RANKING OF SIRE BREEDS AND BEEF CROSS BREEDING OF DAIRY AND BEEF COWS

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Summary

There is general agreement across countries on the ranking of beef breeds for production and carcass traits. Differences between dairy and early maturing beef breeds in growth and slaughter traits are small, but the latter have lower feed intake and better carcass conformation. Late maturing beef breeds also have lower feed intake and better carcass conformation and in addition, have a higher growth rate, kill-out proportion and carcass muscle proportion. When factors such as age and fatness are accounted for, differences between breeds in meat quality traits are small.

Differences amongst breed types in kill-out proportion can be explained by differences in gut contents (consequent on differences in feed intake), differences in the proportions of gastrointestinal tract and metabolic organs, differences in hide proportion, and differences in offal fats. Growth is an allometric, rather than an isometric, process. Some parts, organs and tissues grow relatively more slowly than the animal overall, and so become decreasing proportions over time, while others grow relatively faster and become increasing proportions. With increasing slaughter weight, the proportions of non carcass parts, hind quarter, bone, total muscle and higher value muscle decrease, while the proportions of non carcass and carcass fats, fore quarter and marbling fat all increase.

Because of heterosis or hybrid vigour, the productivity of cross-bred cattle is superior to the mean of the parent breeds. While calving difficulty may be slightly higher (probably due to greater birth weight), calf mortality is much reduced in cross-breds. In addition, general robustness and growth rate are increased. There are additive effects of heterosis in the dam and the progeny. When cross-bred cows are mated to a bull of a third breed, >60 % of total heterosis is attributable to the cross-bred cows.

The double muscling phenotype in beef cattle is due to the inactivated myostatin gene, but the inactivating mutation is not the same in all breeds and other genes also contribute to muscling. Compared to normal animals, double muscled animals have lower proportions of digestive tract, internal fats and metabolic organs. This explains their superior kill-out proportion. They also have a smaller hind shin that helps accentuate the muscling in the remainder of the

limb. There are similar degrees of muscular hypertrophy in both the hind and fore quarters. Muscle to bone ratio is about one third greater in double muscled than in normal carcasses. Piedmontese cattle with none, one or two mutated myostatin alleles were compared with normal Herefords and Limousins. In the absence of any mutated allele, Piedmontese were similar to Herefords, with one mutated allele they were similar to Limousins and with two mutated alleles they were immensely superior to Limousins. In fact, the response to the second mutated allele was about three times that to the first. If progeny approximated to the mean of the parent breeds, crossing a double muscled sire with a dairy or early maturing beef cow would result in cattle of similar characteristics to pure-bred late maturing beef breeds. This does not happen because double muscling is dependent on a homozygous myostatin genotype. The progeny of a common cow breed and normal late maturing, or double muscled, sire breeds have similar production traits.

Introduction

The main reason for cross breeding dairy cows with beef bulls is to enhance the beef value of the resultant progeny either through improved animal productivity, improved carcass and meat quality, or improved saleability in a greater range of markets. Aside from any effects of heterosis, and other than where the sire breed is double muscled, the main production traits of cross-bred calves are approximately mid way between those of the two parent breeds. Therefore, when a beef breed (presuming superior beef traits) is crossed with a dairy breed, the progeny will have superior beef traits to pure-bred dairy progeny. This is the basis for the practice of crossing dairy cows with beef breed bulls.

While the monetary contribution of the surplus calves and cull cows on a dairy farm may be an important component of income, the breeding priority for dairy farmers is to ensure sufficient herd replacement heifers of the desired genetic merit. To achieve this, a minimum proportion of the herd must be bred to dairy bulls and surplus cows can be considered for beef crossing. The potential for beef crossing is thus a function of the replacement rate. In recent years, with the increase in dairy genetic merit and the concomitant declining fertility in dairy herds, the proportion of cows required to produce replacement heifers has increased leaving fewer cows available for beef crossing. Since half of all calves are male, the proportion of cows bred to dairy bulls must be double the herd replacement rate plus a margin to cover for factors such as mortality and occasional increases in culling rate (e.g. to facilitate adjustment of mean calving date). Thus, herd replacement rates of 20 %, 30 % and 40 %, for example,

would leave about 50 %, 30 % and 10 %, respectively of cows available for beef crossing. Where the replacement rate is high and beef breed stock bulls are used, cross breeding is only practical in larger herds. Where artificial insemination is used however, the replacement rate, and consequently the number of cows available for beef crossing, is not an issue. During the milk quota era in the European Union there was a rapid increase in genetic merit of Irish dairy cows resulting in fewer cows being required to produce the quota. This necessitated a lower heifer replacement rate leaving a higher proportion of dairy cows available for beef crossing. Following the abolition of milk quotas, it is anticipated that there will be an expansion of dairy herds resulting in increased replacement rates and corresponding reductions in the proportion of cows available for beef crossing.

Relative performance of pure dairy and beef x dairy cattle

Data from Grange Beef Research Centre in Ireland (Keane, More O'Ferrall and Connolly, 1989; More O'Ferrall and Keane, 1990; Keane *et al.,* 1990; Keane and More O'Ferrall, 1992; Keane, 1994; Keane and Allen, 2002) and from the United Kingdom (UK) Meat and Livestock Commission (MLC) (Southgate, Cook and Kempster, 1988; Kempster, Cook and Southgate, 1988) were used to compile a ranking for common production traits of progeny of straight-bred Holstein-Friesians (HF) and crosses out of HF cows and the common beef breeds. In the Grange studies, the animals were reared as steers to around two years of age and serially slaughtered. The MLC animals were also reared as steers in 16- or 24-month production systems and were slaughtered at an estimated constant proportion of subcutaneous fat.

Performance and carcass traits

Ireland: The Grange Beef Research Centre data are summarized in Table 1. There was little difference between pure-bred HF and the progeny of Hereford (HE), Limousin (LM), Romagnola (RO) and Blonde d'Aquitaine (BL) sires in slaughter weight per day of age (a measure of live growth rate to a constant age). Piedmontese (PM) progeny had a lower value, while Simmental (SM), Belgian Blue (BB) and Charolais (CH) progeny had higher values. In overall ranking, CH had the highest and PM had the lowest values. All beef crosses had a higher kill-out proportion than HF. Amongst the beef crosses, LM, PM, BL and BB had the highest kill-out proportions while HF had the lowest. Carcass weight per day of age (the product of slaughter weight per day of age and kill-out proportion) was higher for all beef crosses (except PM which was similar) than for HF. Generally, carcass weight per day of age

was similar for HF, LM and RO, and higher for BL, SM, BB and CH. In summary, BB and CH produced about 10 % more carcass weight per day of age than HF and PM, 6 % more than HE, LM and RO, and 2 % more than BL and SM.

Because of the large measurement units for carcass conformation and fat classes (all carcasses fell into 4 or less conformation and fat classes), the ranking for these traits is not as reliable as for traits measured as continuous variables. Clearly however, all beef crosses were greatly superior (by approximately one class) to HF in carcass conformation with no great difference between the beef crosses. In contrast, there were big differences between the genotypes in carcass fat class ranking with HF, LM, RO and SM broadly similar, HE higher, and BL, BB, CH and PM lower. These fat class values indicate that at approximately the same age, and having grown as indicated by the slaughter weight and carcass weight per day of age rankings, HE were considerably fatter, and BL, BB, CH and PM were considerably leaner than the others. Intake, scaled to mean live weight during the measurement period, was lower for all beef crosses than for HF, with the differences being least for HE and SM and greatest for RO and PM.

UK: The breed ranking of the MLC data is shown in Table 2. There were no double muscled or Italian breeds in the MLC comparisons but Aberdeen Angus (AA) and South Devon (SD), which were absent from the Grange comparisons, were included. Generally, the ranking of the genotypes was similar to the Grange ranking but the differences between the early and late maturing breeds were greater. Compared with HF, AA produced 5 % less slaughter weight and 8 % less carcass weight per day of age. While SD had a similar growth rate to LM it had a lower kill-out proportion and poorer carcass conformation. With the exception of HE and LM which exchange places, the ranking for carcass weight per day of age was the same as the Grange data for those genotypes that were common to the two studies. Because MLC used a 15 point rather than a 5 point scale, measurement of carcass conformation was more precise than in the Grange evaluation. Both LM and CH had markedly superior carcass conformation to HF with the other beef crosses intermediate. While some of the carcass conformation differences between Grange and MLC may have been due to the different measurement scales, they may also have been due to differences in slaughter end point. The Grange animals were slaughtered on a constant age basis resulting in the late maturing genotypes being leaner whereas the MLC animals were slaughtered on a fat constant basis resulting in the late maturing genotypes being heavier. As carcass conformation improves with increasing weight

and fatness, the relatively heavier and fatter late maturing animals in the MLC evaluation would be expected to have relatively better carcass conformation. Because the MLC animals were slaughtered on a fat constant basis any comparison of fat class is meaningless. The MLC intake data are not directly comparable to the Grange intake data because of the differences in slaughter end point. Compared with HF, all beef crosses had higher efficiencies of live weight production ranging from 6 % for AA to 12 % for LM. The intake and efficiency data must be interpreted in the context of the slaughter end point of the comparisons and the ranking could vary with changes in the slaughter end point.

Muscle growth and muscle yield traits

Compared with HF, almost all beef crosses had greater daily muscle growth and all had greater muscle size as measured by *m. longissimus* area scaled for carcass weight (Table 3). However, the differences between HF and the early maturing genotypes were small whereas the differences between HF and the late maturing genotypes were large. Muscle to bone ratio was greater for all beef crosses than for HF. Differences between genotypes in the proportion of higher value muscle were small, ranging (relative to HF) from none for HE to 3 % for some late maturing genotypes.

Meat quality

Meat quality comprises both objectively and subjectively measured traits. Ranking on subjectively measured traits may vary with local culture and experience. Homer *et al.* (1997) compared meat quality for the progeny of early and late maturing beef breeds out of HF cows (Table 4). Straight-bred HF were not included. Despite differences in fatness there were few differences in meat quality traits. AA and BB differed in colour with the latter being lighter. BB also had more tender joints but a similar difference was not found in steaks. It was concluded that there was little difference in meat quality from progeny of different beef sire breeds.

Kill-out proportion, growth of non carcass parts and carcass composition

Kill-out proportion

For descriptive purposes, beef cattle can be broadly divided into three biological types, namely dairy, early maturing beef breeds and their crosses, and late maturing beef breeds and their crosses. These can be represented by HF, HE and CH, respectively. Animals differ in kill-out proportion because of variation in gut contents and in the proportions of their non carcass

parts. Because of potential confounding effects, gut contents are normally excluded from comparisons of non carcass parts which are expressed as proportions of empty body weight (EBW). The proportions (in EBW) of non carcass parts and of the cold carcass for HF, HE and CH steers (More O'Ferrall and Keane, 1990) are shown in Table 5. Although the differences in EBW were statistically significant they were not large. All three genotypes differed in hide proportion which was greatest for HE and least for HF. HF had higher proportions of head/feet/tail and internal organs than HE and CH which did not differ significantly. HF also had a higher proportion of offal fats than HE, which in turn had a higher proportion than CH. Gastrointestinal tract proportion was greater for HF than for HE and CH which did not differ. As a result of these differences, HF had a higher proportion of total non carcass parts, and hence a lower proportion of carcass, than the two beef crosses. Within the beef crosses, HE had a higher proportion of non carcass parts and a lower proportion of carcass than CH. In brief, the lower kill-out proportion of HF compared with the beef crosses was due to higher proportions of external organs, internal organs, offal fats and gastrointestinal tract although these were to some extent offset by a lower hide proportion. The lower kill-out proportion of HE compared to CH was due to higher proportions of hide and offal fats. These may have been offset to some extent by a lower proportion of blood which was not directly measured but estimated by difference.

While differences in the proportions of non carcass parts may explain differences between biological types in kill-out proportion, kill-out proportion is not fixed but varies with factors such as slaughter weight, age and fatness. This is because growth is an allometric, rather than an isometric, process. Some parts and organs grow relatively more slowly than the animal overall and so become decreasing proportions over time, while other parts grow relatively faster than the animal overall and become increasing proportions. Relative growth rate is measured by the regression coefficient b of the allometric equation $y = ax^b$ where y is the part, organ or tissue, and x is the whole unit.

Relative growth of non carcass parts
Allometric growth coefficients for various non carcass parts relative to the empty body are shown in Table 6. With the exception of fats, all parts and organs had growth coefficients <1.0 indicating they grew more slowly than the empty body and so became decreasing proportions of EBW over time. In contrast, the fats grew faster than the empty body (growth coefficients >2.0) and so became increasing proportions of EBW. Nevertheless, the increased

proportion of fats did not completely offset the decreased proportion of all the other non carcass parts and organs resulting in an increased proportion of carcass. This illustrates how kill-out proportion increases with increasing slaughter weight. The proportions of non carcass parts and carcass at 500 kg and 600 kg EBW are also shown in Table 6. With increasing EBW the proportions of hide, external and internal organs, and gastrointestinal tract decreased while the proportions of offal fats and carcass increased.

Carcass dimensions

Carcass dimensions reflect the physical shape of the carcass and when scaled for carcass weight they are a measure of carcass compactness. There were few differences between HF and HE in scaled carcass measurements (Keane *et al*., 1990) but CH had lower values and also had a greater *m. longissimus* area (Table 7).

Carcass weight distribution

The carcass is normally split into two sides which are essentially mirror images of each other and each side comprises a number of joints some of higher value muscle and some of lower value muscle. The higher value muscle is in the pelvic limb (excluding the shin) and loin, while the lower value muscle is in the thoracic limb, thorax and flank. The proportion of these joints in the carcass side is shown in Table 8 for HF, HE and CH (Keane *et al*., 1990). The only differences between HF and HE were a lower proportion of thoracic limb and possibly a higher proportion of ribs for the latter. Both HF and HE had identical proportions of hind and fore quarters. In contrast, CH had lower proportions of fore quarter, thorax and flank, and higher proportions of hind quarter, loin and pelvic limb than both HF and HE. Thus, notwithstanding the differences between the biological types in carcass conformation, differences in the distribution of side weight between the joints were small.

The allometric growth coefficients for the various carcass joints and for the hind and fore quarters (estimated across the HF, HE and CH genotypes) are shown in Table 9. Both limbs and the loin had growth coefficients <1.0, indicating that they became decreasing proportions of the side with increasing side weight. In contrast, the thorax, flank and ribs had growth coefficients >1.0 and so became increasing proportions of the side with increasing side weight. Because most of the latter joints are in the fore quarter, it is not surprising that the fore quarter had a growth coefficient >1.0, while the hind quarter had a growth coefficient <1.0. Joint proportions at 120 kg and 180 kg carcass side weight are also shown in Table 9. The pelvic

limb, for example, decreased from 340 g/kg to 311 g/kg as side weight increases from 120 kg to 180 kg. Overall, the hind quarter decreased from 454 g/kg to 433 g/kg and the fore quarter increased proportionately, as side weight increased from 120 kg to 180 kg.

Carcass composition

The carcass is comprised of three main tissues - fat which can be divided into the subcutaneous and intermuscular depots, bone which includes tendons and connective tissue, and muscle. The carcass composition of the representative biological types is shown in Table 10 (Keane *et al*., 1990). Other than bone proportion which was similar for HF and CH, the genotypes differed in all respects. HE had more fat (both subcutaneous and intermuscular) and less bone and muscle than HF and CH, and HF had more fat (both subcutaneous and intermuscular) and less muscle than CH.

Allometric growth coefficients for the carcass tissues are shown in Table 11. The coefficients for fat were >1.0 indicating a high relative growth rate resulting in an increased fat proportion with increased carcass weight. The coefficient was higher for subcutaneous fat than for intermuscular fat indicating that it increased more rapidly. Bone and muscle had coefficients <1.0 indicating they grew more slowly than the total carcass and so become decreasing proportions over time. The bone coefficient was lower than that for muscle.

Carcass composition at 120 kg and 180 kg side weight (estimated across the three biological types) is also shown in Table 11. As side weight increased from 120 kg to 180 kg, fat proportions increased markedly while muscle and bone proportions decreased.

The change in carcass composition from 120 kg to 180 kg side weight is shown separately for the three biological types in Table 12. At both carcass side weights, HE had more fat and less bone and muscle, than the other two types, while HF had more fat and less muscle than CH. The change in composition from 120 kg to 180 kg carcass side weight was also greater for HE than for the other two types and was greater for HF than CH. For example, from 120 kg to 180 kg side weight, the increases in total fat proportion were 107, 98 and 82 g/kg for HE, HF and CH, respectively, while the corresponding decreases in bone and muscle proportions were 20, 26 and 21 g/kg, and 80, 72 and 61 g/kg, respectively.

Chemical composition

The chemical composition of *m. longissimus,* pelvic limb and flank muscle for the three biological types is shown in Table 13 (Keane *et al*., 1991). Chemical composition was similar for *m. longissimus* and pelvic limb muscle. Compared with these, flank muscle had less moisture and protein, and more lipid (perhaps because of the difficulty in achieving complete separation of muscle and fat in this joint). For all three joints, HF and HE did not differ in moisture concentration but CH muscle had a higher moisture concentration. HE had less protein in the muscle of all joints than both HF and CH which did not differ. HE also had more lipid in the pelvic limb and flank muscles than both HF and CH which did not differ, and had more lipid in *m. longissimus* than CH.

The allometric growth coefficients (Table 14) for moisture, protein and lipid in the carcass side (estimated across the three biological types) indicate that moisture and protein grew more slowly than total muscle, and so became decreasing proportions, while lipid grew more rapidly and thus became an increasing proportion as muscle weight increased. The effects of these changes on muscle chemical composition are also shown in Table 14. As side muscle weight increased from 70 kg to 120 kg, moisture concentration decreased from 728 to 691 g/kg, protein concentration decreased from 216 to 211 g/kg and lipid concentration increased from 56 to 98 g/kg. The values for the individual biological types for total side muscle are shown in Table 15. As side muscle weight increased from 70 kg to 120 kg, composition changed more rapidly for HE (49 g/kg lipid) than for HF (43 g/kg lipid) and CH (35 g/kg lipid).

While there may be large differences between beef and dairy breeds in muscle chemical composition, differences in meat quality are small. The data in Table 16 (Keane *et al*., 2001) are from a comparison of Holsteins (high dairy genetic merit), Friesians (standard dairy genetic merit, <12 % Holstein genes) and Charolais x Holstein-Friesians. The Charolais crosses had a lower muscle lipid concentration than the dairy breeds but there were few differences between the genotypes in sensory traits.

Cross breeding amongst beef breeds

Cow size

In beef production, maintenance of the cow is a major component of total production costs. As maintenance costs are closely associated with body weight, smaller cows have a lower maintenance requirement and associated feed costs. This may be of little benefit if the value

of the output is also lower, so in practice, producers seek small cows that are highly productive. One method of increasing cow productivity is by crossing with a larger sire breed. This has little effect on the maintenance requirements of the cow but improves the productivity of the progeny. An example of this from the United States (US) is outlined in Table 17 (Germ Plasm Evaluation Program, 1974a). Angus cows were bred to Angus, Hereford, Limousin or Charolais bulls and the male progeny were taken to slaughter. Compared with Angus, breeding to Hereford resulted in a small increase in productivity. Crossing with Limousin resulted in a further increase in productivity, while crossing with Charolais resulted in a marked increase in productivity. Compared with pure Angus calves, Charolais cross calves were 21 kg heavier at weaning and gained 11 % faster during finishing. As a result, final live weight was 52 kg heavier and carcass weight was 32 kg heavier. The associated disadvantages were greater calving difficulty and higher calf mortality for the more productive breeds, particularly Charolais.

Carcass data from this breed comparison are shown in Table 18 (Germ Plasm Evaluation Program, 1974b). There were few differences between the pure Angus and the Hereford cross steers, but the Limousin and Charolais crosses had less fat and more meat. There were no differences between the breed types in meat quality traits.

In summary, compared with pure breeding (Angus) crossing with a similar breed (e.g. Hereford) resulted in a small increase in productivity probably due to heterosis. Crossing with more productive breeds resulted in large increases in productivity but there were associated negative effects on calving difficulty and calf mortality. Compared with pure-bred Angus, Limousin x Angus produced 10 % more meat for a small increase in calving difficulty, while Charolais x Angus produced 16 % more meat for a 13 % increase in calving difficulty and a 4 % increase in calf mortality.

Heterosis

The productivity of cross-bred cattle is generally superior to the mean of the parent breeds as a consequence of heterosis or hybrid vigour. This is illustrated in Table 19, which shows a comparison from the US of pure-bred (mean of Angus and Hereford) and cross-bred (mean of Angus x Hereford and Hereford x Angus) cattle (Beef Research Program, 1982). Calving difficulty was slightly higher for the cross-breds, probably because of greater birth weight. Despite this greater birth weight and calving difficulty however, calf mortality was much

reduced in the cross-breds. The cross-breds also had a greater weaning weight (4 %), greater finishing daily gain (2 %), greater final live weight (3 %), and greater carcass weight (3 %). There were few effects on carcass traits (Table 20).

There are additive effects of heterosis in the cow and the progeny (Beef Research Program, 1982). The effect of heterosis in the cow was determined by comparing cross-bred cows with straight-bred cows when both were rearing calves by the same sires of a third breed. Weaning weight was 14.8 % greater per cow exposed to breeding for cross-bred than for straight-bred cows. This advantage was due to a 6.5 % increase in calf crop weaned reflecting a higher pregnancy rate in cross-bred cows and a 4.3 % increase in weaning weight reflecting better milk production by the cross-bred cows. When the advantages of the heterosis on calf survival and growth are combined with those on reproduction and maternal ability, weight of calf weaned per cow exposed to breeding was increased by 23 %. More than 60 % of the total heterosis was attributable to the cross-bred cows.

Following an analysis of 476 cross-bred and 447 straight-bred calves, Cundiff, Gregory and Koch (1982) concluded that weaning weight per cow exposed to breeding was 8.5 % greater for straight-bred cows rearing cross-bred calves than for straight-bred cows rearing straight-bred calves. This advantage was due to a 3 % increase in calf crop weaned, resulting from increased survival of cross-bred calves from birth to weaning, and to a 4.6 % increase in the weaning weight of cross-bred calves.

Data on heterosis have also been published by Davis *et al*. (1998) and by Chase *et al*. (1998). Davis *et al*. (1998) compared straight-bred Hereford, straight-bred Tarentaise and crosses of these two breeds. (Tarentaise are fawn to yellow cattle, used for milk and meat production. They originated in the French Alps and there are breed societies in Canada, U.S. and Australia). Generally, the Tarentaise progeny had higher values than the Hereford progeny for all traits, but the cross-breds (which in the absence of heterosis would be expected to have values mid way between the parent breeds) had values equal to or higher than the Tarentaise values (Table 21). Heterosis was estimated at from 1 % for hip height at weaning to 6 % for daily gain to weaning.

Chase *et al*. (1998) compared straight-bred Hereford, straight-bred Senepol, Hereford x Senepol and Senepol x Hereford cattle. (The Senepol is native to St. Croix, US Virgin Islands

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where it was developed from of cross of Red Poll and a native breed. It is *Bos taurus*, but is tropically adapted and is as heat tolerant as Brahman. This could make it useful for cross breeding although it is recognised that heterosis in *Bos taurus* x *Bos taurus* crosses is less than in *Bos indicus* x *Bos taurus* crosses). The comparative data (Table 22) show that heterosis ranged from 2 % for feed efficiency to 11 % for feedlot daily gain. Surprisingly, the heterosis for carcass weight was only 3 %.

Relative performance of beef sire breeds crossed on beef cows

While in both Europe and North America many beef breeds are straight-bred, there is nevertheless considerable interest in cross breeding. Other than where the beef cows have some genes from the crossing sire breed which could affect heterosis, there seems no obvious reason why the ranking of beef sire breeds should differ between beef and dairy cows.

Production traits – UK and US comparisons

Comparative rankings from the United Kingdom (UK; Southgate, Cook and Kempster, 1982; Kempster, Cook and Southgate, 1982) and the United States (US; Germ Plasm Evaluation Program, 1974a) for 6 beef sire breeds for three production traits are shown in Table 23. In the UK the sire breeds were crossed on Hereford x Friesian and Blue Grey cows while in the US they were crossed on Angus and Hereford cows. For live weight gain, both the ranking of the breeds and the magnitude of the differences were broadly similar for the two comparisons. In the UK comparison, all other breed crosses were superior to the Angus, whereas in the US comparison, Angus, Hereford and Limousin were similar. The Simmental and Charolais breeds were at the top of the rankings in both comparisons but the order were reversed. In both comparisons, the Hereford and Limousin crosses were identical.

Dressing proportion was similar for Hereford and Angus in both comparisons while the late maturing continental breeds had higher values in the UK study but not the US study. The absence of differences in dressing proportion between early maturing and late maturing steers in the US study is not in agreement with the consensus of results in the literature and may have been due to differences in carcass dressing with internal fats remaining with the carcass in the US but not in the UK.

Scaled *m. longissimus* area was similar for Angus and Limousin in the UK study and smaller for all other breeds. In the US study, scaled *m. longissimus* area was similar for Angus, Hereford and South Devon, somewhat larger for Simmental and Charolais, and much larger

for Limousin. A possible explanation for these contrasting findings is the different slaughter end points. In the UK study, all the animals were taken to the same estimated subcutaneous fat proportion which resulted in large differences in carcass weight. In contrast, in the US study, the animals were slaughtered on an age constant basis resulting in relatively small differences in carcass weight.

Carcass and efficiency traits – UK comparison

The carcass traits ranking for the UK study is shown in Table 24. Generally, there were few differences between Angus and Hereford progeny except for carcass conformation which was poorer for the latter. South Devon and Limousin progeny were intermediate between the early maturing and the Simmental and Charolais progeny for carcass and lean growth rates. South Devon progeny had the poorest carcass conformation. Charolais, followed by Simmental, were at the top of the rankings for carcass and lean growth rates but Simmental fell below Limousin for carcass conformation and all genotypes were below Limousin for meat to bone ratio. Despite the large differences in carcass conformation, there were few differences amongst the genotypes in proportion of higher value meat cuts.

Feed intake and efficiency data from the UK study are shown in Table 25. Compared with Angus (which had high intake by normal standards) all other genotypes had lower intakes with little difference amongst them. Hereford had the highest feed efficiency for live weight production while Angus had the lowest. Feed efficiency for carcass production was highest for Limousin followed by Charolais, with Hereford, South Devon and Simmental similar and intermediate. Angus had the lowest feed efficiency for carcass production. The ranking for efficiency of lean tissue production was similar to that for carcass production. There are apparent contradictions in these efficiency data. For example, the late maturing genotypes had higher live weight gains and lower feed intakes than Hereford yet they had poorer efficiency of feed utilisation for live weight gain. The explanation is that feed intake was measured over a fixed period for all genotypes and expressed relative to mean body weight during the period of measurement. Feed efficiency however, was measured on the total feed consumed and total live weight gain produced.   Since the late maturing animals were heavier at slaughter (to ensure the same proportion of subcutaneous fat) they had a greater life time mean live weight resulting in a higher life time maintenance requirement and hence poorer feed efficiency.

Carcass and meat quality traits – US comparison

A ranking of the production data from the US beef breed comparison is shown in Table 26. Birth weight was greater for all breeds than for Angus. There was relatively little difference amongst the Angus, Hereford, South Devon and Limousin breeds for slaughter weight and carcass weight but both Simmental and Charolais had higher values. Meat proportion was higher and fat proportion was lower for the late maturing than for the early maturing breeds. There were no differences between the breeds in meat shear force, tenderness, juiciness or overall acceptability values.

Double muscling in beef cattle

The inactivated myostatin gene is responsible for the double muscling phenotype in beef cattle, but the inactivating mutation is not the same in all breeds. In Piedmontese, the inactivating mutation is due to a single base transition. It has been reported that breed source (Piedmontese or Belgian Blue) of the double muscling allele was not significant for birth weight or carcass composition traits. This implies that the myostatin allele is responsible for all the effects of double muscling. However, Hanset (1982) concluded that selection resulted in an additional increase in muscling of Belgian Blue cattle, homozygous for double muscling, after the myostatin gene was fixed, indicating that other genes were contributing to muscling independent of the inactive myostatin.

Comparison of normal and double muscled cattle

As pure-breds, double muscled cattle are enormously superior to normal cattle in carcass traits. Growth rate does not differ greatly between them but because of a higher kill-out proportion (Table 27) carcass weight is considerably greater for the double muscled type (Fiems *et al*., 1995). There is also a large difference in carcass conformation with many double muscled carcasses grading S (on the SEUROP scale) and normal carcasses of the same breed grading almost two classes lower. Carcass bone proportion does not differ greatly between the double muscled and normal types but the double muscled type has much less carcass fat and much more muscle. This difference in physical composition is reflected in muscle chemical composition, where lipid content is much lower and moisture content is higher for the double muscled type.

In addition to the differences in carcass conformation and composition (Ansay and Hanset, 1979), double muscled animals also have lower proportions of digestive tract, internal fats and

internal organs (Table 28). This largely explains their higher kill-out proportion. They also have a smaller hind shin which helps to emphasise the difference in the remainder of the hind limb. Muscling superiority in the fore quarter is similar to in the hind quarter indicating, contrary to conventional wisdom, that there are similar degrees of hypertrophy in both quarters. Muscle to bone ratio is about 30 % greater in double muscled than in normal carcasses.

Normal and double muscled cattle relative to Friesian or Holstein

As straight-breds, double muscled cattle are as different from normal late maturing breeds (e.g. Charolais, Blonde d'Aquitaine) as the latter are from Holsteins and Friesians. The performance of straight-bred normal and double muscled bulls of the same breeds (Charolais, Belgian Blue) relative to Friesians (Geay *et al*., 1982) or Holsteins (Minet *et al*., 1996) is shown in Table 29. For daily gain, normal Charolais were superior to double muscled Charolais but the difference between normal and double muscled Belgian Blue was small. This implies that double muscling *per se* does not affect growth rate. Feed intake of normal animals was about 10 % lower than for Holsteins or Friesians while the intake of double muscled animals was about 20 % lower. The kill-out superiority of double muscled animals was about double that of normal animals over Holsteins or Friesians and likewise for carcass muscle proportion. Carcass fat proportion of double muscled animals was only one third to one half that for normal animals and muscle lipid proportion showed the same trend. Thus, excepting growth rate, double muscled animals were as superior to straight-bred animals of the same breed as the latter were to Holsteins or Friesians. Consequently, the offspring of a double muscled sire breed and Holstein or Friesian dams, for example, should be similar to normal pure bred animals of the same sire breed if the traits of both sire types were similarly inherited.

The difference in carcass composition between normal and double muscled animals reflects differences in their relative carcass tissue growth patterns. A comparison of the growth coefficients for Hereford and double muscled steer carcass tissues is shown in Table 30 (Shanin and Berg, 1985). The Hereford values are generally in line with those shown earlier for the early maturing biological type (i.e. muscle and bone coefficients <1.0 and a fat coefficient >1.0). Double muscled animals had a bone growth coefficient similar to that for Herefords, but their muscle coefficient was much higher (1.07 v. 0.84) and their fat coefficient was much lower (1.19 v. 1.49). Thus, the changes in carcass composition with changing

carcass weight would be quite different for the two types. This is illustrated in Table 31 which shows the estimated composition for the two types at 130 kg and 190 kg carcass side weights. As Herefords grew from 130 kg to 190 kg side weight, the proportion of fat increased by 54 g/kg while the proportions of bone and muscle decrease by 12 g/kg and 36 g/kg, respectively. In contrast, in the double muscled animals, there was little change in fat proportion with increasing weight, but bone proportion decreased by 12 g/kg while muscle proportion increased by 18 g/kg. (As these are predicted from regression equations they do not necessarily sum to the same total value). Thus, with increasing carcass weight there is a marked change in the carcass composition of Herefords whereas the effect on the carcass composition of double muscled animals is negligible.

Normal and double muscled cattle of similar mature size

Growth of skeletal muscle is at least partly under the control of myostatin but there are several mutations of the gene that affect its activity. Hereford, Limousin and Piedmontese breeds are broadly similar in mature body size but differ in degree of muscularity. Hereford is considered normal for muscularity, Limousin has moderately increased muscularity and Piedmontese has dramatically increased muscularity due to the mutated myostatin gene. Sires of these breed types were bred to cross-bred (composite) cows to produce F_1 calves (Short *et al*., 2002). Bulls from this calf crop were *inter se* mated to F_1 females from the same sire breed to produce F_2 calves. This was designed to allow alleles of major genes segregate independently so that the genotypic and phenotypic effects of these alleles could be studied. F_2 animals of Hereford cross and Limousin cross were both assumed to be normal (++). Piedmontese were classified as P_0 (normal), P_1 (one mutated allele) and P_2 (two mutated alleles). The results are summarized in Table 32. Hereford and normal Piedmontese (P_0) had similar birth weights, slaughter weights, dressing proportions, carcass weights, *m. longissimus* areas and product yields. Piedmontese had a lower fat depth and a greater pelvic area. Thus, for most production traits Hereford and normal Piedmontese were similar. Compared with Hereford and normal Piedmontese, Limousin had a greater birth weight, dressing proportion, carcass weight, *m. longissimus* area and product yield. Fat depth was intermediate between Hereford and normal Piedmontese, and pelvic area was similar to Hereford. Adding one or two alleles of the mutated myostatin gene in Piedmontese had no effect on slaughter weight indicating no effect on growth rate. Otherwise, the means for birth weight, dressing proportion, carcass weight, *m. longissimus* area and product yield increased, while fat depth and pelvic area decreased with increasing number of alleles. Of particular interest is the fact that for the traits

which were affected by the number of mutated myostatin alleles, the response to the second allele was about three times that to the first. In brief, while normal Piedmontese resembled Hereford for most production traits other than fat depth, Piedmontese with one mutated allele resembled Limousin and Piedmontese with two mutated alleles had traits immensely superior to those with one.

In this experiment, the effects of P_0, P_1 and P_2 were evaluated independent of the effects of other genes. The data provide evidence that a major portion of the action of the myostatin gene product is additive. However, there was also evidence of non additivity. This always resulted from the second myostatin allele having a larger effect than the first. Whether this non additivity is real or an artefact due to the shape of the dose response curve of myostatin (and its mutant forms) was not determined.

Other data showed a depression in rate of gain in Piedmontese cross calves but that depression was not caused by the extra myostatin alleles but by other components of the Piedmontese genotype. The linear increase in birth weight and decrease in pelvic area with increasing number of myostatin alleles explains why dystocia is such a problem in double muscled animals.

Breed and double muscling effects on meat quality
Most studies with double muscled cattle indicate that meat tenderness is improved relative to homozygous normal cattle but in many cases only the *m. longissimus* was studied. In addition, there is the question of whether heterozygotes for the double muscling mutation were correctly identified. Thus, the magnitude of the effects on tenderness of one or two copies of the inactivated myostatin gene is not clear.

Cattle with varying proportions (0 %, 25 %, 50 % or 75 %) of Piedmontese inheritance, and with 0, 1 or 2 inactive myostatin alleles were produced by crossing Piedmontese x Hereford (or Angus) females to Piedmontese, Piedmontese x Hereford (or Angus), or Hereford bulls (Wheeler *et al*., 2001). These progeny had 25:75, 50:50 or 75:25 ratios of Piedmontese: Hereford (or Angus) inheritance and had 0 (+/+), 1 (mh/+) or 2 (mh/mh) copies of the inactive myostatin allele.

Tenderness values for two muscles (*m. longissimus* and *biceps fermoris*) are shown in Table 33. Within myostatin genotype, Piedmontese proportion had no effect on muscle tenderness, but as the number of inactive myostatin alleles increased, muscle tenderness increased by on average 0.4 units per allele. The data for the tenderness of four muscles by number of inactive myostatin alleles are shown in Table 34. For normally tender muscles (*longissimus* and *gluteus medius*), the biggest increase in tenderness came from the first inactive allele with less coming from the second. For normally less tender muscles (*semimembranosus* and *biceps fermoris)* the increase from the second allele was at least as great as that from the first. As a result, the tenderness of the *semimembranosus* and *biceps femoris* muscles of cattle with two inactive myostatin alleles was similar to that of the *longissimus* and *gluteus medius* muscles of conventional cattle. From the data it appears there was a tenderness rating ceiling of 6.5 to 7.0. Thus, when normally tender muscles reached this with one inactive myostatin allele there was no room for an effect of the second allele. With normally less tender muscles however, there was scope for both alleles to have an effect.

Cross breeding with double muscled sires
Because of the superior carcass traits of doubled muscled (over normal) animals they appear ideal for crossing on Holstein-Friesian dairy cows which are deficient in the carcass traits in which the double muscled animals excel. However, because of the genetic basis of the double muscled condition, the carcass traits of the cross-bred progeny are not approximately mid way between the two parent breeds but are much closer to those of the non-double muscled parent. As a result, the outcome from crossing a double muscled breed on Holstein-Friesian cows is not much different to that from crossing with normal late maturing breed types.

A comparison of steers out of Friesians dams mated to Friesian, Limousin and Belgian Blue sires is shown in Tables 35 and 36 (Steen and Kilpatrick, 1995). Both beef crosses had superior carcass traits to Friesians but differences between the beef crosses themselves were small (Table 36). In terms of carcass composition, the beef crosses were superior to Friesians, and in some respects, the Belgian Blue crosses were superior to the Limousin crosses in that they had more muscle and less fat. Based on the comparisons of normal and double muscled breeds shown earlier, if the progeny of both these sire breeds out of Holstein-Friesian cows were to rank mid way between the parent breeds, then Belgian Blue crosses should be about one conformation class better, have 50 g/kg less carcass fat and 50 g/kg more carcass muscle

than the Limousin crosses. The actual differences were 0.2 of a conformation class, 26 g/kg fat and 17 g/kg muscle.

Comparisons of progeny from Charolais or Belgian Blue bulls, and Charolais or Piedmontese bulls, and Holstein-Friesian cows are summarized in Table 37 (Hardy and Fisher, 1996; Davies *et al*., 1999). Other than carcass fat proportion which was 18 g/kg lower and carcass muscle proportion which was 19g/kg higher for Belgian Blue, there was little difference between Charolais and Belgian Blue crosses. Charolais crosses were superior to Piedmontese crosses in live and carcass growth rates and in carcass conformation.

The progeny out of Holstein-Friesian cows and two double muscled sire breeds (Belgian Blue and Piedmontese) were compared with Simmental progeny (Grundy *et al*., 2000). The data are summarized in Table 38. Belgian Blue progeny had somewhat higher live and carcass weight gains than Piedmontese progeny. Otherwise, there were few differences between the progeny of the two double muscled breeds. Simmental progeny had a lower kill-out proportion and higher fatness than the progeny of the double muscled breeds.

Data from a number of studies (Hardy and Fisher, 1996; Davies *et al*., 1999; Grundy *et al*., 2000) where various beef breeds were compared with Charolais for crossing on Holstein-Friesian cows are summarized in Table 39. Limousin and Belgian Blue progeny were somewhat inferior to Charolais and Simmental progeny in growth rate and Piedmontese progeny were considerably inferior. Kill-out proportion was higher for the progeny of the double muscled breeds than for the Simmental and Limousin progeny which were similar. This resulted in an improved ranking for the double muscled breeds in carcass gain. Other than carcass fat class, which was higher for Simmental, differences between the progeny groups were small. Carcass fat proportion as lower (although this was not reflected in carcass fat class), and muscle proportion was higher (although conformation was poorer) for the Belgian Blue than for the Charolais progeny.

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Table 1. Ranking of Holstein-Friesians (HF) and beef x HF steers for growth and slaughter traits

Sire breed	HF[1]	HE	LM	PM	RO	BL	SM	BB	CH
Slaughter weight/day (g)	803	103	98	95	101	102	106	104	107
Kill-out (g/kg)	527	102	105	105	104	105	104	105	104
Carcass weight/day (g)	425	105	103	100	104	107	109	109	111
Carcass conformation[2]	2.19	133	136	139	139	132	136	138	143
Carcass fat class[3]	3.52	125	103	86	97	91	103	95	90
Feed intake (g/kg LW)	18.2	98	96	94	92	96	98	97	97

[1]Actual values for HF, values for other genotypes expressed relative to HF value = 100; [2]EU Beef Carcass Classification Scheme, Scale 1 (P = poorest) to 5 (E = best); [3]EU Beef Carcass Classification Scheme, Scale 1 (leanest) to 5 (fattest). LW = Live weight, HE = Hereford, LM = Limousin, PM = Piedmontese, RO = Romagnola, BL = Blonde d'Aquitaine, SM = Simmental, BB = Belgian Blue, CH = Charolais.
Sources: Keane *et al.,* 1989, 1990; More O'Ferrall and Keane, 1990; Keane and More O'Ferrall, 1992; Keane, 1994; Keane and Allen, 2002.

Table 2. Ranking of Holstein-Friesian (HF) and beef x HF steers for growth, slaughter traits and efficiency

Sire breed	HF	AA	HE	SD	LM	SM	CH
Slaughter weight/day (g)	807	95	99	104	104	107	112
Kill-out (g/kg)	500	99	100	102	105	102	105
Carcass weight/day (g)	405	92	99	106	108	110	117
Carcass conformation[1]	460	128	128	120	160	136	157
Efficiency (g LW/kg feed)	162	106	111	108	112	107	108

[1]Scale 1 (poorest) to 15 (best). AA = Aberdeen Angus, SD = South Devon. See Table 1footnotes.
Sources: Southgate, Cook and Kempster, 1988; Kempster, Cook and Southgate, 1988.

Table 3. Ranking of breeds (HF=100) for muscle weight and m. *longissimus* area

Sire breed	HF[1]	HE	LM	PM	RO	BL	SM	BB	CH
Muscle weight (g/day)	256	102	109	113	115	116	116	119	117
M. longissimus area[2]	22.3	103	117	118	117	110	108	112	114
Muscle: bone ratio	3.22	105	117	115	114	115	109	117	116
Higher value muscle (g/kg muscle)	446	100	102	103	103	101	102	102	102

[1]Actual values for HF, values for other genotypes expressed relative to HF=100; [2]cm^2/100 kg carcass. See Table 1 footnotes.
Sources: Keane *et al*., 1989, 1990; More O'Ferrall and Keane, 1990; Keane and More O'Ferrall, 1992; Keane, 1994; Keane and Allen, 2002.

Table 4. Meat quality[1] of progeny from Holstein-Friesian cows and various beef sire breeds

Sire breed	HE	AA	PM	LM	BB	CH	s.e.
pH$_{24}$	5.78	5.84	5.78	5.77	5.72	5.75	0.04
Colour (EEL value)[2]	23.1[ab]	21.6[b]	23.3[ab]	23.8[a]	24.6[a]	23.5[ab]	0.72
Fat depth (mm)	7.91[ab]	9.04[a]	5.15[c]	5.56[c]	4.88[c]	6.35[bc]	0.46
Drip loss (g/kg)	12.7	11.8	14.4	14.4	14.6	14.3	1.4
Juiciness[3]	4.4	4.5	4.5	4.3	4.2	4.4	0.12
Tenderness[3]	3.9[a]	3.8[a]	3.8[a]	3.8[a]	4.5[b]	4.0[a]	0.08
Flavour[3]	4.6	4.8	4.7	4.6	4.7	4.7	0.08

[1]Means for steers and heifers; [2]Higher values indicate lighter colour; [3]Scale 1 (low) to 8 (high). [a,b]Values within a row without a common superscript differ significantly (P<0.05) in this and subsequent tables. See Table 1 footnotes.
Source: Homer *et al.*, 1997.

Table 5. Non carcass parts and carcass as proportions (g/kg empty body weight) for steers of three biological types

Biological type[1]	HF	HE	CH	s.e.d.
Empty body weight (kg)	516[a]	505[a]	532[b]	3.6
Hide	67[a]	79[c]	72[b]	1.3
Head/feet/tail	59[a]	57[b]	58[ab]	0.4
Internal organs	36[a]	34[b]	33[b]	0.4
Offal fats	67[a]	60[b]	52[c]	1.0
Gastrointestinal tract	110[a]	102[b]	100[b]	1.5
Trim + chill loss	24	23	23	-
Blood + miscellaneous[2]	55	50	56	-
Total parts	418[a]	405[b]	394[c]	2.0
Cold carcass	582[a]	595[b]	606[c]	2.1

[1]HF = dairy, HE = early maturing, CH = late maturing; [2]Not measured, estimated by difference;   See Tables 1 and 4 footnotes.

Sources: More O'Ferrall and Keane 1990; Keane *et al.,* 1990.

Table 6. Allometric regression coefficients and proportions (g/kg) of empty body weight for non carcass parts at 500 kg and 600 kg empty body weights

	Growth coefficient		Empty bodyweight	
	b	s.e.	500 kg	600 kg
Hide	0.64	0.054	79	68
Head	0.64	0.035	37	32
Feet	0.55	0.039	24	20
Internal organs	0.61	0.042	39	33
Internal fat	2.15	0.132	22	35
Caul fat	2.76	0.147	14	30
Stomach[1]	0.53	0.098	41	34
Intestines	0.84	0.077	80	75
Carcass	1.04	0.016	600	611

[1]Rumen + reticulum + abomasum.

Source: Estimated from More O'Ferrall and Keane, 1990.

Table 7. Carcass measurements for steers of three biological types (per 100 kg carcass)

Biological type	HF	HE	CH	s.e.d.
Carcass length (cm)	43.3[a]	42.1[a]	40.6[b]	0.69
Leg length (cm)	23.5[a]	22.6[ab]	22.2[b]	0.49
Carcass width (cm)	16.4[a]	15.7[ab]	15.0[b]	0.39
Leg width (cm)	15.0[a]	14.4[a]	13.9[b]	0.38
M. *longissimus* (cm^2)	22.3[a]	22.4[a]	25.4[b]	0.73

See Tables 1, 4 and 5 footnotes.

Source: Keane *et al.*, 1990.

Table 8. Carcass joint proportions (g/kg) for steers of three biological types

Biological type	HF	HE	CH	s.e.d.
Thoracic limb	135[a]	130[b]	137[a]	1.3
Thorax	325[a]	324[a]	315[b]	2.8
Flank	47[ab]	49[a]	44[b]	1.2
Ribs	106	111	107	2.2
Loin	54[a]	54[a]	56[b]	0.7
Pelvic limb	334[a]	332[a]	341[b]	2.2
Hind quarter	435[a]	435[a]	442[b]	2.7
Fore quarter	565[a]	565[a]	558[b]	2.7

See Tables 1, 4 and 5 footnotes.

Source: Keane *et al.,* 1990.

Table 9. **Allometric regression coefficients for joints and quarters relative to carcass side weight, and joint proportions (g/kg) at 120 kg and 180 kg carcass side weight**

	Growth coefficient		Carcass side weight	
	b	s.e.	120 kg	180 kg
Thoracic limb	0.77	0.020	143	131
Thorax	1.17	0.016	364	393
Flank	1.30	0.068	44	50
Ribs	1.40	0.045	52	62
Loin	0.86	0.035	58	55
Pelvic limb	0.76	0.020	340	311
Hind quarter	0.88	0.011	454	433
Fore quarter	1.09	0.020	546	567

Source: Keane *et al.,* 1990.

Table 10. Carcass composition (g/kg side) of steers of three biological types

Biological type	HF	HE	CH	s.e.d.
Subcutaneous fat	98[a]	126[b]	83[c]	3.8
Intermuscular fat	134[a]	144[b]	118[c]	3.7
Bone + other tissue	170[a]	155[b]	168[a]	1.9
Muscle	598[a]	575[b]	630[c]	5.6

See Tables 1, 4 and 5 footnotes.
Source: Keane *et al.*, 1990.

Table 11. **Allometric regression coefficients for carcass tissues relative to carcass side weight, and tissue proportions (g/kg) at 120 kg and 180 kg carcass side weight**

	Growth coefficient		Carcass side weight	
	b	s.e.	120 kg	180 kg
Subcutaneous fat	2.37	0.113	72	124
Intermuscular fat	1.83	0.072	110	154
Total fat	2.06	0.083	182	278
Bone + other tissue	0.63	0.036	166	142
Muscle	0.73	0.027	651	580

Source: Keane *et al.,* 1990.

Table 12. Side composition (g/kg) of steers of three biological types at 120 kg and 180 kg carcass side weight

Carcass side weight	120 kg			180 kg		
Biological type	HF	HE	CH	HF	HE	CH
Subcutaneous fat	71	92	54	123	154	96
Intermuscular fat	115	124	92	160	169	132
Total fat	185	216	146	283	323	228
Bone + other tissue	171	158	170	145	132	149
Muscle	644	626	684	572	546	623

See Tables 1 and 5 footnotes.
Source: Estimated from Keane *et al.*, 1990.

Table 13. Chemical composition of joint muscle for steers of three biological types

Biological type	HF	HE	CH	s.e.d.
Moisture (g/kg)				
M. longissimus	712[a]	711[a]	718[b]	2.3
Pelvic limb	718[ab]	715[a]	721[b]	2.3
Flank	684[a]	687[a]	695[b]	3.1
Protein (g/kg)				
M. longissimus	227[a]	220[b]	223[ab]	2.1
Pelvic limb	219[a]	213[b]	219[a]	1.8
Flank	212[a]	204[b]	213[a]	2.0
Lipid (g/kg)				
M. longissimus	52[ab]	58[a]	49[b]	3.3
Pelvic limb	53[a]	61[b]	50[a]	3.1
Flank	91[a]	103[b]	83[a]	4.2

See Table 1, 4 and 5 footnotes.

Source: Keane *et al.,* 1991.

Table 14. Growth coefficients of muscle constituents, and mean muscle chemical composition (g/kg) at 70 kg and 120 kg carcass side muscle weight

	Growth coefficient		Side muscle weight	
	b	s.e.	70 kg	120 kg
Moisture	0.92	0.014	728	691
Protein	0.96	0.028	216	211
Lipid	2.06	0.160	56	98

Source: Keane *et al.,* 1991.

Table 15. Chemical composition (g/kg) of total side muscle for steers of three biological types at 70 kg and 120 kg carcass side muscle weights

Side muscle weight (kg)	70 kg			120 kg		
Biological type	HF	HE	CH	HF	HE	CH
Moisture	725	722	736	688	680	705
Protein	219	212	218	213	205	214
Lipid	56	66	46	99	115	81

See Tables 1 and 5 footnotes.

Source: Estimated from Keane *et al.*, 1991.

Table 16. Muscle chemical composition[1] and quality traits[2] of Holstein (HO), Friesian (FR) and Charolais x Friesian (CH) steers

Sire breed	HO	FR	CH	s.e.
Chemical composition (g/kg)[1]				
Moisture	728	722	734	6.8
Protein	208[a]	211[a]	217[b]	3.7
Lipid	51[a]	56[a]	37[b]	7.6
Quality traits				
Juiciness[2]	4.9	4.5	4.2	0.48
Tenderness[2]	4.6	4.7	3.7	0.55
Flavour[2]	3.9	3.7	3.5	0.31
Overall acceptability[2]	3.4	3.4	3.0	0.33

[1]Mean of 7 joints from carcass side; [2]Scale 1 (low) to 8 (high). See Table 4 footnotes.

Source: Keane *et al.*, 2001.

Table 17. Production data for steer progeny of four sire breeds mated to Angus cows

Sire breed	Angus	Hereford	Limousin	Charolais
Calving difficulty (%)	5.3	4.7	10.2	18.9
Calf mortality (%)	2.1	0.0	2.4	6.3
Birth weight (kg)	34.5	36.6	38.4	40.8
200-day weight (kg)	213	221	226	234
Finishing gain (g/day)	1021	1039	1044	1134
Final live weight (kg)	460	470	482	512
Dressing (%)	61.5	61.4	62.0	61.7
Hot carcass weight (kg)	293	300	304	325

Source: Germ Plasm Evaluation Program, Report No. 1, 1974a.

Table 18. Carcass data for steer progeny of four sire breeds mated to Angus cows

Sire breed	Angus	Hereford	Limousin	Charolais
Fat trim (g/kg)	230	235	179	187
Bone (g/kg)	116	117	124	126
Meat (g/kg)	655	648	697	687
Shear force (kg)	3.2	3.4	3.4	3.1
Tenderness[1]	7.4	7.4	7.3	7.6
Acceptability[1]	7.3	7.3	7.2	7.4

[1]9 point hedonic scale with higher scores greater.
Source: Germ Plasm Evaluation Progam, Report No. 3, 1974b.

Table 19. Production data for pure-bred and cross-bred Angus and Hereford cattle

Type	Pure[1]	Cross[2]
Calving difficulty (%)	5.1	6.8
Calf mortality (%)	3.1	0.5
Birth weight (kg)	36.2	37.0
200-day weight (kg)	208	216
Finishing gain (g/day)	1039	1062
Final live weight (kg)	461	473
Dressing (%)	61.0	61.2
Hot carcass weight (kg)	290	299

[1]Mean of Angus and Hereford; [2]Mean of Angus x Hereford and Hereford x Angus
Source: Beef Research Program, Progress Report No. 1, 1982.

Table 20. Carcass data for pure-bred and cross-bred Angus and Hereford cattle

Type	Pure	Cross
Fat trim (g/kg)	219	230
Bone (g/kg)	116	117
Meat (g/kg)	661	651
Sheer force[1]	3.2	3.2
Tenderness[1]	7.4	7.5
Acceptability[1]	7.3	7.3

[1]See Tables 18 and 19 footnotes.
Source: Beef Research Program, Progress Report No. 1, 1982.

Table 21. Comparison of straight-bred Hereford (H) and Tarentaise (T) cattle and their cross-breds

Type	HxH	H x T	T x T	Heterosis (%)
Birth weight (kg)	39.2	40.8	38.9	4.2
Calving difficulty score	1.4	1.3	1.4	5.0
Weaning weight (kg)	221.0	241.4	239.4	5.1
Daily gain to weaning (kg)	0.96	1.05	1.05	6.4
Hip height at weaning (cm)	109.4	111.9	111.6	1.1

Source: Davis *et al.*, 1998.

Table 22. Comparison of pure Hereford (H) and Senepol (S) and their crosses for production and carcass traits

Type	H x H	H x S	S x S	S x H	Heterosis (%)
Birth weight (kg)	31.4	35.5	34.3	33.6	3.5
Weaning weight (kg)	186	237	225	199	5.1
Daily gain to weaning (g)	753	983	928	807	5.4
Final live weight (kg)	377	452	426	402	6.4
Daily gain in feedlot (kg)	1.38	1.36	1.07	1.35	10.6
Daily intake (kg)	7.7	8.9	7.9	8.3	9.9
Gain/feed (g/kg)	180	154	135	166	1.7
Hot carcass weight (kg)	233	280	276	246	3.4
M. longissimus area (cm^2)	66.3	74.5	69.9	69.9	6.0

Source: Chase *et al.*, 1998.

Table 23. Relative (AA = 100) performance of progeny from different sire breeds and the same dam breeds

Sire breed		AA	HF	SD	LM	SM	CH
Live weight gain (g/day)	UK	865	103	106	103	112	110
	US	1053	100	106	100	110	112
Dressing proportion (g/kg)	UK	518	100	102	104	102	104
	US	613	100	101	101	99	100
M. longissimus area (cm^2)[1]	UK	0.287	94	94	100	96	94
	US	0.251	99	101	110	102	104

[1]Per kg carcass. See Tables 1 and 2 footnotes.
Source: UK = Southgate, Cook and Kempster, 1982; Kempster, Cook and Southgate, 1982.
　　　　US = Germ Plasm Evaluation Program, Report No. 1, 1974a.

Table 24. Relative (actual values for AA =100) ranking of sire breeds for steer progeny production traits

Sire breed	AA	HE	SD	LM[1]	SM	CH
Carcass growth (g/day)	419	103	110	112	117	119
Lean growth (g/day)	303	102	109	113	116	119
Conformation (15 pt scale)	10.0	93	84	113	104	111
Meat : bone ratio	4.03	97	96	103	97	98
Higher price cuts (g/kg carcass)	440	101	101	103	102	102

[1]Missing values estimated for LM. See Tables 1 and 2 footnotes.
Sources: Southgate, Cook and Kempster, 1982; Kempster, Cook and Southgate, 1982.

Table 25. Relative (actual values for AA = 100) ranking of sire breeds for intake and efficiency traits

Sire breed	AA	HF	SD	LM[1]	SM	CH
Feed intake (g/kg LW)	26.4	95	94	93	95	93
Efficiency[2] *for:*						
Live weight	91	104	96	99	96	98
Carcass weight	47	104	104	110	103	107
Lean tissue weight	34	104	104	110	102	107

[1]Missing values estimated for LM; [2]g product per kg feed consumed; See Tables 1 and 2 footnotes.
Source: Southgate, Cook and Kempster, 1982.

Table 26. Relative (actual values for AA = 100) ranking of steer progeny of beef sire breeds for production and carcass traits

Sire breed	AA	HE	SD	LM	SM	CH
Birth weight (kg)	35.8	104	109	110	115	116
Weaning weight (kg)	212	101	102	104	107	108
Slaughter weight (kg)	468	100	103	103	109	109
Carcass weight (kg)	296	99	103	101	106	109
Meat (g/kg carcass)	655	101	101	107	104	106
Fat (g/kg carcass)	227	98	95	77	80	78

See Tables 1 and 2 footnotes.
Source: Germ Plasm Evaluation Program, Progress Report No. 1, 1974a.

Table 27. Carcass traits of normal and double muscled Belgian Blue bulls

Type	Normal	Double muscled
Carcass weight (kg)	427	477
Kill-out (g/kg)	655	687
Conformation[1]	12.8	17.4
Carcass composition (g/kg)		
Fat	212	110
Bone	132	129
Muscle	656	761
Chemical composition (g/kg muscle)		
Lipid	32	9
Protein	226	230
Moisture	741	757

[1]Scale P=3 to S=18.
Source: Fiems *et al., 1995.*

Table 28. Ranking of traits (proportions) for double muscled bulls relative to normal bulls (=100)

Shin joint	80	Digestive tract	83
Bone	93	Kidney fat	79
Fore muscle	121	Internal organs	79
Hind muscle	123	Fat in the 7th rib	67
Muscle: bone ratio	133		

Source: Ansay and Hanset, 1979.

Table 29. Performance of normal and double muscled cattle relative to Friesian or Holstein (=100)

Sire breed	Charolais[1]		Belgian Blue[2]	
Type	Normal	Double muscled	Normal	Double muscled
Daily gain	128	114	90	95
Feed intake	91	77	89	83
Kill-out	109	119	113	120
Muscle proportion	111	125	106	130
Fat proportion	61	24	96	46
Muscle lipid	-	-	49	17

Sources: [1]Geay *et al.*, 1982, relative to Friesian = 100; [2]Minet *et al.,* 1996, relative to Holstein = 100.

Table 30. Allometric growth coefficients (b values) for muscle, fat and bone relative to carcass side for Hereford and double muscled steers

Type	Hereford	Double muscled
Muscle	0.841	1.070
Fat	1.488	1.189
Bone	0.722	0.711

Source: Shanin and Berg, 1985.

Table 31. Estimated carcass composition (g/kg) of Hereford (HE) and double muscled (DM) cattle at 130 kg and 190 kg side weights

Side weight	130 kg		190 kg	
Type	HE	DM	HE	DM
Fat	266	179	320	173
Bone	119	114	107	102
Muscle	599	684	563	702
Muscle : bone ratio	5.02	5.98	5.25	6.89

Source: Shanin and Berg, 1985.

Table 32. Comparison of Hereford (HE) Limousin (LM) and Piedmontese (PM) progeny of three myostatin genotypes

Sire breed/type	HE	LM	PM_0	PM_1	PM_2
Birth weight (kg)	35.9	39.0	35.7	37.0	40.1
Slaughter weight (kg)	475	480	464	465	458
Dressing (%)	57.5	58.8	57.9	59.7	63.2
Carcass weight (kg)	273	282	269	278	291
M. longissimus area (cm^2)	74.3	81.4	74.3	86.4	109
Product yield (%)[1]	50.7	52.3	50.4	52.5	56.5
Fat depth (mm)	9.8	7.4	6.3	5.6	2.6
Pelvic area (cm^2)	170	174	184	174	168
Liver weight (kg)	4.93	5.04	5.13	5.00	4.42
Efficiency[2]	13.7	15.4	12.6	13.2	15.2

[1]Of edible product; [2]Product/Mcal. feed energy. P_0 = normal Piedmontese, P_1 = one mutated allele, P_2 = two mutated alleles.
Source: Short *et al*., 2002.

Table 33. Effect of myostatin genotype and percentage Piedmontese on muscle tenderness rating[1]

Myostatin genotype	+/+			mh/+			mh/mh	
% Piedmontese	0	25	50	25	50	75	50	75
Longissimus	6.2	6.5	6.2	6.9	7.0	7.0	6.9	7.2
Biceps femoris	5.0	5.4	5.1	5.8	5.6	5.6	6.3	6.3
Mean	5.6	5.9	5.7	6.3	6.2	6.1	6.5	6.5

[1]Scale 1= tough to 8= tender.
Source: Wheeler *et al*., 2001.

Table 34. Effects of myostatin genotype on tenderness ratings[1] of four muscles

Myostatin genotype	+/+	mh/+	mh/mh	Mean
Longissimus	6.3	7.0	7.1	6.8
Gluteus medius	6.0	6.5	6.7	6.4
Semimembranosus	5.6	5.8	6.0	5.8
Biceps femoris	5.2	5.6	6.3	5.7
Mean	5.8	6.2	6.5	-

[1]Scale 1 = tough to 8 = tender.
Source: Wheeler *et al.*, 2001.

Table 35. Slaughter traits of steers out of Friesian dams and Friesian, Limousin and Belgian Blue sires

Sire breed	Friesian	Limousin	Belgian Blue
Carcass weight (kg)	297	316	318
Fat class[1]	3.4	3.4	2.9
Conformation class[1]	2.1	3.2	3.4
M. longissimus area (mm^2/kg carcass)	20.6	23.9	25.2
Internal fats (g/kg live weight)	14.8	12.2	12.1

[1]See Table 1 footnotes.
Source: Steen and Kilpatrick, 1995.

Table 36. Carcass composition of steer progeny of Friesian dams and Friesian, Limousin and Belgian Blue sires

Sire breed	Friesian	Limousin	Belgian Blue
Saleable meat (g/kg)	694	718	732
Higher priced meat (g/kg)	431	440	445
Marbling score	3.3	2.9	2.5
Carcass composition (g/kg)			
Muscle	611	635	652
Fat	228	222	196
Bone	152	138	144

Source: Steen and Kilpatrick, 1995.

Table 37. Comparison of progeny from Holstein-Friesian dams and Charolais or Belgian Blue, or Charolais or Piedmontese, sires

Sire breed	Charolais[1]	Belgian Blue[1]	Charolais[2]	Piedmontese[2]
Live weight gain (kg/day)	1.24	1.20	0.98	0.90
Carcass gain (g/day)	696	692	553	523
Fat class[3]	2.87	2.97	3.85	3.85
Conformation class[3]	3.70	3.53	3.05	2.70
Feed efficiency[4]	-	-	7.8	8.0
Carcass composition				
Fat	190	172	-	-
Bone	150	148	-	-
Muscle	661	680	-	-
Muscle : bone ratio	4.42	4.60	-	-

[1]Young bulls; [2]Means of bulls and heifers; [3]See Table 1 footnotes; [4]Feed/live weight gain.
Sources: [1]Hardy and Fisher, 1996; [2]Davies *et al.,* 1999.

Table 38. Comparison of progeny[1] of Holstein-Friesian dams and Simmental, Belgian Blue or Piedmontese sires

Sire breed	Simmental	Belgian Blue	Piedmontese
Live weight gain (kg/day)	1.19	1.15	1.11
Kill-out (g/kg)	535	556	560
Carcass gain (g/day)	632	639	622
Dry matter intake (kg/day)	7.2	7.1	7.0
Feed efficiency[2]	6.1	6.3	6.4
Fat class[3]	3.59	2.98	3.01
Conformation class[3]	2.94	3.05	2.79

[1]Mean of bulls and heifers; [2]Feed/live weight gain; [3]See Table 1 footnotes;
Source: Grundy *et al.,* 2000.

Table 39. Relative (Charolais=100) finishing performance and slaughter traits for progeny[1] of late maturing non doubled muscled and doubled muscled sire breeds.

Sire breed	CH[2]	LM	SM	BB	PM
Live weight gain (kg/day)	1.10	97	100	97	93
Kill-out (g/kg)	560	100	99	103	103
Carcass gain (g/day)	625	97	100	99	95
Fat class[3]	3.36	-	124	103	102
Conformation class[3]	3.38	-	91	95	88
Intake (g/kg LW)	20.1	-	101	100	98
Efficiency (kg feed DM/kg LWG)	7.75	-	97	100	103
Carcass composition (g/kg)					
Fat	190	-	-	91	-
Bone	150	-	-	99	-
Muscle	661	-	-	103	-

[1]Out of Holstein-Friesian cows; [2]Actual values for CH; [3]See Table 1 footnotes. LW = live weight, DM = dry matter, LWG = live weight gain.

Sources: Compiled from Hardy and Fisher, 1996; Davies *et al.,* 1999; Grundy *et al.*, 2000.