BEEF CROSS BREEDING OF DAIRY AND BEEF COWS

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Summary

The rationale for crossing dairy cows with beef bulls is to increase the beef productivity and value of the progeny. The proportion of dairy cows available for beef crossing is determined by the dairy herd replacement rate. The performance of cross-bred cattle is generally superior to the mean of the parent breeds because of heterosis. This is most pronounced for reproduction, maternal and calf survival traits. Crossing dairy cows with early maturing beef breeds (e.g. Angus, Hereford) has little effect on growth but improves carcass conformation and reduces feed intake. Crossing with most late maturing beef breeds also improves carcass conformation and reduces feed intake, but in addition, growth rate, kill-out proportion and carcass muscle proportion are increased. Cross breeding can have small negative effects on dam milk production, and subsequent reproduction can be impaired following a long gestation or difficult calving. There is little advantage in crossing with double muscled sire breeds (e.g. Belgian Blue, Piedmontese) compared with the larger conventional late maturing breeds (e.g. Charolais, Blonde d'Aquitaine). There are few effects of sire breed on meat quality.

Introduction

The main reason for crossing dairy cows with beef bulls is to increase the value of the progeny for beef production either through improved animal productivity, improved carcass and meat quality or improved saleability through greater acceptance in a wider range of markets. Ignoring any contribution from heterosis, and other than where the sire breed is double muscled, the main production traits of cross-bred calves are generally mid way between those of the two parent breeds. Therefore, if a beef breed (e.g. Charolais) has superior beef traits to a dairy breed (e.g. Holstein-Friesian), then crossing the two will result in progeny with superior beef traits to the dairy breed. While increasing the value of the surplus calves on dairy farms can increase income, the most important issue for the dairy enterprise is to ensure adequate dairy herd replacements of the desired genetic merit. To achieve this, a minimum proportion of the herd must be bred to dairy bulls leaving the surplus 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 safety margin to allow for factors such as mortality, infertility and the flexibility to adjust herd mean calving date if necessary. Thus, for example, herd replacement rates of 20 %, 30 % and 40 % plus a 5 % safety margin would leave about 50 %, 30 % and 10 %, respectively of dairy cows available for beef crossing. When breeding is by natural service and where the replacement rate is high, beef crossing is only practical in large herds. Where artificial insemination (AI) is used however, a high replacement rate does not preclude cross breeding as any cows available for beef crossing can be bred by AI.

Beef crossing on dairy cows

Relative productivity of pure Holstein-Friesians and beef breed × Holstein-Friesians

Data from Grange Research Centre (Keane *et al.,* 1989, 1990; More O'Ferrall and Keane, 1990; Keane and More O'Ferrall, 1992; Keane, 1994; Keane and Allen, 2002) were used to compile a ranking for some common production traits of progeny from straight-bred Holstein-Friesians (HF) and crosses of HF with the common beef breeds. The animals were reared as steers to around two years of age and were serially slaughtered on an age/date basis.

Relative growth and slaughter data for HF and beef breed × HF steers are summarized in Table 1. There was little difference between HF and the progeny of Hereford (HE), Limousin (LM), Romagnola (RO) or Blonde d'Aquitaine (BA) sires in slaughter weight per day of age, which is a measure of growth rate and live weight at a constant age. Piedmontese (PM) progeny had a lower growth rate while Simmental (SM), Belgian Blue (BB) and Charolais (CH) progeny had higher growth rates. All beef crosses had higher kill-out proportions than HF. Amongst the beef crosses, LM, PM, BA and BB had the highest kill-out values while HE 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 the same) than for HF. Carcass weight per day of age was similar for HE, LM and RO, and higher for BA, SM, BB and CH. In summary, BB and CH produced about 10 % more carcass weight for age than HF and PM, 6% more than HE, LM and RO, and 2 % more than BA and SM.

All beef crosses were superior to HF in carcass conformation with relatively small differences between the various beef crosses. In contrast to the conformation ranking, there were big differences between the genotypes in fat class ranking. For HF, LM, RO and SM, fat class was broadly similar; HE had a higher value, while BA, BB, CH and PM had lower values. These fat class values indicate that at approximately the same age, HE were considerably fatter, and BA, BB, CH and PM were considerably leaner than the others. Intake, scaled to mean body weight at time of measurement, was lower for all beef crosses than for HF. HE and SM showed the least intake differences from HF while RO and PM showed the greatest differences. Aberdeen Angus was not included in these comparisons but on the basis of published data (Kempster *et al.*, 1982, 1988; Southgate *et al.*, 1982, 1988), its ranking is similar to that for Hereford.

Relative carcass and meat quality traits of pure dairy and beef x dairy cattle

Muscle growth: Compared with HF, nearly 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 2). Differences between HF and HE were small. These results are similar to those of Kempster *et al.* (1988) who also reported relative (HF=100) values for muscle growth of 95 and 108 for Aberdeen Angus (AA) and South Devon (SD), respectively. Corresponding values for scaled *m. longissimus* area were 107 and 103. Differences between HF and the late maturing beef crosses were large for both muscle growth and scaled *m. longissimus* area. Muscle to bone ratio was greater for all the beef crosses than for HF. Kempster *et al.* (1988) reported relative muscle to bone ratios of 110 and 108 for AA and SD, respectively. Differences between HF and the beef crosses in the proportion of higher value muscle were small, ranging from none for HE to 3 % for some late maturing beef crosses.

Meat quality: Meat quality comprises both objectively and subjectively measured traits. Ranking on subjectively measured traits may vary with local culture and preference. Homer *et al*. (1997) compared the meat quality of progeny from early and late maturing beef sire breeds and HF dams (Table 3). Straight-bred HF were not included. Despite differences in fatness there were few differences in meat quality traits. Muscle colour was lighter for BB than AA, and BB also had more tender joints but not steaks. Overall, there was little difference amongst the beef crosses in meat quality.

Because the comparison of Homer *et al.* (1997) excluded pure dairy animals, data from a comparison (Keane *et al.,* 2001) of pure dairy strains and beef crosses (Charolais × Holstein-Friesians) are shown in Table 4. The dairy strains were pure-bred Holsteins and standard Irish Friesians (<12% Holstein genes). The Charolais crosses had a lower proportion of muscle lipid than the dairy strains but there were no differences amongst the genotypes in sensory traits. Taken together, the data of Homer *et al.* (1997) and Keane *et al.* (2001) indicate that there are few differences in meat quality amongst pure dairy and beef × dairy cattle.

Dairy cow performance as affected by sire breed of calf

Sire breed type and calving data

Surveyed calving traits for Holstein-Friesian dairy cows mated by AI to a range of beef breed bulls are shown in Table 5 (Department of Agriculture, Food and Rural Development, 1998). Because there were only 5 and 10 bulls, respectively for Blonde d'Aquitaine and Belgian Blue the results for those breeds should be interpreted with caution. Mean breed calving difficulty ranged from 1.9 % for Hereford to 6.3 % for Blonde d'Aquitaine. However, within each breed there was wide variation (e.g. 0 to 6.1 % for Hereford and 1.0 to 17.8 % for Blonde d'Aquitaine).

There was little relationship between the incidence of calving difficulty and calf mortality which did not vary much between breeds. Of the 7 breeds surveyed, 5 had a calf mortality incidence of 1.5 to 2.0 % and the remaining two were 2.3 % (Limousin) and 2.6 % (Belgian Blue). Mean gestation length varied from 281 days for Aberdeen Angus to 288 days for Blonde d'Aquitaine; Hereford and Belgian Blue had the same gestation length of 283 days. For Aberdeen Angus and Hereford, the range in gestation length was 2 days, for Blonde d'Aquitaine and Belgian Blue it was 3 days, and for Charolais, Simmental and Limousin, it was 4, 5 and 6 days, respectively.

Missing from Table 5 are data for Holstein-Friesians. Dillon *et al.* (2001) reported mean gestation lengths of 281 and 284 days for medium genetic merit Irish Holstein-Friesians and high genetic merit Dutch Holstein-Friesians, respectively. Thus, crossing dairy cows with Aberdeen Angus, Hereford or Belgian Blue bulls does not extend gestation length compared to Holstein-Friesian breeding, but crossing with the other beef breeds extends mean gestation length by up to 5 days.

Data on calf birth weights vary greatly amongst different studies but all are agreed that Holstein-Friesians and the early maturing beef breeds (Angus, Hereford) have similar birth weights while the late maturing breeds have heavier birth weights. Baker *et al.* (1990) gave the following birth weights for progeny of various sire breeds mated to Hereford and Angus cows: Angus 30 kg, Friesian and Hereford 32 kg, Limousin 33 kg, South Devon and Blonde d'Aquitaine 34 kg, Simmental 35 kg, Maine Anjou and Charolais 36 kg, and Chianina 37 kg.

Calf breed type and dairy cow performance

More O'Ferrall and Ryan (1990) crossed Friesian cows with bulls of three contrasting biological types (Friesian, Hereford and Charolais). The beef breeds were chosen to represent both the traditional early maturing breeds (Hereford) and the large late maturing breeds (Charolais). A total of 22 bulls (fairly equally distributed amongst the breeds) and 318 calvings were evaluated. Milk yield for the current and subsequent lactations was expressed relative to Friesian = 100. There were no significant differences in milk yield but there was a tendency for milk yield to be lower in cows bred to the beef bulls (Table 6). Calf birth weight was similar for Friesian and Hereford sires, but was 4-5 kg heavier for Charolais sires. Compared to Friesian, gestation length for Hereford and Charolais was longer by 3 and 4 days, respectively. There was no difference in the incidence of calving difficulty from using Friesian or Hereford sires but using Charolais sires resulted in a significantly higher incidence of calving difficulty. Days to first service was similar for all breeds, and days open was similar for Friesian and Hereford sires but cows that calved to Charolais sires took 5-6 days longer to become pregnant. Services per conception were similar for Friesian and Hereford sires but significantly more services per conception were required for cows that calved to Charolais sires. In brief, the effects of calf sire breed on milk production were small but they were negative for the beef sire breeds with no difference between Hereford and Charolais. Despite a 3 days longer gestation length for Hereford there were no differences between cows calving to Friesian and Hereford sires in calving and reproduction traits. Breeding to Charolais resulted in greater calving difficulty and impaired reproduction. There was a reduction of 9 kg milk and 0.6 days lactation length for each one day delay in calving date after January 1. This may be a function of the grazing season ending or cows being dried off on a fixed date.

Differences between sire breeds in cow performance may be solely due to the differences in gestation length and calf birth weight or there may be specific breed effects. This can be tested by comparing cows that produced male and female calves because the latter have a shorter gestation length and a lower birth weight. While there was no significant difference in milk production between cows that produced male and female calves, cows that had female calves produced 4 % more milk in both the current and subsequent lactations. Birth weight was 3 kg heavier for male calves but gestation length was only one day longer. There were no effects of calf gender on reproduction traits. Thus, it appears that differences in calving and reproduction traits are more particularly breed effects rather than gestation length or calf birth weight effects.

Cross breeding amongst beef breeds

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 lower maintenance requirements and costs. Thus, the objective should be to obtain high producing progeny from relatively small cows.

Different sire breeds crossed on a common cow breed

Crossing with a larger sire breed has little effect on the maintenance requirements of the cow but increases the productivity of the progeny. An example from the United States (Germ Plasm Evaluation Program, 1974) is outlined in Table 7. Angus cows were bred either to Angus, Hereford, Limousin or Charolais bulls and the male progeny were reared to slaughter. Compared to Angus, crossing with Hereford resulted in a small increase in productivity. Crossing with Limousin resulted in a further productivity increase, and crossing with Charolais resulted in a marked productivity increase. Compared with Angus steers, Charolais crosses were 21 kg heavier at weaning and gained 11 % faster during finishing. As a result, final live weight was 52 kg greater and carcass weight was 32 kg greater. The disadvantage was greater calving difficulty and higher calf mortality from using Charolais sires.

There were few differences between the Angus and the Hereford crosses in carcass traits but Limousin and Charolais cross carcasses had less fat and more meat. There were no differences amongst the breed types in meat quality traits.

In brief, compared to pure Angus, Hereford crosses produced 2 % more carcass and had lower calving difficulty and calf mortality (probably due to heterosis), Limousin crosses produced 4 % more carcass but had greater calving difficulty, while Charolais crosses produced 11 % more carcass with further increases in calving difficulty and calf mortality.

Exploiting heterosis

Productivity of cross-bred cattle is generally superior to the mean of the parent breeds because of heterosis. This was illustrated in a study in the United States where the mean values for pure-bred Angus and Hereford cattle were compared with the mean values for Angus × Hereford and Hereford × Angus cattle (Germ Plasm Evaluation Program, 1974). Calving difficulty was slightly higher for the cross-breds, probably because of the greater birth weight. Despite the greater birth weight and higher calving difficulty however, calf mortality was lower. Cross-breds also had greater weaning weight (4 %), and greater carcass weight (3 %). There was little difference in carcass traits.

Following an analysis of 476 cross-bred and 447 straight-breed calves, Cundiff *et al.* (1982) concluded that weaning weight per cow exposed to breeding was 8.5 % higher 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 crossbred calves from birth to weaning, and to a 4.6 % increase in weaning weight of the cross-bred calves.

To determine the effect of heterosis in the cow, cross-bred cows were compared 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 cows 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 to a 4.3 % increase in weaning weight, reflecting higher milk production by cross-bred cows.

When the advantages of the heterosis for calf survival and growth were combined with those for 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.

Davis *et al.* (1998) compared straight-bred Hereford, straight-bred Tarentaise and crosses of these two breeds. (Tarentaise are fawn to yellow cattle, which are used for milk and meat. They originated in the French Alps and have breed societies in Canada, U.S. and Australia). Generally, the straight-bred Tarentaise had higher values than the straight-bred Herefords 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. Heterosis was estimated at from 1 % for hip height at weaning to 6 % for daily gain.

Likewise, Chase *et al.* (1998) compared straight-bred Hereford, straight-bred Senepol, Hereford × Senepol and Senepol × Hereford cattle. The main production traits of feedlot gain, final live weight and feed intake had heterosis values of 6 - 11 % while carcass and tissue colour traits had heterosis values of 3 -14 % (Table 8).

Growth patterns of different biological types

Cattle breed types can be divided into three main biological types, namely dairy, early maturing beef breeds and their crosses, and late maturing beef breeds and their crosses. Representative examples of these three types are HF, HE and CH, respectively. Detailed comparisons of these biological types have been carried out (More O'Ferrall and Keane, 1990; Keane *et al.*, 1990, 1991).

Non-carcass parts and kill-out proportion

Animals differ in kill-out proportion because of differences in gut contents and in the proportions of non carcass parts. Due to the confounding effects of differences in gut contents, non carcass parts are generally expressed as proportions of empty body weight. The proportions of non carcass parts and of cold carcass in the empty body weight for HF, HE and CH steers are shown in Table 9. All three genotypes differed in hide proportion which was greatest for HE and least for HF. HF had higher proportions of external (head/feet/tail) and internal organs than HE and CH which did not differ. HF also had a higher proportion of offal fats than HE which in turn had a higher proportion than CH. Gastrointestinal tract proportion was also greater for HF than for HE and CH which did not differ. Overall, HF had a higher proportion of total non carcass parts and hence a lower proportion of cold carcass than the two beef crosses. Amongst the beef crosses, HE had a higher proportion of non carcass parts and a lower proportion of carcass than CH. Thus, the lower kill-out proportion of HF compared with the beef crosses was due to higher proportions of external and internal organs, offal fats and gastrointestinal tract. The lower kill-out proportion of HE compared to CH was due to higher proportions of hide and offal fats.

Carcass composition

The carcass comprises of three main tissues - fat (both the subcutaneous and intermuscular depots), bone (including tendons and connective tissue) and muscle. Carcass composition for HF, HE and CH is shown in Table 10. Bone proportion was similar for HF and CH but lower for HE. HE had more fat (both subcutaneous and intermuscular) and less bone and muscle than both HF and CH, and HF had more fat (both subcutaneous and intermuscular) and less muscle than CH.

The carcass composition data were subjected to allometric regression analysis. The allometric (growth) coefficients for the fat depots were considerably >1.0 indicating high relative growth rates leading to increasing proportions of fats with increasing carcass weight (Table 11). The growth coefficient for subcutaneous fat was higher than for intermuscular fat indicating that the former increased more rapidly with increasing weight. Bone and muscle growth coefficients were both <1.0 indicating they grew more slowly than the carcass and so became decreasing proportions with increasing carcass weight. The bone coefficient was lower than that for muscle.

Estimated composition at 120 kg and 180 kg carcass side weight for the three biological types is also shown in Table 11. As side weight increased, fat proportions increased considerably while muscle and bone proportions decreased considerably. At both 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 rate of change in composition was also greater for HE than for the other two types and was greater for HF than CH. For example, over the 60 kg increase in side weight, the increases in total fat proportions were 107, 98 and 82 g/kg for HE, HF and CH, respectively. The corresponding reductions in bone and muscle proportions were 20, 26 and 21 g/kg, and 80, 72 and 61 g/kg, respectively.

Muscle chemical composition

The chemical composition of total side muscle for HF, HE and CH at 70 kg and 120 kg carcass side muscle weight is shown in Table 12. At both side muscle weights, HE had less moisture and protein and more lipid than HF, which in turn had less moisture and more lipid than CH.

Progeny from normal and double muscled sire breeds

Relative performance of normal and double muscled animals

As straight-breds, double muscled cattle (e.g. Belgian Blue, culard Charolais, Piedmontese) are as different from conventional late maturing breed types (e.g. normal Charolais, Limousin, Blonde d'Aquitaine) as the latter are from Holstein-Friesians. The relative performance (compared to Friesians or Holsteins) of straight-bred normal and double muscled cattle of the same breeds (Charolais and Belgian Blue) is shown in Table 13 (Geay *et al.*, 1982; Minet *et al.*, 1996). For daily gain, normal Charolais were superior to double muscled Charolais while for Belgian-Blue the difference was in the opposite direction. This suggests that double muscling *per se* does not affect growth rate. Intake of normal animals was about 10 % lower than that of Holstein-Friesians, while intake of double muscled animals was a further 10% lower. The kill out superiority of double muscled animals over Friesians/Holsteins was about double that for normal animals and likewise for muscle proportion. Fat proportion of double muscled animals relative to Holsteins/Friesians was only one third to one half that for normal animals and muscle lipid proportion followed the same trend. Thus, with the exception of growth rate, double muscled animals are as superior to straight-bred normal animals of the same breed as the latter are from Friesians/Holsteins. Therefore, if the production traits of both types were similarly inherited, the offspring of double muscled sires and Holstein-Friesian dams, for example, would be similar to normal pure-bred progeny of the same sire breed.

Performance of progeny of normal and double muscled breeds

Comparisons of progeny from Charolais or Belgian Blue bulls, or Charolais and Piedmontese bulls, and Holstein-Friesian cows, are shown in Table 14 (Hardy and Fisher, 1996; Davies *et al.,* 1999). Other than carcass fat proportion which was somewhat lower, and carcass muscle proportion which was somewhat higher for Belgian Blue progeny, Charolais progeny were marginally superior. Charolais progeny were similar or superior to Piedmontese progeny. Thus, when crossing Holstein-Friesian dairy cows with beef bulls, there is little advantage in progeny production traits from using double muscled Belgian Blue sires compared to normal Charolais sires, and none from using double muscled Piedmontese over normal Charolais sires. This is because double muscled sires do not transmit their superiority to their cross-bred offspring proportionately to normal sires. However, there may be an advantage to the double muscled sire breeds in terms of shorter gestation length and a lower incidence of calving difficulty as indicated earlier.

Normal and double muscled cattle of similar mature size

Pleiotropism is the concurrent response in other traits to selection for a specific trait. Control of skeletal muscle growth is at least partly through the hormone myostatin. There are several mutations of the myostatin gene that affect the activity of myostatin and cause double muscling. Hereford, Limousin and Piedmontese breeds are 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 inactivated myostatin gene. Sires of these breed types were mated 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 identified. Both Hereford cross and Limousin cross F_2 animals were assumed to be normal. Piedmontese F_2 were classified as P_0 (normal), P_1 (one mutated allele) and P_2 (two mutated alleles).

The results are summarized in Table 15. Hereford and normal Piedmontese had similar birth weights, slaughter weights, dressing proportions, carcass weights, *m. longissimus* areas and product yields, but Piedmontese had a lower fat depth and a greater pelvic area. Thus, for meat production traits Hereford and normal Piedmontese were broadly similar. Compared with Hereford and normal Piedmontese, Limousin had 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 mutated alleles. Of particular interest is the fact that of the traits that were affected by the number of mutated alleles, the response to the second allele was about three times that to the first. Thus, 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.

These data suggest that a major portion of the action of the myostatin gene product was additive but there was also evidence of some non additivity which always arose from the second allele having a larger effect than the first. Addition of one and two mutated alleles linearly increased birth weight and linearly decreased pelvic area. This is why dystocia is such a problem in double muscled animals.

Breed and double muscling effects on meat quality

While the inactivated myostatin gene is responsible for the double muscling phenotype in cattle, the inactivating mutation is not the same in all breeds. In Piedmontese, the inactivating mutation is due to a single base transition (Wheeler *et al*., 2001). 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) observed that genetic 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.

Some studies with double muscled cattle indicate that meat tenderness is improved relative to homozygous normal cattle but in most cases only the *m. longissimus* was studied. In addition, there have been some questions on 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 (Wheeler *et al*., 2001).

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.

The data for tenderness of four muscles (*longissimus dorsi*, *gluteus medius*, *semimembranosus* and *biceps femoris*) by number of inactive myostatin alleles are shown in Table 16. Within myostatin genotype, Piedmontese proportion had no effect on muscle tenderness but as the number of inactive myostatin alleles increased, muscle tenderness increased by about 0.4 units per allele. For the normally tender muscles (*longissimus* and *gluteus*) the biggest increase in tenderness came from the first inactive allele with less or none coming from the second. For the normally less tender muscles (*semimembranosus* and *biceps fermoris*), the increase from the second allele was at least as great as from the first. As a result, the tenderness of the *semimembranosus* and *biceps fermoris* of cattle with two inactive myostatin alleles was similar to that of *m. longissimus* and *gluteus medius* of conventional cattle. It appears that there was a tenderness ceiling of 6.5 to 7.0. Normally tender muscles reached this with one inactive myostatin allele leaving no room for an effect of the second allele. With normally less tender muscles, there was scope for both alleles to have an effect.

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Table 1: Ranking of Holstein-Friesian (HF = 100) and beef × HF steers for production traits

Sire breed	HF[1]	HE	LM	PM	RO	BA	SM	BB	CH
Slaughter weight/day (g)	803	101	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	103	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 the beef crosses are expressed relative to HF = 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).
HE = Hereford; LM = Limousin; PM = Piedmontese; RO = Romagnola; BA = Blonde d'Aquitaine; SM = Simmental; BB = Belgian Blue; CH = Charolais; LW = Live weight
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=100) and beef × HF steers for muscle traits

Sire breed	HF	HE	LM	PM	RO	BL	SM	BB	CH
Muscle weight (g/day)	256	102	109	113	115	116	116	119	117
M. longissimus area[1]	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]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 3:Meat quality of progeny[1] from Holstein-Friesian cows and beef sire breeds

Sire breed	HE	AA	PM	LM	BB	CH	s.e.
pH (24 h post slaughter)	5.78	5.84	5.78	5.77	5.72	5.75	0.04
Colour (EEL value)[2]	23.1^{ab}	216^{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 4: Muscle chemical composition[1] and meat quality traits[2] of Holstein (HO), Frisian (FR) and Charolais × Holstein-Friesian (CH) steers

Sire breed	HO	FR	CH	s.e.
Chemical composition (g/kg)				
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[3]	4.9	4.5	4.2	0.48
Tenderness[3]	4.6	4.7	3.7	0.55
Flavour[3]	3.9	3.7	3.5	0.31
Overall acceptability[3]	3.4	3.4	3.0	0.33

[1]Mean of 7 joints from the entire side; [2]Mean of *m. longissimus* and *m. semimembranosus* [3]Scale 1 (low) to 8 (high). See Table 3 footnotes.
Source: Keane *et al.*, 2001

Table 5: Calving traits for beef breed bulls mated to Holstein-Friesian cows

Sire breed		AA	BA	BB	CH	HF	LM	SM
No. bulls		19	5	10	32	94	29	40
Calving difficulty (%)	Mean	2.7	6.3	3.7	4.7	1.9	4.2	3.6
	Range	0.3-8.5	1.0-17.8	1.3-5.2	1.2-19.6	0.0-6.1	0.2-18.8	1.0-9.8
Calf mortality (%)	Mean	1.5	1.5	2.6	2.0	1.5	2.3	1.9
	Range	0.0-4.2	0.4-2.9	0.8-4.1	0.3-4.2	0.2-3.3	0.6-8.6	0.1-3.9
Gestation length (days)	Mean	281	288	283	286	283	286	285
	Range	280-282	286-289	281-284	283-287	282-284	284-290	283-288

See Table 1 footnotes.
Source: Department of Agriculture, Food and Rural Development, 1998

Table 6: Production and reproduction traits of Friesian cows mated to Friesian, Hereford and Charolais bulls

Sire breed	Friesian	Hereford	Charolais
Current lactation[1]	100 (4179)	98	97
Subsequent lactation[1]	100 (4081)	99	99
Calf birth weight (kg)	42.2	43.1	47.3
Gestation (days)	283	286	287
Calving difficulty score[2]	1.69	1.70	1.97
Days to 1st service	68	69	67
Days open	86	85	92
Services per conception	1.6	1.5	1.9

[1]Relative to Friesian = 100, actual Friesian yield (kg) in brackets; [2]Scale 1 (no assistance) to 5 (Caesarean)
Source: More O'Ferrall and Ryan, 1990

Table 7: Production data for 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/d))	1021	1039	1044	1134
Final live weight (kg)	460	470	482	512
Dressing (g/kg)	615	614	620	617
Hot carcass (kg)	293	300	304	325

Source: Germ Plasm Evaluation Program, 1974

Table 8: Comparison of straight-bred and reciprocal crosses for Hereford (H) and Senepol (S) cattle

Breed type	H × H	H × S	S × S	S × 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 feed 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
Marbling score	370	381	370	369	1.4
Lean colour score	2.2	2.5	2.4	2.7	13.9
Warner-Bratzler score (kg)	4.8	4.3	4.5	5.3	2.2

Source: Chase *et al.*, 1998

Table 9: Non carcass parts and cold carcass (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, [3]CH = late maturing.
[2]Not measured, estimated by difference. See Table 1 and Table 3 footnotes.
Sources: More O'Ferrall and Keane 1990; Keane *et al.*, 1990

Table 10: Carcass composition (g/kg) 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 and other tissue	170[a]	155[b]	168[a]	1.9
Muscle	598[a]	575[b]	630[c]	5.6

See Table 1 and Table 3 footnotes.
Source: Keane *et al.*, 1990

Table 11: Side composition (g/kg) of steers of three biological types at 120 kg and 180 kg carcass side weights

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 Table 1 footnotes.
Source: Estimated from Keane *et al.*, 1990

Table 12: 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		**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 Table 1 footnotes.
Source: Estimated from Keane *et al.*, 1991

Table 13: 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
Daily feed intake	91	77	89	83
Kill-out proportion	109	119	113	120
Muscle proportion	122	148	106	130
Fat proportion	67	28	97	46
Muscle lipid proportion	-	-	48	17

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

Table 14: Comparison of progeny from Holstein-Friesian dams and normal Charolais or doubled muscled Belgian Blue or Piedmontese sires

Sire breed	**Charolais**[1]	**B. Blue**[1]	**Charolais**[1]	**Piedmontese**[2]
Daily gain (kg)	1.24	1.20	0.98	0.90
Carcass gain (g/d)	696	692	553	523
Fat class[2]	2.87	2.97	3.85	3.85
Conformation class[2]	3.70	3.53	3.05	2.70
Feed conversion ratio	-	-	7.8	8.0
<u>*Carcass composition (g/kg)*</u>				
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; [2]See Table 1 footnotes.
Sources: [1]Hardy and Fisher, 1996; [2]Davies *et al.*, 1999

Table 15: 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 (g/kg)	575	588	579	597	632
Carcass weight (kg)	273	282	269	278	291
M. longissimus area (cm^2)	74.3	81.4	74.3	86.4	109
Yield (g/kg)[1]	507	523	504	525	565
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 (g)[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 16: 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