*, 1976, 1979, 1982a; Cundiff, 1992.
†Sensory panel scores: 1 = extremely undesirable to 9 = extremely desirable.
MARC, Meat Animal Research Center.

Table 21.10. Sire breed comparisons for shear force and sensory quality from cycle IV of the MARC GPE study*.

Category/breed	Shear force (kg)	Tenderness†	Flavour intensity†	Juiciness†
Hereford, Angus	5.7	4.7	4.8	5.1
Galloway	5.8	4.8	4.8	5.1
Shorthorn	5.9	4.7	4.8	5.1
Charolais	5.9	4.6	4.8	5.0
Piedmontese	5.4	5.0	4.7	5.1
Salers	6.3	4.5	4.8	5.0
Gelbvieh	5.6	4.7	4.7	5.0
Pinzgauer	5.1	5.1	4.8	5.1
Nellore	7.2	4.0	4.7	4.8
Texas Longhorn	6.1	4.8	4.8	5.1

*Age-constant (426 days) values. Dams were Angus and Hereford. Source: Wheeler *et al.*, 1996.
†Sensory panel scores: 1 = extremely tough, bland, or dry to 8 = extremely tender, intense or juicy.
MARC, Meat Animal Research Center.

Liboriussen *et al.* (1977) reported that sire breed means were similar among Simmental, Charolais, Danish Red and White, Romagnola, Chianina, Hereford, Blonde d'Aquitaine and Limousin for shear force, sensory juiciness and cooked colour. Sensory tenderness and flavour of the semitendinosus muscle were slightly more desirable for Blonde d'Aquitaine and Limousin than for Hereford progeny (other breeds were intermediate), although breed differences were non-significant for the longissimus dorsi muscle. Homer *et al.* (1997) reported no significant sire breed differences among Limousin,

Table 21.11. Breed characterization for shear force and sensory quality from cycle V of the MARC GPE study*.

Category/breed	Shear force (kg)	Tenderness†	Flavour†	Juiciness†
Hereford, Angus	5.4	5.3	4.9	5.3
Belgian Blue	5.9	4.9	4.9	5.0
Piedmontese	5.4	5.0	4.8	5.0
Brahman	7.3	4.0	4.8	4.8
Boran	6.6	4.5	4.8	5.0
Tuli	5.7	5.0	4.9	5.2

*Age-constant (447 days) values. Dams were Angus, Hereford and MARC III composite. Source: Cundiff *et al.*, 1997.
†Sensory panel scores: 1 = extremely tough, bland, or dry to 8 = extremely tender, intense or juicy.
MARC, Meat Animal Research Center.

Charolais, Belgian Blue, Piedmontese, Angus and Hereford for tenderness, juiciness or flavour of sirloin steaks, although roasting joints from Belgian Blue crosses were more tender than those from other sire breed groups. More O'Ferrall *et al.* (1989) reported that shear force was lower for Simmental than for several other sire breeds, although sensory tenderness did not vary significantly across breeds. In that same study, sensory juiciness, flavour desirability and flavour intensity were slightly better for Hereford than for Charolais or Simmental, while overall acceptability was similar across sire breeds.

Skelley *et al.* (1980) reported no difference in subjective lean colour or firmness of steer carcasses from progeny of Holstein, Polled Hereford, Charolais or Simmental sires (cows were Angus), although carcass fat tended to be softer and more yellow for Holstein progeny. Although variation between breeds was not significant for shear force, Hereford crosses had slightly more desirable sensory ratings than Charolais crosses for tenderness, juiciness, flavour intensity and flavour desirability. Knapp *et al.* (1989) found that Holsteins were similar to English and Continental European beef breeds in most palatability traits of cooked beef and had fewer tough steaks than cattle of *B. indicus* breeding. May *et al.* (1993) reported no significant differences between steaks from Wagyu-cross and Angus steers in shear force or sensory palatability traits.

Shackelford *et al.* (1994a) found significant differences among 28 sire lines in subjective colour, texture and firmness of carcass lean, but concluded that genetic variation was small relative to environmental variation in the incidence of the unacceptable dark, firm and dry (DFD) condition. There was some evidence of genetic trend toward darker meat in some breeds. *B. indicus* breeds were similar to most *B. taurus* breeds in subjective colour score of uncooked lean.

Cattle of high percentage *B. indicus* breeding tend to have lower marbling scores at a given age and produce less tender steaks than *B. taurus* breeds (Table 21.8; Peacock *et al.*, 1982; Crouse *et al.*, 1989; DeRouen *et al.*, 1992). Tenderness is often lower for *B. indicus* than for *B. taurus* at the same level of marbling (Koch *et al.*, 1988; Wheeler *et al.*, 1994), suggesting that factors other than marbling account for a significant portion of the tenderness difference. Increased activity of calpastatin in *B. indicus* may account for some of the reduced tenderness (Johnson *et al.*, 1990; Wheeler *et al.*, 1990; Whipple *et al.*, 1990; Shackelford *et al.*, 1991; O'Connor *et al.*, 1997).

Variation in tenderness is significant within as well as across breeds. In cycle IV of the GPE study, Wheeler *et al.* (1996) noted that the mean estimated purebred difference in shear force between the most and least tender breeds (i.e. Pinzgauer and Nellore) corresponded to 4.76 genetic standard deviations, whereas the total range within a breed is approximately 6 genetic standard deviations.

Genetic Effects on Attributes of Fat

A high level of cholesterol in the blood has been identified as a possible risk factor for coronary heart disease in humans. In recent years, health consultants in many countries have encouraged diets with decreased levels of cholesterol and fat and lower ratios of saturated-to-unsaturated fatty acids. Intake of cholesterol and most saturated fatty acids (stearic acid, for one, may be an exception) tends to raise blood cholesterol. Intake of unsaturated fatty acids in lieu of saturated fatty acids may decrease blood cholesterol. Compositional differences in fatty acids may also play a significant role in determining palatability and sensory characteristics of beef. For example, Melton *et al.* (1982) found that desirable flavour of ground beef was associated with increased oleic (C18 : 1) acid in the neutral lipids and with decreased concentrations of C18 : 0 and C18 : 3 in the neutral and polar lipids. Larick *et al.* (1989) suggested that the difference in flavour of longissimus muscle of American bison might be related to a greater proportion of polyunsaturated fatty acids as compared with Hereford or Brahman.

Cholesterol content

Subcutaneous fat clearly has a higher cholesterol content than does longissimus muscle on a wet-weight basis (Eichhorn *et al.*, 1986a, b; Wheeler *et al.*, 1987). Animals with increased subcutaneous fat would, in general, be expected to have more cholesterol in the total carcass. Interestingly, limited evidence suggests that intramuscular fat differences do not have a significant association with cholesterol content in longissimus muscle. Rhee *et al.* (1982) evaluated longissimus muscle steaks from carcasses of eight subjective marbling-score categories, ranging from 'practically devoid' to 'moderately abundant' and found no effect of marbling score on cholesterol content of cooked steaks. Among uncooked steaks, Rhee *et al.* (1982) reported that the only significant difference was that those with 'practically devoid' marbling had significantly less cholesterol than did those of all seven other marbling categories. Wheeler *et al.* (1987) reported that cholesterol content of longissimus muscle did not vary significantly as cattle increased in age, weight and intramuscular fat.

On a within-tissue basis, most studies have found non-significant or relatively small differences between breeds in cholesterol content. Eichhorn *et al.* (1986a) reported that breed type did not significantly affect cholesterol content of the longissimus or triceps brachii muscles in a study of meat from mature cows of 15 breeds and crosses. Wheeler *et al.* (1987) reported no difference between Chianina and British crosses in cholesterol content in the longissimus muscle or subcutaneous fat, even though Chianina had a lower content of ether-extractable fat in the uncooked longissimus muscle and lower serum cholesterol. Baker and Lunt (1990) reported that sire breed did not significantly affect cholesterol content in longissimus muscle tissue, even though total lipid content of muscle tissue was higher in Angus-sired calves than in calves sired by Charolais or Piedmontese. Koch *et al.* (1995) reported that *B. taurus* cattle had a higher content of cholesterol in subcutaneous fat but less in the longissimus muscle as compared with bison (American buffalo) or *B. taurus* × bison hybrids. Rule *et al.* (1997) reported higher cholesterol content of ground carcass (composite of muscle and adipose) tissue in moderate-growth as compared with high-growth steers, a difference which the authors suggested might be attributed to the increased overall fatness of the moderate-growth animals. There was no significant difference between genetic types in cholesterol content of defatted longissimus muscle of steers.

Fatty acid profile

Several studies have reported significant breed effects on fatty acid composition, although breed type has sometimes been confounded with other potential effects, such as age, weight and overall fatness. Evidence suggests that fat depots tend to become more unsaturated as an animal increases in age and/or fatness (Zembayashi and Nishimura, 1996; Malau-Aduli *et al.*, 1997), although these relationships do not hold up consistently across animal types (i.e. sexes and breeds) in various studies. There is evidence that fatty acid composition varies across tissue type or lipid source (Eichhorn *et al.*, 1985; Zembayashi and Nishimura, 1996), which is important because some tissues (e.g. subcutaneous fat) can be removed before eating whereas intramuscular fat is generally consumed.

Sumida *et al.* (1972) reported that breed type (Hereford, Angus and crosses among Hereford, Angus and Charolais steers) did not affect the ratio of total unsaturated to saturated fatty acids and that most breed-type comparisons for proportions of individual fatty acids were also non-significant. Gillis *et al.* (1973) reported that the proportions of several individual fatty acids varied significantly among breeds in both intramuscular and subcutaneous lipid, although the ratios of unsaturated to saturated fatty acids were quite similar across breed types. In a study of meat from mature cows of 15 breeds and crosses, Eichhorn *et al.* (1986a) reported that breed effects on total saturated, unsaturated and polyunsaturated fatty acid proportions were significant for the longissimus muscle and subcutaneous adipose tissue but not for the triceps brachii muscle or perinephric adipose tissue. In total lipid extracts of longissimus muscle, breed-type means ranged from 5.1 to 12.5% for total polyunsaturated fatty acids and from 40.9 to 48.3% for total saturated fatty acids. Mills *et al.* (1992) reported that muscle of Angus–Charolais–Simmental cross steers contained slightly more total saturated fat, including a higher content of stearic acid, than muscle from Holstein steers. Total saturated fat other than stearic acid was similar between muscle of Holsteins and crossbreds.

May *et al.* (1993) reported a higher ratio of monounsaturated to saturated fatty acids in subcutaneous and intramuscular adipose tissue for Wagyu-cross than for Angus steers, although it was unclear whether part of the difference might have been attributable to confounding effects of overall fatness. Zembayashi *et al.* (1995) found that Japanese Black (Wagyu) steers had a higher content of monounsaturated fatty acids in subcutaneous and intramuscular neutral lipids than Holstein, even when adjusting for difference in slaughter age and carcass fatness. Zembayashi and Nishimura (1996) found that dam-breed comparisons of Japanese Black versus F_1 Japanese Black × Holstein were usually non-significant for percentages of individual or group total fatty acids in subcutaneous and intramuscular lipids. The effect of individual sire (only one sire breed was used) was significant for total saturated, polyunsaturated and unsaturated fatty acids in subcutaneous neutral lipid (but not in intramuscular neutral lipid or phospholipid) and for some individual fatty acids in each lipid source, even after removing the effect of carcass fat percentage.

Average fat thickness and fatty acid content of subcutaneous adipose tissue were found to be less, whereas the degree of unsaturation of fatty acids was greater for Brahman than for Hereford both among mature cows (Huerta-Leidenz *et al.*, 1993) and in their male progeny (Huerta-Leidenz *et al.*, 1996). Covariate adjustment for body fatness did not remove the significant breed-type effects for most of the variables in the cow study. Perry *et al.* (1998) reported that subcutaneous fat from Brahman × Hereford steers had a higher proportion of unsaturated fatty acids and a lower melting-point than fat from Hereford, Simmental × Hereford, or Holstein × Hereford, independent of carcass fatness.

A series of recent studies was conducted in Australia to determine genetic effects on fatty acid profiles of beef. Heritability estimates of fatty acids were rather low in weaners, but quite promising in slaughter animals (0.23, 0.57 and 0.15 for total saturated, monounsaturated and polyunsaturated fatty acids, respectively) for the triacylglycerol fraction of adipose tissue (Malau-Aduli *et al.*, 1998). Among feedlot animals of several breed types, ranging from early- (Jersey × Hereford) to late- (Charolais × Simmental × Hereford) maturing, Jersey crosses had the highest concentration of monosaturates and the lowest level of polyunsaturates in intramuscular fat (Siebert *et al.*, 1996). Limousin cows had higher percentages of saturated fatty acids and lower percentages of mono- and polyunsaturated fatty acids than Jersey cows in fat extracted from shoulder muscle, although differences between these two breeds were non-significant among yearling heifers (Malau-Aduli *et al.*, 1997). Comparisons among grass-fed animals were made between calves sired by Angus, Belgian Blue, Hereford, Jersey, Limousin, South Devon and Wagyu bulls mated to Hereford dams (Deland *et al.*, 1998; Siebert *et al.*, 1998). Concentration of monounsaturated fatty acids in longissimus muscle phospholipids and subcutaneous adipose tissue tended to be greatest for calves sired by Wagyu, Jersey and Belgian Blue, and least for calves sired by Angus, Hereford and Limousin. Proportion of total saturated fatty acids was lowest for Wagyu- and highest for Limousin-sired calves in subcutaneous adipose tissue, but did not differ significantly among sire breeds when measured in muscle phospholipids.

Fat colour

In some markets, white fat is preferred to yellow fat. The degree of yellowness is associated with concentration of β-carotene. Death *et al.* (1996) reported that the degree of yellowness was greater in the subcutaneous and intermuscular fats of Hereford × Jersey than Hereford × Friesian heifers. Kruk *et al.* (1998) found that β-carotene concentration and degree of yellowness in subcutaneous fat were higher as the proportion of Jersey relative to Limousin breeding increased. Their preliminary results indicated possible effects of a major gene, because individuals that had extreme values for β-carotene concentration and degree of yellowness of fat were observed among purebred Jersey, $\frac{3}{4}$ Jersey, and F_1 animals, but not among purebred or $\frac{3}{4}$ Limousin animals.

Prospects for Genetic Improvement in Meat Traits

Consumer demand for beef

The beef industry has been forced to give greater attention to consumer issues in response to negative publicity regarding health effects of meats and to increased competition from pork and poultry. General trends in consumer preferences are toward leaner meat products with predictable eating qualities and simple preparation requirements. Health consultants have encouraged diets with decreased levels of cholesterol and fat and lower ratios of saturated-to-unsaturated fatty acids. Consumers are also demanding improved consistency in sensory attributes of cooked beef, with tenderness probably being the most important of these, followed by flavour. The industry is responding by producing leaner animals and by trimming excess fat during processing, although consistency of tenderness remains less than desired.

General trends notwithstanding, consumer preferences remain variable for factors such as leanness, marbling and serving size. Consequently, alternative market categories with different target specifications continue to exist. An important challenge for the cattle industry is to maintain appropriate genetic variability to accommodate variable market demands, while providing improved product consistency within a given market category.

Consistency in eating quality

Excessive genetic variation has often been cited as an important contributor to a lack of consistency in sensory attributes of beef. However, considering that the market does have an array of demand categories to accommodate variable product specifications, it is more important to improve product consistency within a given market category than to reduce variation in general. The use of processing treatments (e.g. post-mortem storage, mechanical tenderization, electrical stimulation, addition of enzymes) has been suggested to improve consistency of palatability, but an accurate method of determining which carcasses need treatment is needed. Genetic improvement in palatability is limited by a lack of cost-effective methods for measurement. Improvement in the industry's ability to accurately classify animals and carcasses into eating quality categories is critically needed.

In some markets, marbling score (intramuscular fatness) has been used as an indicator of eating quality and as a determinant of carcass price, although such use has been controversial. Although intramuscular fat content is associated with consumer desirability of beef, the relationship is too weak to provide consistently accurate classification of carcasses into categories of eating quality (Smith *et al.*, 1987; Wheeler *et al.*, 1994). Higher levels of intramuscular fatness are desirably associated with shear force, calpastatin activity, meat colour, flavour intensity, juiciness and tenderness. Interestingly, estimates of the phenotypic correlations tend to be lower than the corresponding genetic correlations. Thus, it could be concluded that intramuscular fat content is more useful for genetic evaluation than for market classification, at least in populations in which its genetic correlation with lean yield is not significantly antagonistic. A more direct measure of palatability (e.g. shear force), or perhaps a combination of criteria, is needed to properly classify carcasses for market value and would be useful for genetic evaluation as well.

Shear-force evaluation of cooked meat is one of the most heritable traits associated with meat quality, it is closely genetically correlated to sensory attributes, and it has few, if any, genetic antagonisms with other traits. Thus far, routine measurement of shear force has been considered too costly to implement in commercial beef-packing facilities. A potential limitation of shear force, and probably other methods, is that measurement of one muscle might not accurately predict tenderness of other muscles (Shackelford *et al.*, 1995).

Multiple strategies, both genetic and non-genetic, might be needed to improve the consistency of eating quality. Methods to improve average palatability will also improve consistency, because fewer unacceptable products will be produced. Choice of breeds, seedstock selection, animal management and post-mortem treatment all represent potential methods of improving palatability of beef. An improved ability to accurately sort products into palatability categories is critical for enhancing consistency and will improve the effectiveness of genetic evaluation.

Genetic evaluation and improvement

Extensive genetic variation exists between and within cattle breeds for carcass composition and tenderness. Breed preferences tend to vary across regions and market categories because of differences in production systems and consumer demands. Heterosis effects tend to be relatively unimportant for most meat traits. However, crossbreeding has the potential to improve meat traits through complementary mating systems and blending of breeds. For example, Cundiff (1997) noted that certain crosses of Continental European × British inheritance are more likely to provide optimal levels of carcass weight, lean yield and marbling than most single breeds. Similarly, crosses between *B. indicus* and *B. taurus* can provide adaptability to tropical or subtropical climates, while maintaining a higher level of meat tenderness than purebred *B. indicus*. Terminal mating systems with specialized sire and dam lines are recommended when production constraints in the cow herd dictate the use of dam genetic types that are not optimal in terms of meat quality.

Cattle-industry programmes for genetic evaluation, many of which are sponsored by breed organizations, are increasingly expanding to include meat traits. The number of seedstock with estimated breeding values for body composition traits should increase rapidly with the adoption of ultrasound technology. Genetic improvement in these traits could occur relatively rapidly, considering that they are moderately to highly heritable, but this will depend on the intensity with which selection pressure is applied. Selection responses in sensory attributes of beef are expected to occur more slowly, because heritability is lower and evaluation methods are more difficult to implement.

Advances in molecular technology hold promise for genetic evaluation of meat traits, because marker-based selection has the potential to avoid some of the difficulties (e.g. trait measurement, long generation interval) associated with traditional evaluation methods. Results of genome studies in cattle are quite preliminary at present, but useful applications are anticipated in the future. This research should improve our basic knowledge of the underlying regulation of lean : fat deposition and muscle development. Marker-based genetic evaluation could be beneficial for improvement of sensory attributes, which are more costly to measure and less heritable than composition traits. Novel alleles with desirable effects could be introgressed into ‘recipient’ populations.

As the ability to genetically alter carcass merit in cattle populations increases, it is important to consider the effects of such changes on correlated responses in other traits. For most meat traits, relatively few significant genetic antagonisms are obvious when based on across-study averages, although estimates tend to vary considerably across studies. It is uncertain to what extent this across-study variation in genetic correlation estimates reflects sampling errors versus true population differences. In some populations, selection for leanness could have antagonistic effects on intramuscular fat and sensory perception of tenderness, flavour intensity and juiciness. Fortunately, the magnitude of these genetic relationships is not very strong within many breeds, indicating that simultaneous improvement in composition and sensory quality could be possible if selection pressure is exerted on each trait. Selection for carcass merit should be reasonably compatible with increased growth rate in most populations. Perhaps of greater concern, albeit based on limited evidence, is that selection for leanness could be antagonistic to reproductive efficiency. Increased use of terminal mating systems is suggested when it is desirable to maintain a different genetic potential for body composition in the cow herd from that in slaughter progeny.

Conclusions

Appropriate breeding system design, utilization of breed differences and seedstock selection are important if the beef industry is to improve product quality and consistency while maintaining production efficiency. The potential to genetically change lean : fat composition of beef is high, but the potential impact on other traits needs to be considered. Potential improvement of sensory attributes within a breed is currently limited by measurement cost and low heritability, and so the utilization of between breed differences is important. Development of a cost-effective strategy for accurate assessment of sensory attributes of beef would enhance genetic evaluation and improve the consistency with which product quality meets consumer expectations. The development of ultrasound and molecular technologies has the potential to significantly enhance genetic improvement of meat traits.

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