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## Genetic improvement of meat quality in sheep and cattle

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### ABSTRACT

Genetic variations in body composition are apparent as differences among breeds, crosses, selected strains and sire groups. Crossbreeding, use of terminal sires and selection within breeds has tended to concentrate on total meat output rather than quality, despite consistent consumer signals against fat. Evidence suggests that, in males selected using live animal ultrasound measurements of fat and muscle depths, about half of the selection pressure available to improve growth rate should be sacrificed in order to maximise economic response through decrease in carcass fat content.

Genetic variations in lean/fat partitioning to different regions and muscles of the carcass, and in traits affecting the wider sensory appeal of cooked meat, are also important to the range and consistency of meat products. Indirect live animal indicators are vital to minimising the high cost of progeny testing. Meat product tenderness is one example. Much of the variation is under the control of the calpain system for which genetic differences have been found among breeds and crosses, related families, selection lines, and in strains segregating for major genes and genetic markers (e.g. calpastatin and the CSSM18 and TGLA122 markers of the callipyge gene in sheep). Decreased post mortem tenderness is associated with decreased proteolytic enzyme activity which in some cases is related to increased lean growth rates in the live animals as well.

Between and within muscle variations in actin/myosin interactions, lipid, myoglobin contents and solubilities can also give rise to genetic variations in tenderness, meat flavour, colour and the heat gellation properties of myosin. The biochemical basis of these effects suggests useful indicator traits (e.g. LDH and ICDH enzyme activity associations with fibre type, intra-muscular fat and haem iron contents) which are likely to offer innovative genetic solutions to long-term industry competitiveness.

### INTRODUCTION

Meat is eaten to be enjoyed, not just for its nutritional value (Lister 1995). Many of our meat processors and exporters seem reluctant to even accept that they are part of the meal industry, emphasising throughput efficiencies for traditional products (e.g. procurement and processing costs), rather than new convenience foods that satisfy and entertain. It is therefore not surprising that geneticists and breeders have been slow to explore more consumer-oriented notions of quality meat.

Recent reviews (e.g. Dikeman 1990, Kemp 1994, Wood *et al.* 1994), have highlighted the considerable evidence of genetic variation in body composition in livestock. These variations are apparent as differences among breeds and crosses, among selected strains, and in the moderate heritabilities found for carcass composition, even on a percentage or weight-adjusted basis. Industry has a variety of breeding methods for exploiting these variations, notably those based on crossbreeding and making use of terminal sires in crosses with environmentally adapted and reproductively efficient dam breeds. Selection strategies are more suited to longer-term improvement goals, but effects are usually cumulative across several generations.

Indicators of sensory value also show evidence of variations that are both repeatable, to allow control over the consistency of meat products, and heritable (Renand 1995, Wood and Cameron 1994). The genetic relationships of such indicators with one another and with productive efficiency are of particular significance. Firstly, because

there could be some surprising associations – it is unlikely that evolutionary adaptations will have played a significant role in moulding desirable gene combinations affecting the sensory qualities of our meat products. Secondly, because associations with traits affecting the costs of production and processing will influence the economic efficiency of quality meat production.

### Fat content of carcasses and muscles

Breed variation in gross carcass composition has been known for many years, for example, for sheep in this country, as presented by Bennett and Kirton (1983) and Kirton *et al.* (1995, 1996). As judged by the breeds currently predominant on New Zealand farms, this research has had little impact on our sheep industry beyond efforts to exploit average breed differences in growth rate. Although some of the fatter breeds such as the Southdown have declined in popularity and have been improved in terms of their lean growth abilities, little use has been made of breed differences and hybrid vigour by crossbreeding to high lean growth rate terminal sire breeds. McEwan *et al.* (1995) quote evidence that crossbred progeny from terminal sires comprised only 14% of lambs slaughtered in 1993.

Selection methods have also tended to concentrate on total meat output, in part due to the simplicity of recording effort involved and the difficulties of measuring meat composition in the live animal. This attitude has persisted despite consistent market signals against fat (e.g. Waldron *et al.* 1991), highlighted in most current carcass payment and classification schemes, and for which accurate and

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cost-effective live animal evaluation methods are now available (e.g. using ultrasound). Evidence suggests that about half of the selection pressure that is available to improve growth rate should be sacrificed in rams, in order to maximise economic response through reduced carcass fat content (Waldron *et al.* 1992; NZABT 1994). Few New Zealand sheep breeders are making such extreme changes to their immediate selection goals, although some are incorporating leaner fast-growing breeds and strains into their ram-breeding flocks (e.g. Landcorp's Lamb Supreme programme – Nicoll 1995).

For cattle, multivariate predictions based on the extensive within-breed genetic parameters for Charolais cattle of Renand *et al.* (1994), show that selection for improved growth is expected to increase leanness and reduce fat and would also reduce the intermuscular fat content of the longissimus muscle. Furthermore, selection for high lean and low fat simultaneously (i.e. for lean growth rate, or strictly, lean % minus fat %), would reduce by half the gains that could otherwise be achieved in carcass weight-for-age, closely in line with evidence from sheep. Renand (1995) concluded that the contrast between the lean and fat contents of beef carcasses is the major determinant of genetic variability in carcass quality.

In the recently published gene map for the pig (Andersson *et al.* 1994), a chromosome has been identified carrying genes for backfat depth. Further study is likely to reveal other alleles of these genes.

As a consequence of associations with eating characteristics (e.g. texture, tenderness, flavour) there seems to be a real need to consider intra-muscular (marbling) fat independently of total carcass fat in breed improvement programmes (Wood and Cameron 1994, Wood *et al.* 1994). The data of Renand *et al.* (1994) indicate that some degree of genetic independence exists, in cattle ( $rg = 0.66$ ) as well as in pigs (Wood *et al.* 1994). Other evidence has been reviewed by Kemp (1994), who notes an average heritability of 0.4 for marbling score in beef cattle.

Characteristic breed differences in fat partitioning to subcutaneous versus intra-muscular depots have also been found for sheep and cattle (Kemp 1994, Renand *et al.* 1994), as well as for pigs. Fast-growing, lean European 'white' pigs which show low carcass marbling compared to dark-skinned Durocs and the fatter American breeds have been noted by Wood *et al.* (1994), who suggest that breeders should be cautious about making further reductions in marbling below the current low levels of many modern strains (Wood and Cameron 1994). The Duroc's high concentration of marbling relative to backfat is also associated with increased tenderness, juiciness and redness, and the changes in muscle characteristics are suggestive of an increase in the concentration of red oxidative muscle fibres (Wood *et al.* 1994). Such results point to associations of eating qualities with lean as well as with fat, and at the level of individual muscles as well as at the carcass level.

### **Muscle growth and development and muscle fibre physiology**

During the last 15 years many factors affecting the relative rates of protein synthesis and degradation have

been highlighted and indicators of differences between animals revealed in the development of myofibres and muscle mass. In cattle, Picard *et al.* (1995) demonstrated that castration at 4 months of age gave rise after puberty to smaller muscle fibres (lower protein/DNA ratio), a lower proportion of fast-twitch glycolytic fibres and a lower proportion of heavy chain myosin in semitendinosus muscle, suggesting that androgens slow down the effect of age on the metabolic transformation of muscle fibres and modulate the effects of genes encoding myosin isoforms.

Little quantitative genetic information is available on the phases of muscle development and their impact on the growth rates of different muscles. Our analyses of the Renand *et al.* (1994) data for the longissimus muscle of Charolais sires, indicate that fibre size changes (protein/DNA ratio) are more responsive (approximately three-fold) to simultaneous selection for high lean and low carcass fat percentage (i.e. high lean growth rate), than to selection for carcass weight itself.

Also of interest to improvement programmes are the associations between muscle biochemistry and meat quality traits, which have prompted caution in applying breeding programmes focused exclusively on gross measures of growth and development (e.g. Ashmore, 1974; Valin *et al.* 1982). Muscles have different functional properties related to evolutionary requirements for body function, reproduction and survival rather than their eating qualities. To serve these functions they vary greatly within the animal, not only in their fibre and protein properties but also in other, associated compositional characteristics. These variations affect the processing and eating qualities of differentiated meat products based on individual muscles or selected combinations of muscles.

Muscle fibres are commonly classified on the basis of the metabolic pathway from which the fibre derives its high energy phosphate to support its contractile activity (Ashmore 1974). This classification system has also proved useful in reconciling the many varying processing and eating qualities of different muscles, especially for sheep (Ashmore and Vigneron 1988, Valin *et al.* 1982) and their reaction to pre-slaughter management (Monin 1981). The connective tissue contents of different muscles and the degree of collagen cross-linking are also related to their functional requirements and to age (Ashmore and Vigneron 1988).

Variability in the metabolic types of muscle fibres is one of the main factors involved in meat quality differences, arising from their characteristic changes postmortem and affecting their tenderness, juiciness and flavour (Rabat *et al.* 1995). These differences may be estimated from their lactate dehydrogenase (LDH), and isocitrate dehydrogenase (ICDH) or citrate synthetase activities. Cluster analysis of the sheep muscle variations obtained by Briand *et al.* (1981) shows that joint variation in LDH and ICDH activities was highly diagnostic of variations in the metabolic profiles of different muscles.

Vigneron *et al.* (1986) showed that the fibre populations of different muscles differed significantly among breeds. The Romanov showed a lower proportion of fast-twitch white fibres and the Merino d'Arles and

Precoce breeds a high total fibre number in the small scutoauricularis muscle of the ear which they advocate as a good live animal indicator of meat quality variations among animals. High heritabilities of total fibre number and the proportion of fast:slow fibres were found for this muscle. Meat from animals with a higher proportion of red fibres was more juicy and had more flavour than those with a higher proportion of white fibres. Ashmore and Vigneron (1988) also demonstrated high heritabilities of fibre characteristics and indicated that the fibre type composition is associated with several important technological capabilities of meat from different muscles: onset of rigor, evolution of texture, colour conservation, water retention, emulsifying capacity of muscle proteins and their responses to electrical stimulation.

Our recent multivariate predictions based on within-breed genetic parameters for Charolais cattle (Renand *et al.* 1994), show that selection for improved growth should increase leanness, reduce intramuscular fat content of the longissimus muscle, increase ultimate pH and collagen content, reduce the solubility of collagen and increase the oxidative activity and diameter of its muscle fibres. Selection for lean growth rate would be associated with similar changes in ultimate pH but reduced collagen and haem pigment contents of the longissimus, increased collagen solubility and fibre size, as well as greatly enhanced responses in carcass lean content. It would also be genetically associated with increased glycolytic activity of this muscle. The restrictions on carcass growth needed to control concomitant changes in intramuscular fat were minimal and were genetically associated with a metabolic profile towards low LDH and high ICDH activities (i.e. a strong metabolic shift from glycolytic to oxidative fibre types). The proportion of heavy chain myosins would also increase, especially if changes in collagen content were to be avoided as well.

Gonzalez and Pazos (1995) studied beef breed variations in several metabolic indicators of meat quality in longissimus muscles, but failed to detect significant characteristic breed differences. Angus purebred and crossbred muscles had higher haem pigment contents than those of Hereford purebreds and crosses. High LDH activities, typical of muscles high in oxidative fast-twitch fibres were found, higher in Angus than in Hereford. The M4 isoenzyme predominated. ATP-ase activity was also higher in Angus than in Hereford purebreds and crosses, and increased in proportion to the Brahman influence in the cross.

A double-muscling gene has been identified in Belgian Blue cattle (Hanset and Michaux 1985) and possibly the Charolais, Limousin and Simmental breeds as well. The gene markedly increases the percentage of lean (from 58.7% to 70.5%) and reduces the percentage of fat (22.1% to 12.8%) in the 7th rib cut, gives higher proportions of high priced cuts in the hind quarters but is associated with higher calving difficulties (Hanset *et al.* 1987). A marker linked to the gene has been identified (Georges *et al.* 1990).

### Connective tissue and collagen effects

Connective tissue is an integral component of muscle and has an important effect on meat qualities. Collagens

impact on the so-called "background toughness" of meat and are negatively associated with major price differences between different cuts of meat (Kuypers and Kurth 1995). When meat is cooked the collagen fibres contract strongly, forcing water out of the denatured myofibrillar structure, increasing fibre density and shear force. Key enzymes have been identified which affect the cross-linking of collagen molecules characteristic of different collagen types and which vary with animals, and are closely associated with the thermal stability of collagen (Horgan *et al.* 1991). Meat toughness arising from collagen variations can be predicted from the activities of these enzymes (Harper *et al.* 1995), and a number of candidate genes associated with lysyl hydroxylase, lysyl oxidase, prolyl hydroxylase, collagenase (as well as fibrinectin and collagen 2a.1) have been identified.

Some evidence of antagonistic genetic variations have been found (Young *et al.* 1993; Young and Dobbie 1994; Renand *et al.* 1994). Young *et al.* (1993) and Young and Dobbie (1994) showed higher muscle collagen contents in weight-selected lines than in controls but no detectable differences in shear force; high lean growth rate Texel-sired lambs had similar collagen contents and properties to Romney-sired lambs. Kuypers and Kurth (1995) found evidence of weaker associations with collagen following intensive selection for growth of breast muscle in turkeys.

### Tenderness

Glycolytic effects prior to and immediately following slaughter can also give rise to between-animal and within-animal (muscle) variations in tenderness (Shorthose and Harris 1991). Fast glycolysing muscle has lower shear force, faster early rates of ageing to 24 hours, and is more tender. Thus tenderness is promoted by a rapid attainment of a low pH/high temperature condition, which supposedly releases or activates proteolytic enzymes of the lysosome. It is a complex process affected by a large number of interacting factors such as glycolysis, rate of pH decline, osmolarity of muscle cells, temperature and including genetic factors characteristic of different species, breeds, strains and families (Dransfield 1994). Variation in heritability estimates for meat tenderness/shearforce, probably reflects the variety of underlying contributing factors (Kemp, 1994).

Koohmaraie (1992a,b) demonstrated that much of the variation of the rate of postmortem proteolysis can be attributed to the calpain proteolytic system. Calpastatin has been shown to be an important regulator both in vivo and in postmortem muscle. Genetic variations in this system are evident. For example in studies of sheep in which the Callipyge gene is segregating, Kerth *et al.* (1995) found that animal variations in calpastatin were positively associated with 36% of the variation in shear force and negatively associated with 55% (49%) of the variations in initial (sustained) tenderness. For beef cattle, post-rigor calpastatin has been shown to be highly variable among animals, highly heritable (0.65+0.19), to be negatively associated with average daily gain (-0.52) and intramuscular fat content (-0.34), and positively associated with % retail product yield (0.44, Shackelford *et al.* 1994).

### Callipyge gene effects

Shay *et al.* (1995) have confirmed the location of the gene on chromosome 18 of the sheep in the interval spanned by the markers CSSM18 and TGLA122, although some unusual inheritance features suggesting dominant negative imprinting are evident (Cockett *et al.* 1995). The gene became apparent in an American Dorset flock selected with emphasis on leg conformation. It has pronounced effects on muscle development. Animals display increased muscle size in the loin and leg, leaner carcasses, increased feed efficiency, but tougher meat (Carpenter and Solomon, 1995).

Recent evidence confirms earlier reports of higher eye muscle area (30-69%), similar slaughter or carcass weights but higher dressing %, lower carcass fat thickness (24-45%), internal fat weights and muscle marbling scores, reduced lung and liver weights and small intestine mass, more efficient liveweight gain under rapid growth, higher nitrogen balance and utilisation of crude protein, higher serum growth hormone and IGF-1, reduced serum insulin (39%) and IGF-1 under restricted feeding (20%), increased circulating IGF BP-2, higher yield of trimmed cuts and high value cuts from the carcass (by 3-8 percentage points), higher but variable muscle weight advantages from the leg and loin regions (20-42%) but not for slow-twitch muscles in the shoulder (Al-Hassan and Roberts 1995, Brown *et al.* 1995, Goodson *et al.* 1995, Hill *et al.* 1995, Hossner *et al.* 1995, Koochmarai *et al.* 1995, Meyer *et al.* 1995a,b). Meat from Callipyge animals has shown similar pH and temperature declines on ageing, lower muscle fragmentation indices (27-37%) and higher shear force in longissimus and semimembranosus muscles. It responds to electrical stimulation, calcium ion infusions, and to hydrodyne treatment, but the meat tends to be tougher for some muscles and less acceptable in terms of tenderness, flavour and juiciness (Carpenter and Solomon 1995, Khosraviani *et al.* 1995, Koochmarai *et al.* 1995, Meyer 1995, Solomon *et al.* 1995). The animals show higher calpastatin and millicalpain levels but no difference in microcalpain, increased satellite cell proliferation, and suggestions of higher capacity for protein synthesis. Genotype x muscle interactions were found for sensory panel tenderness and connective tissue ratings.

Carpenter and Solomon (1995) showed that ageing decreased the shear force of both normal and Callipyge chops, but not the hypertrophied muscles of beta-adrenergic agonist-treated lambs, which may be due to higher levels of calpastatin. The ageing curves of electrically stimulated and calcium infused Callipyge lambs and untreated normal lambs (the most tender treatments for each genotype) were initially parallel (similar rates of tenderisation), but although tenderisation of the Callipyge lambs continued beyond 15 days they remained tougher. Callipyge lambs had lower sensory scores for texture, flavour and juiciness which may be due to lower fat concentrations. Other observations indicate their muscles have larger fast-twitch fibres, fewer oxidative fibres and higher concentration of protein. Hydrodyne shock wave treatment gave a 40% improvement in tenderness in both groups of lambs.

### Genetic associations with production

For sheep selected over several generations and widely divergent in weaning weight, Oddy *et al.* (1995) demonstrated that genotypic differences in the rates of protein gain were almost exclusively driven by the rate of protein degradation. Evidence from the plasma metabolic profiles of sheep selected for and against lean growth rate also point to genetic variations in protein degradation (Cameron and Cienfuegos-Rivas 1994).

Scheurs *et al.* (1995) report markedly decreased proteolytic capacity of both the calpain and cathepsin enzyme systems in chickens selected for fast growth, while chickens with efficient protein metabolism (FC line) showed intermediate calpain/calpastatin values but increased cathepsin and cystatin activities. Both showed similar rates of pH decline post-mortem to commercial broilers, and all were higher than protein-inefficient Leghorn egg-laying chickens. Leghorns showed higher myofibrillar fragmentation indices and lower shear force values for their breast muscles. The FC line showed lower shear force values than Leghorns and broilers which may need longer ageing times than 24 hours.

Speck and Clarke (unpublished) have shown breed, strain and sire variations in shear force and ultimate (24 hour) pH, and their association with the depth of longissimus muscles in sheep. They have also found higher tenderness in body weight-selected Romney lines compared with their unselected controls. Studies of calpain system enzymes are in progress.

A line of New Zealand Angus cattle selected for yearling body weight under a single (medium) level of feeding (Morris *et al.* 1993; Morris and Cullen 1995), shows no difference in tenderness relative to unselected controls, but there was a 20% lower calpastatin concentration in the weight selected herd (C.A. Morris and P.A. Speck, unpublished). Thus, calpastatin was more closely associated (negatively) with gain than tenderness. Different calpastatin results from the Trangie herd (Australia), selected for gain, suggest that comparisons of calpastatin at different feeding levels should be conducted.

The cellular location of the calpains and calpastatin relative to each other and their *in vivo* regulation, have important implications in the regulation of muscle protein turnover and in variations in eating qualities associated with the conversion of muscle to meat postmortem (Goll *et al.* 1995). These workers propose that mechanisms involving the nature of the actin/myosin interaction are important, especially the proportion of myosin linkages that are in a strong binding state and processes which are responsible for the subsequent weakening of this interaction during ageing. Genetic variations in actin/myosin interactions in post-mortem muscle (such as variations in the amount and type of nucleotide binding) have received little attention to date. They are likely to affect tenderness in animals and in different muscles of the same animal.

Knowledge of the interrelationships between *in vivo* and post-mortem proteolytic effects for muscles of different metabolic types is vital. Firstly, because it is unlikely that evolutionary adaptations have been important in di-

rectly moulding desirable gene frequencies and gene combinations for traits affecting the sensory properties of our meat products. Secondly, because rates of muscle growth and development are of major importance to the economic efficiency of quality meat production.

**Water-holding and gelation properties of meat**

The water-holding capacity of meat (drip loss) affects consumer acceptance and the final weight of product . It is held to be caused by myofibrillar shrinkage which forces fluid into the extracellular spaces and from there to the surface of the meat. Moderate heritabilities have been found for this meat quality trait in cattle (Renand 1995), estimated either directly as drip loss (0.31) or indirectly using a pressure probe (0.15) or butyrometer (0.22).

In pigs, the recessive Halothane gene, also known as the ryanodine receptor gene, increases the rate of glycolysis in muscle during the postmortem period, due to release of calcium ions from mitochondria into the sarcoplasm, causing a rapid reduction in pH and the precipitation of proteins (reduced protein solubility) on the myofibrils. This increases drip loss and the scattering of incident light giving rise to pale soft exudative meat. The condition is part of the porcine stress syndrome, which can result in sudden death and increased susceptibility to poor preslaughter handling. Extreme leanness and ‘enhanced’ body conformation (thicker deeper muscles) are found in homozygous pigs, as exemplified by the Pietrain breed - evidence of an important negative association between meat and carcass qualities (Wood *et al.* 1994). Blood and more recently ryanodine receptor markers and now DNA sequences for the gene itself will facilitate its genetic control in sire-breeding herds (Renand 1995).

Conversely, a delayed fall in postmortem pH can give rise to dark firm and dry meat, a condition which is influenced by breed and preslaughter handling of pigs (Wood *et al.* 1994).

Another major gene (unfavourable dominant), the ‘acid meat’ (RN) gene in pigs, increases the glycogen level and branching enzyme activity in the myofibres, giving rise to a lowered protein content, ultrastructural abnormalities and resulting in decreased technological abilities associated with high lactic acid levels postmortem (Le Roy *et al.* 1994).

Myosin and several other myofibrillar proteins exist in various isoforms depending on fibre type. Differences associated with protein solubility (Susuki and Cassens 1980; Xiong *et al.* 1995) are likely to account for variability (e.g. in gelling behaviour and gel characteristics) and flavour of processed muscle foods made from different cuts or muscles (Boyer *et al.* 1995).

**Meat flavour and colour**

Muscle fibre types also vary in the levels of the more aliphatic and aromatic amino acids on their surfaces (Boyer *et al.* 1995). Muscle phospholipid content is one such characteristic variation affecting meat flavour - it determines desirable cooking aromas and is very sensitive to oxidation causing off-flavours and odours (Rabat *et al.* 1995). Glycolytic muscles contain less phospholipids than oxidative muscles.

Oxymyoglobin autoxidation is involved in the development of metamyoglobin giving rise to an unattractive colouration on the surface of meat (colour instability). In cattle, the longissimus lumborum muscle has high and psoas major muscle low, colour stability. Protein degradation during ageing can be a sensitive indicator of cells exposed to oxygen radicals, with possible repercussions and associations on and with meat tenderness as well (Mercier *et al.* 1995).

Evidence of genetic effects on colour and flavour were reviewed by Dikeman (1990), Kemp (1994), Wood and Cameron (1994) and Renand (1995).

**CONCLUSIONS**

A variety of factors have been identified which directly or indirectly influence biochemical processes affecting the sensory properties of meat, including age, breed, sex, as well as preslaughter and post mortem processing conditions (Dransfield 1994). However, there has been relatively little study of between animal variations in product quality itself or of genetic associations among different meat quality traits. A summary of genetic parameters taken from Renand (1995), is presented in Table 1.

These results point to low heritabilities of meat quality traits from taste panel evaluations, no doubt related to the low sensitivity of these evaluations, especially those that do not ensure careful control of background environment effects (Shorthose and Harris, 1991). The physical and chemical indicators studied, however, show higher levels of genetic contribution to between-animal variability, especially those that are closer to the biological components involved in meat qualities. Thus, tissue

**TABLE 1:** Genetic parameters of meat quality (literature summary from Renand 1995).

	Heritability coefficients	Genetic correlations with	
		Carcass gain	Carcass fatness
<b>Taste panel evaluations</b>			
Tenderness	0.22	+0.01	+0.25
Juiciness	0.10	+0.24	+0.01
Flavour	0.13	-	
Colour	0.15	-	
Acceptability	0.17	-	
<b>Physico-chemical measurements</b>			
Shear force	0.27	+0.02	-0.06
pH at 24 h post mortem	0.17	-0.09	-0.09
Colour <sup>1</sup>	0.27	+0.28	-0.16
Water holding capacity <sup>2</sup>			
Pressure probe	0.15	-0.07	-0.13
Drip loss	0.31	-0.10	-0.02
Butyrometer	0.22	+0.08	-0.02
<b>Biochemical composition and fibre characteristics</b>			
Lipid	0.36	-0.34	+0.27
Dry matter	0.30	-	
Nitrogen	0.34	-	
Mean fibre diameter	0.34	+0.13	+0.12

<sup>1</sup> reflectance  
<sup>2</sup> water loss

development factors beyond those associated with breed and strain variation in fat content can give rise to differences in processing performance and eating qualities among animals of a similar age.

Genetic correlation estimates reported by Renand (1995) were variable and had high standard errors. Their average values tended to be much lower than those coming from his own more discriminating studies (e.g. Renand *et al.* 1994) in which a variety of indicator traits were evaluated, and those for pigs summarised by Wood and Cameron (1994).

While genetic influences have been shown to be important, the underlying basis of gene effects is only now starting to emerge, and at an increasing pace as genetic markers which impact on meat quality are revealed (Renand 1995). Improved understanding of the calpain system and its underlying genetic control has received much attention recently. Some important antagonisms with productive attributes affecting the efficiency of animal production are also emerging, and these are not necessarily the same for all muscles of the carcass and for all production and processing systems, as emphasised by Shorthose and Harris (1991). It is clear from their review, which stresses the complexity of inter-relationships among meat quality traits, that future genetic studies will need to embrace the reactions of different cuts and muscle products to different culinary methods as well.

Much work remains to be done to provide the genetic information needed to incorporate objectives for improved meat quality into selective breeding programmes for sheep and beef cattle. It is clear that multiple-trait selection indices will be needed to cope with the antagonisms that appear to be involved, a task that will require much extension effort and a consistent long-term focus on specified breeding goals if meaningful progress is to be realised. Even now, the important antagonism of leanness with fast growth is not well recognised in the breeding programmes currently being deployed by our sire-breeding industries. Generally, faster lean growth seems to be favourably associated with improved meat flavour, colour, juiciness and (sometimes) tenderness, although there is reduced tenderness in the case of the Callipyge gene and probably also for other genes involved in proteolysis. Fortunately, a number of quantitative trait indicators as well as genetic markers capable of being evaluated in the live animal are emerging from current research, and characteristic breed variations which can be exploited through crossbreeding are becoming identified. Muscle variations within the animal also offer opportunities to develop more specialised and better-matched meat production and processing methods capable of providing competitive sector-linked, "conception-to-consumption" delivery systems for an enhanced array of differentiated meat products.

## **Animal behaviour and stress: impacts on meat quality**

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### **ABSTRACT**

Animal behaviour can deleteriously affect meat quality through three different pathways: exertion/activity, physiological stress responses and perceptions of welfare. In this review of published work we will describe each pathway, and discuss methods for minimising their impacts on both the physicochemical and animal welfare aspects of meat quality. We conclude that whereas the physicochemical quality of meat can be improved by some post-slaughter carcass handling treatments, public perceptions of meat quality can only be enhanced by improved animal handling practices to reduce stress.

### **INTRODUCTION**

Meat quality has usually been defined in terms of the physicochemical properties of meat (e.g. tenderness, flavour, colour, juiciness). However, many present day consumers have a broader definition of what constitutes meat quality. The physicochemical properties of meat are still very important, but issues such as food safety, food health and animal welfare will also influence which meat products customers will buy.

### **Meat quality: physicochemical aspects**

The physicochemical properties of a piece of meat are determined by many factors from the farm to the plate. These include: the age of the animal, the particular muscle the cut the meat comes from, the manner in which the animal was slaughtered, the carcass processing methods employed, the duration and temperature of storage, and the cooking method employed. Of these, meat pH, plays a major role in determining the overall acceptability of the