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Effect of Heterozygosity at the Double-muscle Locus on the Performance of Market Calves

W. C. Rollins, R. B. Thiessen, F. D. Carroll, and Moira Tanaka

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UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURAL SCIENCES

Trials conducted at the University of California (Davis) demonstrated the feasibility of producing market calves heterozygous for the double-muscling gene. On average, these calves compared to normal calves reached market weight at an earlier age, had carcasses with significantly more lean meat and lower quality grade, but with a negligible difference in meat acceptability, as shown by taste panel evaluations.

THE AUTHORS:

W. C. Rollins is Professor Emeritus, Department of Animal Science, and Geneticist in the Experiment Station, Davis.

R. B. Thiessen is Senior Scientific Officer, A.R.C., Animal Breeding Research Organization, Edinburgh, Scotland.

F. D. Carroll is Professor Emeritus, Department of Animal Science, and Nutritionist in the Experiment Station, Davis.

Moira Tanaka was Staff Research Associate, Department of Animal Science, Davis.

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INTRODUCTION

The body shape (conformation) associated with bovine muscular hypertrophy, commonly known as double-muscling, is a phenotypic expression of a homyzygous mutant genotype resulting from a monohybrid autosomal mode of inheritance (Rollins *et al.*, 1972). There is some evidence that the gene for double-muscling, while tending toward recessiveness in the British beef breeds, may tend towards dominance in some European continental breeds (Rollins, 1969*a*).

Double-muscled cattle have been reported to produce carcasses with 20 percent to 130 percent more lean meat and 30 percent to 50 percent less fat than normal cattle. Furthermore, due to reduced offal weight, double-muscled animals dress higher (Vissac, 1968; Pomeroy and Williams, 1962; Butterfield, 1966; Rollins, Julian, and Carroll, 1969).

Double-muscling has been reported over the years in many breeds throughout the world. Among the traditional beef breeds (Angus, Hereford, and Shorthorn) in this country, its highest rate of occurrence at present is in the Angus.

The double-muscled animal is not a useful market animal for the USA beef industry because of undesirable side effects, namely, calving problems (Hanset, 1967), reduced viability (Paci, 1935; W. C. Rollins, unpublished data), and questionable meat quality (tender, but too dry and bland in flavor, W. C. Rollins, unpublished data).

It, therefore, seemed logical to compare heterozygous calves with normal calves under controlled conditions to ascertain if the heterozygous calf, as an intermediate type, might have a positive net balance of advantages over disadvantages endowed by the mutant gene, thus making it competitive with the normal type market animal.

The experimental data in this study have been restricted to the above named breeds, because for many years they constituted the main component of the national beef herd. Evidence will be presented to support the following thesis:

> Fertilization of normal cows of the Angus, Hereford, or Shorthorn breeds with semen from double-muscled Angus bulls will produce heterozygous market calves that are leaner, but still of acceptable beef type and quality at desirable market weights and ages. Heterozygous heifer calves should be marketed and not saved for breeding.

METHOD

In this report the following symbolism is used:

m = the gene for muscular hypertrophy (double-muscled)

\+ = its normal allele

Genotype	Corresponding phenotype
mm	. . . Typical double-muscled animal which is extreme in appearance
m +	. . . Resembles the normal type, but on average is somewhat more muscular. Does not appear to be double-muscled.
+ +	. . . Normal type

Pictures of yearling bulls representing the three genotypes are presented in figure 1.

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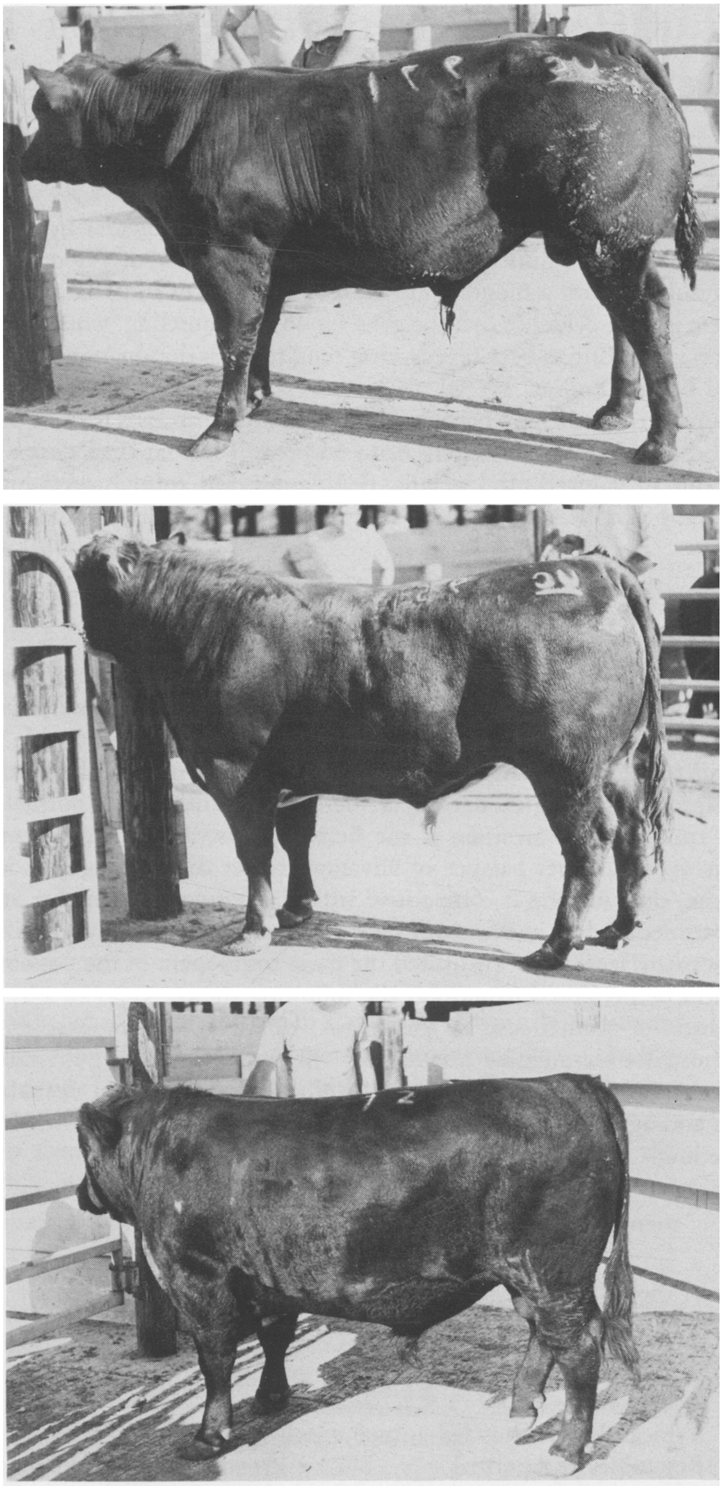

Fig. 1. Conformation of fed yearling bulls of three genotypes: (top) *mm*; (middle) *m*+; bottom ++.

Because *m* + calves are most efficiently produced by mating *mm* bulls to + + cows, such a system was compared under controlled conditions with one in which + + bulls were mated to + + cows. Consideration was given to as many of the factors as possible that influence the net return from a market calf—namely, conception rate, ease of calving, postnatal viability, growth rate, feed utilization, body composition and meat quality.

MATERIALS, RESULTS AND DISCUSSION

Conception rate

The *mm* bull × + + cow breeding system preferably calls for artificial insemination (AI) because *mm* bulls, although apparently equal to + + bulls for semen quality and libido, would on average have greater difficulty than + + bulls in natural service, especially under range conditions, because of locomotion problems of an anatomical nature (Oliver and Cartwright, 1968; W. C. Rollins, unpublished data). In small level pastures and drylots, however, *mm* bulls perform satisfactorily in natural service.

Ten *mm* Angus bulls were tested at the University of California, Davis (UCD) in natural service and/or artificial insemination on varying numbers of cows from one to 103. Each of these bulls proved to be fertile by producing one or more calves and when used in natural service had satisfactory libido.

Semen from each of the bulls was collected and frozen. For all of the bulls except one, the frozen semen was of acceptable quality. In the one exception the semen was from a bull that was very satisfactory in settling cows in natural service.

Under controlled conditions *mm* Angus bull 856 and + + Angus bull CO5 were used in AI on + + cows of comparable breeds to produce part of the 1970 calf crop. Eight cows were exposed to 856. The results were a conception rate of 87.5 percent and a 2.41 average number of inseminations per conception. Comparable figures for CO5 were 17 cows exposed resulting in a conception rate of 94.1 percent and a 1.75 average number of inseminations per conception.

Similarly *mm* Angus bull 981 and + + Angus bull C18 were used in AI to produce part of the 1974 and 1976 calf crops. Eighteen cows were exposed to 981. His conception rate was 77.8 percent and the average number of inseminations per conception was 1.43. For C18 the corresponding figures were 28 cows exposed, a conception rate of 71.4 percent and an average number of inseminations per conception of 1.35.

These results are similar to those reported from France, Italy, and Belgium, where *mm* bulls are in use in AI studs; experimentally in France but on a widespread commercial basis in Italy and Belgium (Rollins, 1969b).

Ease of calving

The UCD method for scoring ease of calving is the same as that in use at the U.S. Meat Animal Research Center (MARC), ARS-NC-13, March, 1974. This enabled us to compare ease of calving at the two locations (table 1). At UCD the sires in use were *mm* and + + Angus, while at MARC they were + + Angus. At each location the cow herds consisted of parous cows. At MARC, the cow breeds were Angus and Hereford, while at UCD they were Angus, Hereford, and Shorthorn.

From table 1 it is apparent that cows mated to *mm* bulls at UCD calved as easily or more so than those mated to the + + bulls at UCD and MARC.

TABLE 1.
TYPE OF PARTURITION FOR COWS MATED TO + + BULLS COMPARED WITH THOSE MATED TO *mm*.

Genotype and breed of sire	Number of sires	Location	Breed of dam*	Number of calves	Percent born with: No difficulty†	Percent born with: Calf-puller	Percent born with: C-section	Percent born with: Posterior presentation	Dead at or shortly after birth (percent)
+ + Angus	35	MARC	Angus and Herford	206	93	3	1	3	2
+ + Angus	4	UCD	Angus, Hereford, and Shorthorn and crosses thereof	39	97	0	0	3	0
mm Angus	7	UCD	Angus, Hereford and Shorthorn, and crosses thereof	119	100	0	0	0	1

*At UCD all cows and calves are nondouble muscled, i.e., they are not *mm*.
†No assistance or minor hand assistance.

Viability to yearling age of calves

Viability to yearling age of live born *m*+ and + + calves produced in the UCD herd is presented in table 2. The *m*+ calves were sired by several *mm* Angus bulls and the + + calves by several + + Angus bulls. The data presented support the hypothesis that *m*+ calves are no less viable than + + calves. Hybrid vigor due to crossbreeding favored the + + calves, since 70 percent of them were crossbred while 53 percent of the *m*+ were.

TABLE 2.
RELATIONSHIP OF LIVE-BORN CALF GENOTYPE
TO CROSSBREEDING AND VIABILITY TO ONE YEAR OF AGE

Genotype*	Number	Percentage crossbred	Percentage viability (yearlings)
m+	137	53	96
+ +	50	70	94

*On the basis of pedigree.

Growth and Feed Utilization

Literature review

Reports in the literature on the effect of double-muscling on growth and feed utilization are mainly for European breeds.

For early growth, before 8 months of age, when milk is a major constituent of the ration, Raimondi (1961) reported essentially equal rates of gain for double-muscled and normal calves. Neuvy and Vissac (1962) reported superior gains for the double-muscled, and Carbone (1940) reported superior gains for the normal. In the last case cited, the double-muscled calves' feed intake was 10 percent less than that of the normal calves.

Valls-Ortíz, Ménissier, and Vissac (1972) reported two studies in France in which *m*+ calves were compared with + + calves for growth from birth to 60 days of age (an age at which milk-fed veal calves are marketed in some regions). In the first study six double-muscled and six normal Charolais bulls were mated to normal cows in the provinces of Rhone and Aveyron. In the former province the cows were mainly of dairy breeds, while in the latter they were generally of unimproved local breeds or beef breeds and, as a result, were not such good milkers as those in Rhone. In the Province of Rhone the *m*+ calves gained 1.22 kg per day, which was a 2.1 percent increase over the + + calves' gain. In the Province of Aveyron the *m*+ calves gained 1.00 kg per day, which was 1.2 percent less than the normal calves' gain.

In the second study offspring were produced by 37 double-muscled and 83 normal Charolais bulls mated to normal cows in the provinces of Aveyron, Haute-Loire and Rhone. The *m*+ calves gained 1.14 kg per day, which was 2.0 percent more than the + + calves' gain. A statistical test of significance for this difference was not reported.

However, it was reported that the *m* + calves were heavier than the + + calves (P < .01) at birth and at 60 days of age.

In summary these data suggest an advantage in growth rate for double-muscled over normal calves when fed an adequate milk ration. For a ration which included roughage and concentrates as well as milk (milk rationed), there appeared to be little difference between the two types provided the double-muscled calves consumed as much feed as the normals.

For growth from 5 to 15 months of age, with milk absent from the rations, four out of seven cases reviewed showed double-muscled calves consumed less feed than normals and in each case gained less (Trillat, 1967; Hanset and Demoulin, 1966; Grenet, 1964). In the last study cited feed consumption was reported in terms of dry matter consumed per 100 kilograms of liveweight. In two cases double-muscled calves consumed an equal or greater amount of feed than the normals and outgained them (Raimondi, 1961, and Trillat, 1967). In the former study the average initial weight of the double-muscled calves was 2 percent greater than that of the normal calves. Both groups consumed the same amount of feed. In the remaining case, in which Charolais heifers were on pasture, the normals outgained the double-muscled calves (Vissac, Menissier, and Perrau, 1973). Although no feed consumption figures are available for the last reference cited, it is likely that the double-muscled heifers consumed less than the normal heifers. In four out of six of the above cases, for which requisite data are reported, double-muscled calves required fewer units of feed per unit of gain than normals. In two of the trials reported above (Hanset and Demoulin, 1966) the double-muscled calves had lighter initial weights than the normals (2.3 percent and 7.7 percent, respectively) and gained less (.9 percent and 2.2 percent, respectively) but in each case consumed about 22 percent less feed. This far greater feed utilization efficiency (in terms of units of feed per unit of gain) for the double-muscled calves reflects the leaner composition of their gains. An analysis of the seventh, eighth and ninth rib cut averaged over bulls and heifers gave 72.7 percent lean meat, 13.2 percent fat, and 14.1 percent bone for the double-muscled calves and 58.5 percent lean meat, 26.1 percent fat, and 15.4 percent bone for the normal calves.

Bibe *et al.* (1974*a*) reported on a growth comparison between *m* + and + + calves for the period 8 to 15½ months of age. Twenty-seven *m* + and 26 + + calves were produced from matings of three double-muscled and three normal Charolais bulls to normal cows of the French Pie Noir, a dairy breed. Sex of calf effects and length of time on feed were adjusted by least squares analysis. The ration consisted of a mixture of two-thirds dried alfalfa, one-third dried beet pulp and contained 100 g of digestible nitrogen per kilogram. Average daily gain for the *m* + calves was 1.192 kg, which was 2.4 percent superior to the gain of the + + calves. The *m* + calves consumed 2.5 percent less feed per day and required 5.2 percent less feed per kg of gain than the + + calves. The authors in a following paper (1974*b*) reported that the *m* + calves had leaner carcasses (P < .05) than the + + calves.

Bouton *et al.* (1978) compared the growth and carcass composition of 14 *m* + and 19 + + Angus × Jersey steers. They were on pasture for 7 months following weaning at 8 months of age and later were fed a hay-lupin ration in the feedlot to about 500 days of age. The *m* + steers had significantly heavier and leaner (as indicated by less subcutaneous fat and larger ribeye areas) carcases at a significantly younger age than the + +.

These results suggest that for non-milk rations consisting of roughage and/or concentrates *mm* animals tend to have less appetite and as a consequence tend to gain less. However, the double-muscled calves tended to utilize their feed more efficiently than the normals, which reflected a leaner composition of their gains.

The effect of concentrates in the ration on the growth of double-muscled Charolais steers was shown by Neuvy and Vissac (1962). By varying the proportion of concentrates to roughage in their feeding trials, it was shown that at the higher level of concentrates the double-muscled steers outgained the normal steers, but at the lower level the reverse was true.

Paci (1935) reported average monthly weights from birth to 12 months of age of double-muscled (DM) and non-DM Piedmont calves raised on their owners' farms. At all ages the DM were heavier than the non-DM calves. For example, at 6 months the advantage was 15 percent while at 12 months it was 14 percent. However, a serious limitation of these data was the failure to report male and female weights separately, especially in view of a 72 bull:28 heifer sex ratio at birth for the DM calves as contrasted to a 54 bull:46 heifer ratio for the non-DM calves.

Trials conducted at UCD

In the trials conducted at UCD the *m* + offspring of three *mm* Angus bulls (herd numbers 856, 644, and 981) were compared with the + + offspring of two + + Angus bulls (herd numbers CO5 and C18). 856 and 644 were tested in one trial along with CO5 (Trial I) and 981 in another trial along with C18 (Trial II).

The *mm* bulls were purchased as weanling or yearling calves from three different breeders who produced them inadvertently through unplanned *m* + X *m* + matings. In a sense it might be said we selected these *mm* bulls at random.

In order to test the *m* + calves more stringently we selected the + + sires that were to produce the + + control calves on the basis of merit. CO5 (Executor of Hidden Hills, 3853809) was a PRI Certified Meat Sire (Koch, 1972, p. 152) while C18 (Ankonian TN Emulous 27140, 6639774) was a reference sire in the Angus Sire Evaluation, the results of which are summarized in the Group 3 Report, Fall 1975, of the American Angus Association. In the test just mentioned, registered Angus bulls were evaluated (ranked) on the basis of progeny tests for breeding values for the traits 205-day adjusted weight, yearling adjusted weight, carcass cutability and USDA carcass quality grade.

Since 981 was progeny-tested with reference sire C18, his breeding value can be ranked with those of the 54 Angus sires tested. Appendix 1 sets forth the method for making this comparison.

Frequency distributions of genotype and breed of calves used in the growth and body composition studies and that of their dams are presented in table 3.

The dams of the 1970 calf crop (from which the calves used in Trial I were drawn) were members of the U.C. experimental herd described in table 2 (Rollins *et al.*, 1972). The dams of the 1974 and 1976 calf crops (from which the calves used in Trial II were drawn) in the main were Herefords from the University's commercial range herd.

As can be seen in table 3 some of the dams producing *m* + calves were themselves *m* + . Mated to *mm* sires they could produce *mm* or *m* + calves.

An index (named I_2) for measuring muscularity of conformation was developed by Rollins *et al.* (1972). As shown in table 3 of that reference, there was no overlap in the I_2 distributions of *mm* and *m* + calves. Hence, *mm* and *m* + calves resulting from *mm* × *m* + matings were distinguishable.

Since the *m* + calves were produced by both *m* + and + + dams, whereas the + + calves had only + + dams, this raises the question of whether or not *m* + dams have a different milk production from + + dams. The report of Lavin Arenas (1964), using

TABLE 3
FREQUENCY DISTRIBUTIONS OF GENOTYPE AND BREED OF CALVES AND THEIR DAMS* USED IN THE GROWTH AND BODY COMPOSITION STUDIES

Cattle unit, breed, and genotype	Trial I (1970) *m*+ calves: Number of calves	*m*+ calves: Proportion of total number	+ + calves: Number of calves	+ + calves: Proportion of total number
Calves (total)	33	—	14	—
Angus	20	.61	7	.50
Crossbred	13	.39	7	.50
	Number of dams		Number of dams	
Dams (total)	33		14	
Angus	20	.61	7	.50
Hereford	3	.09	3	.21
Shorthorn	0	0	1	.07
Crossbred	10	.30	3	.21
Genotype (dam)				
+ +	13	.39	14	1.00
m+	9	.27	0	0
+ + or *m*+	11	.33	0	0

	Trial II (1974 and 1976) No. *m*+ calves			No. + + calves		
	1974	1976	Total	1974	1976	Total
Calves (total)	7	17	24	12	13	25
Angus	0	2	2	0	2	2
Crossbred	7	15	22	12	11	23
	Number of dams			Number of dams		
Dams (total):	7	17	24	12	13	25
Angus	0	2	2	0	2	2
Hereford	6	13	19	11	10	21
Crossbred	1	2	3	1	1	2
Genotype (dam):						
+ +	6	16	22	12	13	25
m+		1	2	0	0	0

*The calves' sires were Augus.

Asturienne cattle, suggests that the presence of the *m* gene in heterozygous condition depresses milk yield compared with normal, and that in homozygotes (*mm*) milk yield is depressed further. Studies in the Piedmont and Charolais breeds provide other evidence of a marked depressing effect on total and daily milk yield of the double-muscled (*mm*) condition (Raimondi, 1963; Anonymous, 1966; Vissac, Logeay, and Perreau, 1970; Vissac *et al.*, 1974).

These studies suggest that if there was some effect on milk production of the *m* gene in heterozygous condition it would be toward depressing it, rather than elevating it. Hence, if the use of *m* + dams introduced a bias in the comparison of weaning weights of *m* + and + + calves, it was apt to favor the + + calves.

Since all calves had Angus sires, they were either Angus or crossbred. Within each trial, the similarity in proportion of these two breed types for *m* + and + + calves suggested little to be gained by the adjustment of traits for crossbreeding effects. By a similar line of reasoning no adjustment of traits was made for the effects of breed or crossbreeding of dam.

The 1970 calf crop was sired by 856, 644, and CO5. Sires 856 and 644 each produced *mm* and *m* + offspring, while CO5 produced + + offspring. The calves were weaned around 6 months of age, and each calf's weight was adjusted to 180 days of age and for age of dam. The following least squares model was used to compare the *m* + with the + + calves:

$E(Y_{ijk}) = \mu + a_i + b_j$ wherein the deviations from the general mean (μ) are: a_1 for male progeny, a_2 for female progeny; b_1 for *m* + progeny of *mm* sire 856, b_2 for *m* + progeny of *mm* sire 644 and b_3 for + + progeny of + + sire CO5.

Although a comparison of *m* + with + + calves was the main objective, a comparison of the growth rates of *mm* with + + was of interest to see how it would compare with the trials just reviewed of European cattle.

Seven *mm* calves were compared with 14 + + controls. The data were adjusted for effects of sex, breed, and age of dam. The calves suckled dams to 6 months of age. The dams were on good feed. The *mm* calves gained .907 kg per day from birth to weaning, which was a 7.0 percent advantage over the + + calves. In the same trial, 33 *m* + calves outgained the + + calves by 7.5 percent, but neither of these differences were statistically significant.

For the period 180 days (weaning) to 365 days of age, the calves were on an *ad lib* ration of 75 percent roughage and 25 percent concentrates for bulls and 70 percent roughage and 30 percent concentrates for heifers. The *mm* calves gained .708 kg per day, which was 13.8 percent less than that of the + + ($P < .05$). The *m* + calves gained 4.4 percent more than the + + calves ($P > .05$).

For two months of the growth period under discussion feed intake was measured for six *mm*, 20 *m* + and 14 + + calves of those on trial. Daily feed intake was measured in units of weight of feed per unit of metabolic body size (Kleiber, 1932). The *m* + calves consumed 2.0 percent more feed per day than the + + calves. Since this was a nonsignificant difference the *m* + and + + feed intake data were combined and labeled non *mm*. The *mm* calves consumed 11.0 percent less feed than the non *mm* ($P < .0005$) (Nott, 1973).

This reduced appetite of *mm* calves undoubtedly accounted for a significant amount of the reduction in their growth rate, compared to the performance of the + + calves.

Although there were no significant differences between the growth rates and feed intakes of *m* + and + + calves, the poor performance of the *mm* calves on the high roughage ration under discussion led to a decision to compare *m* + and + + under the more stringent conditions of the following trial.

The relative performance of *m* + and + + calves were compared for two rations, one consisting of 80 percent concentrates and the other solely of alfalfa cubes. These rations are further described in table 4.

TABLE 4.
COMPOSITION OF POSTWEANING FEEDLOT RATIONS
(APPROXIMATELY 90 PERCENT DRY MATTER)

a_1: High-concentrate ration for 1974 calf crop

Ingredient	Percent
Barley	72.0
Alfalfa	8.0
Sudan	4.0
Molasses dried beet pulp	4.0
Fat	2.0
Molasses	5.0
Cottonseed meal	3.0
Urea	1.0
Trace minerals	.4
Dicalcium phosphate	.3
Oystershell	.3
Ration analysis, on an as-fed basis*	
Crude protein, percent	13.2
Digestible protein, percent	9.5
Metabolizable energy, kcal/g	2.56

a_2: Alfalfa cube ration for 1976 calf crop
(composition determined from proximate analysis).

Proximate analysis	
Crude protein, percent	25.6
Digestible protein, percent†	15.5
Metabolizable energy, kcal/g†	1.96

*Estimated from Tables of Feed Composition (NAS-NRC, Publication 1684, 1969).
†Estimated from the proximate analysis using tables in J. H. Meyer and L. G. Jones, 1962, Bulletin 784. California Agricultural Experiment Station.

Pre-slaughter traits studied were average daily gain from 205 days of age (weaning) to 365 days of age, 205-day adjusted weight, 365-day adjusted weight, amount of feed consumed daily and units of feed per unit of weight gain. At the start of the feeding trial the *m* + calves on average were .5 percent lighter in weight than the + + calves. Due to the smallness of this difference, body weight effect was not considered in comparing the feed efficiency of the two groups. Post-slaughter traits studied in this trial will be discussed in the section on body composition.

The calves were sired by bulls 981 and C18, each used on the same cow herd to produce two calf crops, one in 1974 and the other in 1976. The 80 percent concentrate ration was fed to the 1974 calf crop and the alfalfa cube ration to the 1976 calf crop.

The factorial model used to test for the existence of a ration by genotype interaction is given in Appendix 2 and the results of the test in table 5. The statistical method used is given on pages 362 and 363 of Scheffé (1959).

In summary, the level of roughage in the feedlot rations did not effect the relative growth rate, feed consumption or feed efficiency of calves heterozygous for the double-muscling gene *m*, (*m* +), and calves lacking the double-muscling gene, (+ +), (i.e. the ac interaction term approached statistical significance in none of the traits studied, table 5). Hence, in making feedlot decisions on whether to buy feeder calves heterozygous for the double-muscling gene, (*m* +), or those lacking it, (+ +), there is no need to take into consideration the level of roughage in the ration to be fed.

Since the interaction effects in the model given in Appendix 2 proved to be nonsignificant they were deleted and the main effects were estimated in a least squares analysis.

Averaged over the 1974 and 1976 calf crops for the period 205 to 365 days of age, the *m* + calves gained 1.28 kg per day, which was 4.6 percent more than the + + calves gained. Daily feed consumption was 8.95 kg for calves of both genotypes. Feed efficiency measured as kilograms of feed per kilogram of gain was 7.22 for the *m* + calves, which was 5.6 percent less than for the + + calves, ($P < .05$). For the suckling period, birth to 205 days, the *m* + calves gained .81 kg per day, which was .6 percent less than the + + calves gained.

Averaged over the 1970, 1974, and 1976 calf crops the *m* + calves gained 3.0 percent more than the + + from birth to weaning. However, they weighed 2.8 percent less at birth. This reduced their weaning weight advantage over the + + calves to 1.6 percent. From weaning to 365 days of age the *m* + calves compared with the + + calves gained 4.7 percent more. None of these differences were statistically significant.

As previously mentioned, since 981 was progeny-tested with reference sire C18, his breeding value can be ranked with those of the 54 Angus sires tested by the American Angus Association. For 205-day adjusted weight, 981 was ranked between the 43rd and 44th bull while for yearling adjusted weight, he was ranked between the seventh and eighth bull.

It appears reasonable to say that for growth rate, the 54 bulls in the test constitute a sample of the top end of the bulls in the Angus breed, since their breeders are dedicated to performance testing and picked their better bulls to enter in the test. In support of this latter statement the report gives weight ratios of individual performance for weaning weight and yearling weight of 31 and 25, respectively, of the 54 sires entered in the test. For weaning weight these averaged 114 and for yearling weight, 111.

Heritability is around 30 percent for weaning weight and 50 percent for yearling weight. If we assume, as the other evidence that has been presented suggests, that the gene for double-muscling, *m*, has little direct effect upon growth rate under conditions of the cow-calf system in the USA, then 981's rank for weaning weight (between the 43rd and 44th bull) is not surprising since he was competing in a progeny test with a highly selected group of Angus bulls.

On the other hand, 981's high ranking for yearling weight (between the seventh and eighth bull) most likely reflects a leaner composition of the postweaning gains for his *m* + calves as compared with the + + calves of the 54 bulls in the test. Evidence for a leaner composition of *m* + gains will be presented later.

In conclusion, it appears that the double-muscling gene, *m*, has little direct effect

TABLE 5.
RESULTS OF TESTS FOR RATION BY GENOTYPE INTERACTIONS

Source of variation	Degrees of freedom	Mean squares				
		205-day adjusted weight	Average daily gain	365-day adjusted weight	Daily feed consumed	(kg of feed) per (kg of gain)
a (Ration)	1	231	11,935**	25,425**	210	129,032**
b (Sex)	1	3,570*	7,875**	40,755**	741**	26,912**
c (Genotype)	1	55	325	496	1	3,784*
ab (Ration X Sex)	1	2,556*	231	703	21	15,138**
ac (Ration X Genotype)	1	0	91	210	45	220
bc (Sex X Genotype)	1	325	171	1,596	105	60
abc (Ration X Sex X Genotype)	1	55	190	903	78	60
Error	41	553	109	831	55	695

*$p \leqq .05$.
**$p \leqq .01$.

upon growth rate except early in life on an adequate all-milk diet, under which conditions its effect is positive. It can, however, effect growth rate indirectly through restriction of appetite and leaner composition of postweaning gains.

The restrictive effect of the *m* gene on appetite was reported for calves with an *mm* genotype in the literature reviewed and in the trials at UCD. There is no evidence, however, to suggest that it affects the appetite of calves with an *m*+ genotype in the British beef breeds in the USA.

The leaner composition of postweaning gains for *m*+ calves in part explains their superiority over + + calves for growth rate and feed utilization, when the latter is measured as units of feed per unit of gain.

Body Composition

Literature review

As the name of the trait suggests the homozygous genotype (*mm*) for muscular hypertrophy or double-muscling endows a bovine with a striking increase in muscularity. The following review of the literature bears out this thesis.

In six studies, namely, Pomeroy and Williams (1962), Raimondi (1962), Butterfield (1966), Hanset and Demoulin (1966), Rollins, Julian, and Carroll, (1969) and MacKellar and Ouhayoun (1973), the double-muscled cattle, on average, had a muscle to bone ratio 60 percent greater than that of their normal controls. Fat to bone ratio (reported in five of the studies) was, on average, 26 percent smaller for the double-muscled cattle than for the normal controls. On average, in four of the studies in which it was reported, the ratio of doublemuscled animals to normal was .98 for skeletal weight.

The literature also contains two studies in which *m*+ calves are compared with + + calves.

Mason (1963) in a study of British Friesian slaughter steers compares the progeny of a bull (identification no. 45) known to be either *mm* or *m*+ with the progenies of three normal (+ +) bulls. All bulls were presumably mated to + + cows. Thus bull 45's progeny (10 in number) all had *m*+ genotypes or a mixture of *m*+ and + + genotypes. Each of the normal bulls had nine offspring. Dissection of the 10th rib cut yielded on average 57.4 percent separable lean, 18.3 percent separable fat, and 3.69 muscle to bone ratio for bull 45's offspring. The comparable figures for the average offspring of the three + + bulls were 50.8 percent, 24.1 percent, and 3.25 percent.

In the section on growth and feed utilization, a comparison between *m*+ and + + calves made by Bibe, *et al.* (1974a) was reviewed. These authors in a followup paper (1974b) involving the same calves reported that dissection of the 11th rib cut yielded on average 65.0 percent muscle and 20.3 percent fat for the *m*+ calves and 62.8 percent and 23.3 percent, respectively, for the + + calves. Thus, on average, the *m*+ calves' proportion of muscle was 3.5 percent greater and their proportion of fat 12.9 percent less than the corresponding figures for the + + calves. The average chilled carcass weight of the *m*+ calves was 284.5 kg and that of the + + calves 278.3 kg.

Trials conducted at UCD

In the trials at UCD the calves went directly to the feedlot at weaning and were fed to an age constant endpoint of 16 months for bulls and 15 months for heifers. The following body composition traits were studied:

1) cutability percentage—percent closely-trimmed boneless retail cuts from the round, loin, rib, and chuck = 51.34 − 5.784 (fat thickness over ribeye muscle, in.) − .462 (kidney, pelvic and heart fat, %) + .740 (ribeye area, sq. in.) − .0093 hot carcass weight, lb.) (American Meat Science Association and Beef Improvement Federation, 1972.).
2) weight of trimmed retail cuts per day of age—equals carcass weight times cutability percentage (expressed as a decimal fraction) divided by slaughter age in days.
3) percentage of fat in the carcass—an estimate based upon carcass density (see appendix 3).
4) non-fat carcass weight as a percentage of shrunk slaughter weight—an estimate based upon carcass density (see appendix 3).
5) degree of marbling—an estimate of the degree of fat dispersed within the meat and is evaluated at the ribeye muscle (*longissimus dorsi*) between the 12th and 13th rib (estimated by a USDA meat grader).
6) USDA carcass quality grade (estimated by a USDA meat grader).

None of these traits was found to have a statistically significant ration by genotype interaction ($P > .10$ in each instance). The design of the test used is given in appendix 2.

Thus, taking into consideration the growth-related traits previously discussed, for none of the traits studied at UCD, pre- or post-slaughter, was the relative performance of *m* + and + + calves influenced by the percentage of roughage in the feedlot ration fed.

For traits one through six least squares estimates were made of the general mean, u, and of the genotypic difference, *m* + - + +. Separate estimates were made for the 1970 calf crop (trial I) and for the 1974 and 1976 calf crops (trial II). The statistical models used to analyze these two trials have been given previously. These estimates are presented in table 6.

Traits five and six will be discussed further in the following section dealing with meat quality.

Using the average + + calf as a standard, the average *m* + calf was 3.1 percent higher in cutability percentage (i.e. $\frac{(m+ \; - \; ++)}{(\; ++ \;)} 100 = 3.1$), 7.9 percent higher in weight of trimmed retail cuts per day of age, 10.9 percent lower in percentage of fat in the carcass, and 6.7 percent higher in non-fat carcass weight as a percentage of slaughter weight. For these traits in the order given above the *m* + − + + estimate was 5.3, 4.7, 6.3 and 6.9 times its standard error, respectively.

If $\frac{(m+ \; - \; ++)}{(\; ++ \;)} 100 = 6.7$ percent, the estimate found for the trait non-fat carcass weight as a percentage of shrunk slaughter weight, is used as an estimate for the trait we are really interested in, namely, lean carcass weight as a percentage of shrunk slaughter weight such an estimate may be biased downward (see appendix 3).

According to Cole (1966, page 40) an average + + calf with 30 percent carcass fat

TABLE 6
LEAST SQUARES ESTIMATES OF THE GENERAL MEAN, μ, AND OF THE GENOTYPIC DIFFERENCE, $m+\ -\ ++$, FOR BODY COMPOSITION TRAITS

Trait	Trial I: General Mean μ	Trial I: $m+ - ++$ and its standard error	Trial II: General Mean μ	Trial II: $m+ - ++$ and its standard error	Unweighted average of trials I and II: General Mean μ	Unweighted average of trials I and II: $m+ - ++$ and its standard error*	$\left(\frac{m+ - ++}{++}\right)100$
Cutability percentage	51.59	1.51 ± .42	50.32	1.65 ± .42	50.96	1.58 ± .30	3.1
Weight of trimmed retail cuts per day of age, g	313.3	25.17 ± 8.14	315.0	22.72 ± 6.10	314.2	23.95 ± 5.08	7.9
Percentage of fat in the carcass	28.54	-3.01 ± .88	29.55	-3.71 ± .60	29.04	-3.36 ± .54	-10.9
Non-fat carcass weight as a percentage of shrunk slaughter weight	45.53	2.80 ± .73	45.17	3.07 ± .43	45.35	2.93 ± .43	6.7
Degree of marbling, 1/3 grade†	10.25	-2.90 ± .68	11.10	-2.90 ± .62	10.68	-2.90 ± .46	-24.1
USDA carcass quality grade, 1/3 grade‡	9.51	-1.11 ± .32	9.75	-1.11 ± .32	9.63	-1.11 ± .23	-10.8

*Trials I and II are considered independent, because the sires and cow herd used in trial I were unrelated to those used in trial II. In trial I the standard error estimates of $m+ - ++$ are based on 43 degrees of freedom while in trial II the corresponding number is 45.
†slight = 7, 8, 9; small = 10, 11, 12; modest = 13, 14, 15; etc.
‡good = 7, 8, 9; choice = 10, 11, 12; prime = 13, 14, 15.

would have 13 percent bone and 58 percent lean, giving a bone-to-lean ratio .23 (the calves in our study had carcasses averaging about 30 percent fat). With a shrunk slaughter weight of 456.6 kg (1000 lb) it would have 162.9 kg of lean carcass meat ($\frac{1}{1.23}$ (.4388) (456.6) = 162.9). The figure .4388 is the + + average for non-fat carcass weight as a percentage of shrunk slaughter weight, expressed here as a decimal fraction. It is equal to $\mu + 1/2\ (m+ \ - \ ++)$, table 6. Using the estimate being discussed an *m* + calf with 456.6 kg. shrunk slaughter weight would have .067 × 162.9 kg. = 10.9 kg. (24 lb.) more lean carcass meat than a + + calf with the same shrunk slaughter weight. As indicated in appendix 3 the size of this *m* + superiority over + + is probably an underestimate.

For the trait cutability percentage 981 the *mm* Angus bull that sired the *m* + calves in the 1974 and 1976 calf crops ranked between the first and second of the 54 bulls tested in the American Angus Association Sire Evaluation Program (see appendix 1).

In conclusion, a review of the literature and an analysis of trials conducted at UCD leave no doubt that the double-muscle gene, *m*, both in the *mm* and *m* + genotypes is associated with carcasses significantly leaner than those of animals with a + + genotype.

For a given slaughter weight, the increase in lean meat in the carcass of the average *m* + animal over that in the average + + animal's carcass is large enough to be not only statistically significant but also of practical importance to the beef industry.

Meat Quality

USDA carcass quality grade and degree of marbling

USDA carcass quality grade is a traditional standard of carcass quality and, by implication, of meat quality. There is a high correlation between USDA carcass quality grade and marbling score, the more marbling the higher the carcass quality grade. The degree of marbling is also highly correlated with the amount of fat in the carcass. It therefore comes as no surprise that *m* + animals on average have lower carcass quality grades and lower marbling scores than + + animals. In table 6 it is seen that *m* + − + + and its standard error is −2.90 ± .46 for degree of marbling and −1.11 ± .23 for USDA carcass quality grade. The average carcass quality grade for *m* + animals was 9.08 (high good) and for + + animals 10.19 (low choice). Considering the sexes separately, *m* + bulls averaged 8.40 and + + bulls 8.90 while *m* + heifers averaged 10.00 and + + heifers 11.50.

For USDA carcass quality grade 981, the sire of the *m* + calves in the 1974 and 1976 calf crops ranked between and 53rd and 54th of the 54 bulls tested in the American Angus Association Sire Evaluation Program (see appendix 1).

Since the *m* + calf on average produces more lean meat than the + + calf, the practical significance of this *m* + superority should be evaluated in terms of trade-offs against the + + animal's higher average USDA carcass quality grade, such trade-offs reflecting various combinations of markets and consumer preferences.

Taste panel trials and results

Taste panel evaluations were made on meat samples taken from the *longissimus* (loin) and *semimembranosus* (round) muscles of 26 pairs of + + and *m* + animals.

Panel members evaluated the samples for tenderness, juiciness, meat flavor, and overall acceptance. Each trait was scored on a 1 to 9 point scale. For tenderness, 9 = very tender, 7 = tender, 5 = slightly tough, 3 = tough and 1 = very tough. For juiciness, 9 = very juicy, 7 = juicy, 5 = slightly dry, 3 = dry and 1 = very dry. For meat flavor, 9 = very strong, 7 = strong, 5 = moderate, 3 = slight and 1 = none. For overall acceptance, 9 = highly acceptable, 5 = moderately acceptable and 1 = not acceptable.

A description of meat sample preparation and sensory methods used by the taste panel is given in Carroll, *et al.* (1978).

The taste panel results for each trait were statistically analyzed, using the following model:

$$Y_{ijk} = \mu + a_i + b_j + c_1X_{1jk} + c_2X_{2jk} + e_{ijk}$$

where Y_{ijk} = the trait score difference, + + − *m* +, of the k[th] pair in the ij[th] subclass; X_{ijk} = the marbling score difference, + + − *m* +, of the k[th] pair in the ij[th] subclass.

The ij[th] subclass is defined as follows: i, for sex, = 1 for bulls and 2 for heifers. j, for calf crop, = 1 for 1970, 2 for 1974 and 3 for 1976.

$\mu + a_i$ = the average trait difference, + + − *m* +, for the i[th] sex, adjusted for marbling.

$(\mu + a_i) + \frac{\Sigma X_{ijk}}{n_i} c_i$ = the average trait difference, + + − *m* +, for the i[th] sex, not adjusted for marbling.

c_i = the pooled intragroup regression of pairwise trait difference on pairwise marbling difference for the i[th] sex.

Separate regression coefficients were estimated for the sexes, namely, c_1 for bulls and c_2 for heifers, because the average marbling score was considerably higher for heifers than for bulls, namely, 14 and 9, respectively, or decoded, modest and slight plus (table 7).

Estimating + + − *m* + for bulls and heifers separately has the advantage of studying the effect of the *m* gene upon meat quality and acceptance at two distinct levels of marbling, as just indicated, and consequently at two levels of USDA carcass quality grade. For bulls the average carcass quality grade was high good, while for heifers it was average choice.

Although none of the regression coefficients of + + − *m* + for trait scores on + + − *m* + for marbling scores was statistically significant (table 8), there appeared to be a pattern amongst them. If we think of each trait as a measure of meat acceptance, and then look at the distributions of the eight regression coefficients (for four traits X two muscles) within each sex, we find that for bulls the regression coefficients range in value from .01 to .40 averaging .13. For heifers they range in value from −.14 to .07 averaging −.03. These patterns suggest that at the level of finish of bulls, namely, high good, the greater amount of marbling of the + + compared to the *m* + comtributes a bit to the apparently slightly higher acceptability of the + + meat, while for heifers with their higher level of finish, namely, average choice, the higher marbling of the + + appears to have an inconsistent and on average a negligible effect upon the relative acceptance of the + + and *m* + meat samples.

TABLE 7.
TASTE PANEL SCORES (AVERAGED) FOR MUSCLE TRAITS OF BULLS COMPARED TO THOSE OF HEIFERS

	Bull			Heifer		
Trait and muscle	No. of + +, *m* + pairs of meat samples	Marbling score Average*	Trait average	No. of + +, *m* + pairs of meat samples	Marbling score average*	Trait average
Tenderness						
longissimus			6.35			6.77
semimembranosus			4.82			5.12
Juiciness						
longissimus	12	9.00	6.16	14	13.79	6.16
semimembranosus			4.46			4.37
Flavor						
longissimus			5.62			5.75
semimembranosus			5.18			5.21
Overall acceptance						
longissimus	9	8.72	5.58	11	14.00	6.07
semimembranosus			3.74			4.06

*Slight = 7, 8, 9; small = 10, 11, 12; modest = 13, 14, 15; etc.

Once again, thinking of each trait as a measure of meat acceptance, let us study the distributions of the eight values of + + − *m* + (for four traits X two muscles) within each sex (table 8). For bulls the values range from .62 to − .01, averaging .26. For heifers the values range from .41 to −.35, averaging .06. For both bulls and heifers these differences in acceptance of + + and *m* + meat are negligible when compared to the average scores given the meat samples (table 7). These scores range from 6.35 to 3.74, averaging 5.24 for bulls and for heifers range from 6.77 to 4.06, averaging 5.44.

In table 8 we also find the following distributions for + + − *m* + adjusted for marbling: for bulls the range is from .18 to −1.46, averaging −.32, while for heifers the range is from 1.30 to −.86, averaging .29. It should be noted that the standard errors of these values are about twice as large as those for the + + − *m* + values not adjusted for marbling.

The + + − *m* + values adjusted for marbling taken at face value are more favorable for *m* + animals for samples taken from the *longissimus* muscle than for those taken from the *semimembranosus* muscle. For + + − *m* + values not adjusted for marbling, there is no such pattern for bulls, but once again there is for heifers.

In summary, the results presented in table 8 do not consistently favor meat from either + + or *m* + animals, and the difference + + −*m* + adjusted or unadjusted for marbling is consistently small with only two values out of 32 being greater in absolute value than one unit on the taste panel evaluation scales. None of the 32 values is statistically significant. On average, *m* + animals in comparison with + + animals are

TABLE 8
LEAST SQUARES ESTIMATE OF + + -*m* + FOR MUSCLE TRAITS AS SCORED BY TASTE PANEL

Trait and muscle	+ + -*m* + for trait scores scores		+ + - *m* + for trait scores adjusted for + + -*m* + marbling scores		regression of + + -*m* + for trait scores on + + -*m* + for marbling scores	
	Bull	Heifer	Bull	Heifer	Bull	Heifer
Tenderness						
longissimus	.28 ± .57	-.23 ± .54	-1.46 ± 1.33	-.09 ± 1.15	40 ± .28	-.02 ± .15
semimembranosus	-.01 ± .49	.33 ± .46	-.55 ± 1.14	1.30 ± .99	.13 ± .24	-.14 ± .13
Juiciness						
longissimus	.17 ± .34	.16 ± .32	.13 ± .78	.33 ± .68	.01 ± .16	-.02 ± .09
semimembranosus	.42 ± .37	.28 ± .35	.10 ± .86	.73 ± .75	.08 ± .18	-.06 ± .10
Flavor						
longissimus	.01 ± .12	.09 ± .11	-.08 ± .27	-.02 ± .24	.02 ± .06	.02 ± .03
semimembranosus	.08 ± .16	.41 ± .15	.01 ± .37	.53 ± .32	.02 ± .08	-.02 ± .04
Overall acceptance						
longissimus	.62 ± .43	-.35 ± .39	-.89 ± .96	-.86 ± .85	.34 ± .19	.07 ± .10
semimembranosus	.48 ± .41	-.21 ± .37	.18 ± .91	.42 ± .82	.07 ± .19	-.08 ± .10

favored slightly more with samples from the *longissimus* muscle than from the *semimembranosus*.

Estimated effects of marbling on acceptance were small. They were consistent and larger on average for bulls while inconsistent and smaller for heifers. Consistency as used here refers to constancy of sign of the regression coefficients of trait on marbling. For bulls the sign was always positive, meaning that adjustment of $++ - m+$ values for marbling always favored the $m+$ animals. This sex difference in consistency of the regression coefficients may well reflect the lower marbling of bull meat (slight plus, on average) as compared with that of heifers (modest, on average). In other words, at the average level of marbling for bull meat (slight plus) the higher marbling of the meat from $++$ animals compared to $m+$ meat contributed to its slightly greater acceptance while at the average level of marbling of heifer meat (modest) the higher marbling of the $++$ meat compared to the $m+$ meat did not consistently contribute to improved acceptance.

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APPENDIX 1

The Method Used to Include a Double-Muscled Sire (981) in the Angus Sire Evaluation

In the Angus Sire Evaluation (Group 3 Report, Fall 1975, of the American Angus Association [AAA]), each of the 54 sires tested was assigned an EPD (expected progeny difference) value. The sire with the largest positive EPD was considered the best, while the one with the largest negative EPD was considered the worst. The EPDs had an average of zero.

In precise statistical language, an EPD is an estimate of a sire's expected progeny average (EPA) expressed as a deviation from the sample mean, zero.

Upon request, the AAA made available the formulas used to compute the EPDs. The following is taken from that source:

The model used for sire evaluation is that each calf's record $Y_{ijk} = \mu + g_i + s_j + e_{ijk}$, where μ = the overall mean, g_i = management group effects, s_j = sire effects, and e_{ijk} = random effects. The least squares normal equations are reduced in number by absorbing the $\mu + g_i$ equations into the s_j equations. Then the s_j equations are augmented on the lead diagonal with $(\frac{4}{H} - 1)$, where H is the heritability. The heritabilities assumed are 30 per cent for weaning weight, 50 per cent for yearling weight, 40 per cent for per cent cutability and USDA quality grade. The s_j equations are then solved, yielding and EPD value for each sire.

The following regression formula is given in Pirchner (1969, p. 168).

$$b_{BV,PA} = \frac{2n\,H}{4 + (n - 1)\,H} \qquad (1)$$

where BV is the breeding value of a sire, PA is the average of n of his progeny, H is the heritability of the trait and $b_{BV,PA}$ is the regression of BV on PA.

$BV_{981} - BV_{C18} = b_{BV,PA}\,(PA_{981} - PA_{C18})$.

In formula (1) as $n \longrightarrow \infty$, $PA \longrightarrow EPA$ and $b_{BV,PA} \longrightarrow 2$.

Therefore,

$$EPA_{981} - EPA_{C18} = 1/2\,(BV_{981} - BV_{C18})$$

or

$$EPA_{981} = EPA_{C18} + 1/2\,(BV_{981} - BV_{C18})$$

In the terminology of the AAA report EPD 981 is an estimate of EPA_{981}; hence,

$$EPD_{981} = EPD_{C18} + 1/2\,[b_{BV,PA}\,(PA_{981} - PA_{C18})] \qquad (2)$$

For example, consider the trait percent cutability. H = .40. Since $n_{981} = 24$ and $n_{C18} = 25$, use n = 24.5 in formula (1), for $b_{BV,PA}$, which gives $b_{BV,PA} = 1.46$. From a least squares analysis $PA_{981} - PA_{C18} = 1.65$. From the Angus Sire Evaluation Ranking Summary $EPD_{C18} = -.55$. From formula (2) above, we have $EPD_{981} = -.55 + 1/2\,[1.46\,(1.65)] = +.65$. Therefore, 981 ranks between the first (EPD = +.77) and second (EPD = +.52) sires in the Angus Sire Evaluation Ranking Summary.

The formulas discussed in this appendix are appropriate for polygenic variation. The rationale involved in introducing an *mm* sire (981) into a group of + + sires (the 54 sires in the AAA test) is of a *null hypothesis nature.* That is to say, Angus sire 981 having been picked at random would not be expected on the basis of his polygenic genotype to rank high among the 54 Angus sires tested since the latter, as discussed in the text, must certainly represent the upper end of Angus sires. If 981 ranks high among the 54 + + sires tested it appears reasonable to attribute this to the action of the mutant allele, *m*, as a gene with major effect. To a lesser extent, the same reasoning holds if 981 ranks at the lower extreme, or below, of the 54 + + sires tested.

APPENDIX 2

The Factorial Model Used to Test for the Existence of a Ration by Genotype Interaction

$$Y_{ijkl} = \mu + a_i + b_j + c_k + ab_{ij} + ac_{ik} + bc_{jk} + abc_{ijk} + e_{ijkl}$$

a_i = Level of grain fed postweaning
1: High concentrate ration fed to the 1974 calf crop
2: Alfalfa cubes ration fed to the 1976 calf crop
See table 4 for an evaluation of these rations.

b_j = Sex of calf
1: Bull
2: Heifer

c_k = Sire of calves
1: Sire 981 (his offspring are *m* +)
2: Sire C18 (his offspring are + +)

Distribution of Subclass Frequencies

		a_1	a_2
b_1	c_1	5	8
	c_2	5	4
b_2	c_1	2	9
	c_2	7	9

APPENDIX 3

Carcass Density as an Estimator of the Percentage of Fat in the Carcass

Garrett and Hinman (1969) using 48 Hereford steers found a correlation of −.95 between carcass density, X, and percentage of carcass fat (chemical determination), Y. Using linear regression to estimate Y given X the standard error of estimate was 1.9.

To test the applicability of this regression equation to Angus, Hereford, and Shorthorn bulls and heifers of *m* + and + + genotypes, chemical fat determinations were made of the carcasses of five + + and 11 *m* + bull calves and eight + + and eight *m* + heifer calves that had been fed a high concentrate ration. The method of determining the chemical fat in the carcass is given in Garrett and Hinman (1969).

The following data (Garrett and Rollins, unpublished) in which $\hat{Y}$ is the estimate of percentage of carcass fat using the regression equation given in Garrett and Hinman (1969) and Y is the observed percentage of carcass fat (chemical determination) indicate the regression equation over estimates the percentage fat for bull calves and for *m* + calves, the two biases being additive.

+ + heifers			*m* + heifers			+ + bulls			*m* + bulls		
$\hat{Y}$	Y	$\hat{Y}-Y$	$\hat{Y}$	Y	$\hat{Y}-Y$	$\hat{Y}$	Y	$\hat{Y}-Y$	$\hat{Y}$	Y	$\hat{Y}-Y$
37.0	37.0	0	34.0	36.0	−2.0	29.0	29.0	0	29.5	26.0	+3.5
35.0	36.5	−1.5	34.0	33.5	+.5	28.0	23.5	+4.5	26.5	25.0	+1.5
34.5	35.0	−.5	34.0	32.0	+2.0	27.5	26.0	+1.5	15.5	22.5	+3.0
35.0	35.0	0	33.0	32.0	+1.0	26.0	19.5	+6.5	25.0	23.5	+1.5
34.0	33.0	+1.0	32.0	31.0	+1.0	18.0	18.0	0	24.5	20.5	+4.0
34.0	34.0	0	31.5	30.0	+1.5				24.0	21.5	+2.5
33.0	33.0	0	29.5	28.5	+1.0				23.5	20.5	+3.0
30.5	30.5	0	24.5	24.5	0				24.5	16.5	+8.0
									21.0	19.5	+1.5
									21.0	18.0	+3.0
									19.0	15.5	+3.5
ave. = −.12			ave. = +.62			ave. = +2.50			ave. = +3.18		

Our comparisons of *m* + with + + calves are made within sex and then averaged. Hence, our estimate of *m* + − + + for percentage of carcass fat, using the regression equation under discussion, is an underestimate, ignoring sign. That is to say, the *m* + calves relative to the + + calves are still more lean than our estimate shows. Despite the bias resulting from using the regression equation under discussion, the *m* + calves were shown to be significantly leaner than the + + calves, not only in a statistical sense but also in terms of practical importance for the beef industry.

The trait non-fat carcass weight as a percentage of shrunk slaughter weight reflects the fact that using carcass density to estimate percentage carcass fat does not enable a breakdown of the remaining carcass component, non-fat percentage, into the components lean and bone. However, if the ratio of bone to lean in the carcass is the same for *m* + and + + calves on average, then it can easily be proved that the parameter $\frac{(m+\ -\ ++)}{(\ ++\ )}$ 100 for the trait non-fat carcass weight as a percentage of shrunk slaughter weight has the same value for the trait lean carcass weight as a percentage of shrunk slaughter weight.

Experimental evidence indicates that the ratio of bone to lean in the carcass may be less in *m* + than in + + calves on average. Chemical determinations of ash and protein made on the carcasses of the previously mentioned animals and six *mm* animals yielded the following results:

number of animals	genotype	sex	ash/protein
8	+ +	heifer	.25
8	*m* +	heifer	.24
3	*mm*	heifer	.20
5	+ +	bull	.24
11	*m* +	bull	.22
3	*mm*	bull	.18

The ash/protein ratio is a good estimate of the bone/lean ratio. Hence, if we use $\frac{(m+ \;-\; ++)}{(\quad ++ \quad)}$ 100 for non-fat carcass weight as a percentage of shrunk slaughter weight as an estimate of $\frac{(m+ \;-\; ++)}{(\quad ++ \quad)}$ 100 for lean carcass weight as a percentage of shrunk slaughter weight, the latter estimate may be biased downwards.

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