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MUSCLE, FAT AND BONE GROWTH AND DISTRIBUTION AND CARCASS COMPOSITION OF DOUBLE MUSCLED AND NORMAL YOUNG GROWING BULLS

by

KARIMA A. SHAHIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled MUSCLE, FAT AND BONE GROWTH AND DISTRIBUTION AND CARCASS COMPOSITION OF DOUBLE MUSCLED AND NORMAL YOUNG GROWING BULLS submitted by KARIMA A. SHAHIN in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in ANIMAL GROWTH AND DEVELOPMENT.

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Date. January 22 1985

DEDICATION

To the Memory of My Father

SYNOPSIS

Eighteen **Double Muscled** (DM), 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls were serially slaughtered from approximately 250 to 800 kg live weight to determine the influence of 'Double Muscling' and maturity type on tissue growth patterns and compositional differences, tissue distribution and the interdependence of the serial development of muscles and bones.

Relative to carcass weight and total bone, the DM bulls had a higher growth rate for total muscle than did the HE and SY bulls. Compared with the more normal breed types, DM was characterized by a high muscle:live weight ratio, a high proportion of muscle in the carcass, high muscle:bone and muscle:fat ratios and a low proportion of fat.

Breed types differed significantly in the relative growth rate of 5 of the 95 muscles and in 1 of the 9 muscle groups. Individual muscle growth patterns revealed an increasing disto-proximal gradient along the limbs and an increasing caudo-cranial gradient along the whole body. However, within any anatomical region considerable variation with well defined growth gradients was found for individual muscles. In the proximal region of both limbs increasing medio-lateral growth gradients were apparent.

At the same total muscle weight, compared with the other breed types, DM tended to have more of their muscle in the hip and stifle region but less in the distal parts of both limbs and in neck and thorax.

'Double Muscling' preferentially affects the superficial, large, fleshy muscles and those which exibit large contour areas. Muscular hypertrophy followed a disto-proximal gradient along the limbs and an inner-outer gradient across the muscle layers with the superficial and bulkiest muscles being the most hypertrophied. At the same total side muscle, DM had heavier expensive or luxury muscles than normal cattle.

Relative to total side fat, DM did not differ significantly from the other maturity types in growth rates of subcutaneous fat (SCF), intermuscular fat (IMF) and carcass cavity fat (CCF), but relative to fat percent in the side DM tended to have much lower growth rates for subcutanous fat and carcass cavity fat.

At equal total fat, HE bulls tended to partition more of their fat to the subcutaneous depot, whereas DM and SY bulls tended to partition more of their fat to the intermuscular and carcass cavity fat depots. As fattening proceeded, fat partitioning index { SCF/(IMF+CCF) } increased, with HE having a higher fat partionining index than either SY or DM. Principal component analyses were applied to derive an index of fat partitioning independent of fatness. After the effect of fatness had been removed HE still had the higher multivariate fat partitioning index than either SY or DM, which would suggest that fat partitioning among the depots is a breed specific feature even after effects of fatness or mature size are accounted for.

Relative to total side bone, breed types tended to have similar growth coefficients for all bone or bone groups except the vertebral column where HE tended to have a higher growth coefficient than either SY or DM. Compared with the more normal breed types, adjusted to the same total side bone, DM had proportionately less bone weight in the proximal hindlimb and total long bones, but they had proportionately more bone weight in costae and sternum. The hypodevelopment of bones in the muscular hypertrophied animals followed a disto-proximal gradient which was most pronounced in the pelvic limb.

Relative to total side bone, DM had significantly higher growth rate for muscles in the all regions which exhibited gross muscular hypertrophy i.e. proximal hindlimb and proximal forelimb. The superior muscling in DM animals is manifested primarly by a generalized increase in regional muscle growth relative to total bone or regional bone weight.

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Table of Contents

Chapter Page

List of Tables

List of Figures

GENERAL INTRODUCTION

Cattle exhibiting extreme muscular appearance express what is known as 'Double Muscling' or muscular hypertrophy. Depending upon the degree of hypertrophy and the area of enlargement, the condition is known under a variety of names such as culard, doppellender (double loin), a groppa doppia, double rumped, horse rumped, bottle thighed and greyhound belly. Depending upon geographical location it is known as Yorkshire, Teeswater etc. (Shrode and Lush, 1947) and depending on the reduction of fat it is known as half-fatted. The degree of the muscular hypertrophy varies with breed depending on the genetic background, environment, sex and stage of maturity.

This phenomenon has been recognised in many breeds of cattle; in North America its greatest occurrence is in the Angus breed (Thiessen, 1982). 'Double Muscling' is an inherited character which is determined by one major gene (*m*) whose expression is influenced by polygenic (modifying genes) and non-genetic (enviromental) effects (Nott *et al.*, 1979). However, Menissier (1982) suggested the possibility of a polygenic determination of 'Double Muscling' as an all-or-nothing trait. The genetic determination of 'Double Muscling' varies with breed and evolutionary history. The mode of inheritance might be explained by the hypothesis of evolution of dominance proposed by Fisher (1930) as noted by Lauvergne *et al.* (1963). Vissac (1972) pointed out that the penetrance of

'Double Muscling' varied with breed depending upon selection emphasis, that is, selection for or selection against muscle development. In European breeds or those selected for thickness or for draft usage, the 'Double Muscling' phenotype has a selective advantage over the normal, therefore the trait becomes dominant while in dairy breeds and American beef breeds the trait tends to become recessive, since the selection strategies considered the trait as undesirable and therefore it is selected against.

Since there are some difficulties in discriminating between culard and well-muscled animals on one hand and between pure conventional and heterozygous animals on the other hand (Hanset, 1982) the exact genetic determination of 'Double Muscling' in particular cases remains uncertain. The penetrance of the 'Double Muscling' gene ranges from almost complete or complete in the homozygous state to variable expressivity in the heterozygous state. The variability of the expression is attributed to differences in genetic background and environmental influence. Therefore, the mode of expression of the 'Double Muscling' gene lies between recessive to dominant for homozygous, whereas for heterozygous it varies from partial recessive, partial dominance or incomplete dominance depending on the breed and its selection and genetic background.

Compared with normal cattle, Double Muscled cattle have more muscle, less bone, less total fat and very much less subcutaneous fat (Mason, 1963; Oliver and Cartwright, 1968;

West, 1974 and Dumont, 1982). Thiessen (1974) reported that Double Muscled carcasses can produce as much 35% higher muscle:bone ratio than normal ones.

Compared with normal cattle, at the same live weight or carcass weight, Double Muscled have more muscle and superior muscle weight distribution (Vissac, 1968; Vissac *et al.*, 1971; Ansay and Hanset, 1979).

Vissac (1973) and Dumont (1982) demonstrated that the influence of 'Double Muscling' on the skeleton was not the same for all parts of the skeleton. The 'Double Muscling' condition has resulted in some morphological differences in size and shape of long bones. Wriedt (1929) found the limb bones in DM to be shorter than normal and of decreased density. Vissac (1962) reported that the shafts of the long bones were more slender but the epiphyses were larger than normal. Hendrick *et al.* (1973) found that Double Muscled animals possessed lighter, shorter bones that have thinner cortices.

Most previous studies regarding the effect of 'Double Muscling' on carcass composition were carried out on very small numbers. No studies on 'Double Muscling' involved a range in weight which could allow the study of relative growth patterns of muscle, fat and bone and comparisons with the more normal maturity types are very limited.

The main objectives of this study were to determine the influence of 'Double Muscling' compared to more normal maturity types, on: growth patterns of major carcass tissues, carcass composition, growth patterns and distribution of anatomically defined muscle groups, growth patterns and distribution of individual muscles, fattening patterns, fat partitioning among the depots, bone growth patterns and distribution and the interdependence of the serial development of muscles and bones.

Further objectives of this study were to develop methods to identify the 'Double Muscling' condition by application of the discriminant analysis technique and to attempt by use of principal component analyses to derive an index of fat partitioning which is independent of fatness.

I. GROWTH PATTERNS OF MUSCLE, FAT AND BONE AND CARCASS COMPOSITION OF DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen **Double Muscled** (DM), 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls were serially slaughtered from approximately 250 to 800 kg live weight to determine the influence of maturity type and 'Double Muscling' on tissue growth patterns and compositional differences which were examined by using the allometric equation $Y = aX^b$ after transformation to common logarithms ($\log_{10}$). As live weight (LW) increased, the proportions of total side fat (TSF) and subcutaneous fat (SCF) increased, the proportions of total side muscle (TSM) and intermuscular fat (IMF) remained relatively constant and the proportion of total side bone (TSB) decreased. Relative to LW, DM had similar growth rate for TSM and lower growth rates for TSF, SCF and IMF than HE and SY. All breed types had similar growth rate for TSB on LW. **Relative to dissected side weight (DSW) and TSB, the DM bulls had a higher growth rate for TSM than did the HE and SY bulls.** Differences existed between DM and the more normal genotypes in carcass composition. DM was characterized by a high muscle:live weight ratio, a high proportion of muscle in the carcass, high muscle:bone and muscle:fat ratios and a low proportion of fat compared to the more normal genotypes. Objective criteria to discriminate between HE and DM were **SCF, muscle:bone and TSM:IMF** ratios, and between SY and DM

were TSB and muscle:bone ratio.

INTRODUCTION

Carcass composition is characterized by the proportion of muscle, fat and bone in the carcass. The relative proportion of muscle and the relationship between the major carcass tissues (i.e. muscle:bone, muscle:fat and fat:bone ratios) and the amount and distribution of the fat are the major factors determining carcass value. Carcass composition varies with species, breed, slaughter weight, sex, plane of nutrition, stage of development, rate of growth, body weight loss and recovery, external appearance and 'Double Muscling' (Butterfield, 1974). Carcass composition is influenced by the differential growth of the major tissues, muscle, fat, and bone. An understanding of the magnitude and sequence of tissue deposition is a prerequiste to exercising control over carcass composition.

With ever growing demand for lean meat and a declining demand for fat, more interest is developing in the 'Double Muscling' condition in cattle which is characterized by hyperdevelopment of muscle and hypodevelopment of fat, bone and a high muscle:bone ratio (Johnson, 1981 and Dumont, 1982).

Most previous studies regarding the effect of 'Double Muscling' on carcass composition were carried out on very few animals, sometimes only one DM animal was used, and most of the time no statistical analysis was used. The only comparisons made have been at fixed age or live weights. No studies on 'Double Muscling' have been reported where anatomical dissection was carried out over a range of weights allowing examination of tissue growth and development patterns.

This part of the study was designed to investigate the influence of 'Double Muscling' compared to more normal breed types, on growth patterns of carcass tissues and on carcass composition and to develop methods to identify the 'Double Muscling' condition by application of the discriminant analysis technique.

MATERIALS AND METHODS

The experiment was designed to permit comparison of a Double Muscled breed type with the Hereford, as a representative of an early maturing breed, and a Beef Synthetic, as a representative of an intermediate maturing type. Maturity type refers to the propensity of different breeds to lay down fat. Each breed type was represented by eighteen animals obtained from The University of Alberta's beef research herd at Kinsella, Alberta. The Herefords (HE) were purebred, Beef Synthetics (SY) were a composite of approximately 43% Angus, 30% Galloway, and 25% Charolais with minor contributions of other breeds. The Double Muscled animals (DM) were a composite of 54% Angus, 19% Galloway, 10% Limousin, 9% Hereford and 7% Charolais with minor contributions of other breeds. Figure I.1 shows the average breed percentages for the DM population. The DM group had been bred as a closed population where sires were selected on the basis of extreme manifestation of the 'Double Muscling' condition. Within this group the diagnosis of Double Muscled or non-Double Muscled was based on morphological appearance (phenotype) using subjective scores (1 to 5 with 1 and 2 classified as normal and 3 to 5 as moderate to extreme DM). A description of the Double Muscled population was given by Basarab (1981).

The management and breeding plan of the Kinsella beef breeding project were reported in detail by Berg (1978). Briefly all bulls were born in April-May, nursed on their dams without creep feed and weaned in October-November at an average age of approximately 5 months. They were then adjusted to high concentrate test ration (71% barley, 24% oats and 5% pelleted high protein trace mineral supplement) fed *ad libitum* plus 0.9 kg chopped brome-alfalfa hay/head/day on which they remained until they reached the designated slaughter weight.

The eighteen available animals from the Double Muscled population were all sired by homozygous bulls and classified as moderate to extreme for the 'Double Muscling' condition. They were serially slaughtered over a range of live weight from 259-753 kg; slaughter time had to be adjusted to accomodate the capacity of the Meats Laboratory and to available animals, however slaughter weights fell fairly uniformly over the total range of live weights. From a

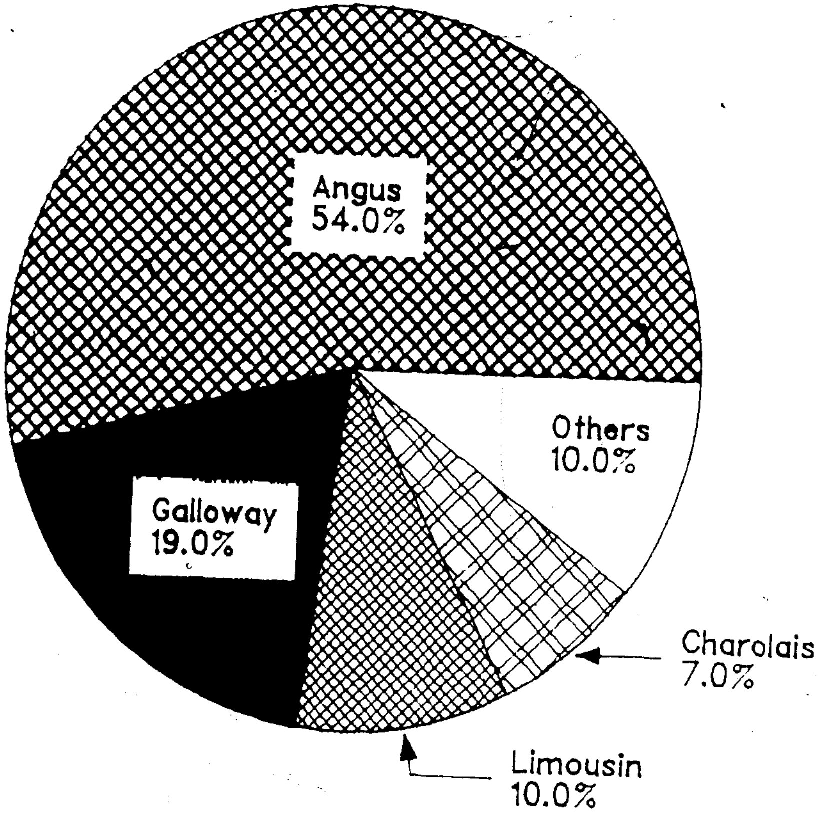


Figure I.1. Average breed percentages for Double Muscled population.

larger number of contemporary dissected HE and SY bulls 18 of each group were chosen to correspond as nearly as possible to the range in weight of the DM group and to have an average similar to the DM group for total muscle (Table I.1). The range in slaughter weights was 322-821 kg for SY and 268-785 kg for HE. Figure I.2 shows the range in live weight at slaughter for each breed type.

On the morning of slaughter each animal was weighed without shrink (farm weight), transported 150 km to a commercial packing plant and reweighed (plant weight or live weight) immediately before slaughter. The head was removed at the atlanto-occipital articulation. The carcass was dressed according to normal commercial practice. After dressing, hot carcass weight was taken after the kidneys with surrounding fat and channel fat were removed from the carcass. The carcass was halved immediately after dressing and stored at 2°C for approximately 24 hr. The left side was transported to The University Meats Laboratory where it was dissected into muscle, fat, bone and 'other tissue' using the total anatomical technique described by Butterfield and May (1966). The sum of the dissected muscle, fat, bone and 'other tissue' was used as dissected side weight (DSW).

Table I.1. Unadjusted means (kg) and standard deviations (S.D.) for live weight, carcass weight, dissected side and major carcass tissues

	Hereford		Beef Synthetic		Double Muscled		Overall	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Age	569.5	116.1	497.2	117.9	530.6	206.5	532.4	152.8
Live weight	612.5	119.9	544.3	128.0	523.2	137.7	556.0	132.0
HCW⁺	364.8	72.0	332.1	84.8	324.1	101.6	340.3	87.0
DSW	176.4	34.9	158.6	41.6	154.2	49.8	163.1	42.8
Major carcass tissues*								
TSM	100.3	18.4	106.4	25.4	107.7	39.2	104.8	28.9
TSF	55.5	16.5	32.0	14.4	28.6	12.5	38.7	18.7
SCF	26.2	9.2	11.7	7.0	10.4	5.7	16.1	7.4
IMF	21.5	5.5	16.2	5.8	13.7	5.5	17.1	6.4
CCF	7.8	3.2	4.1	2.1	4.5	1.8	5.5	2.9
TSB	19.2	3.3	19.1	4.1	16.6	4.4	18.2	4.1
Ratios								
Muscle:bone	5.21	0.39	5.59	0.64	6.35	1.11	5.71	0.90
Muscle:fat	1.94	0.53	3.82	1.69	4.47	2.76	3.40	2.15
SCF:IMF	1.20	0.25	0.68	0.23	0.72	0.19	0.87	0.32
SCF:(IMF+CCF)	0.88	0.17	0.54	0.17	0.55	0.15	0.65	0.22
TSM:SCF	4.29	1.56	13.18	12.61	14.43	12.26	10.63	10.99
TSM:IMF	4.89	1.11	7.06	1.99	8.94	4.87	6.96	3.48

⁺ The abbreviations are defined in the text

* The remaining components (i.e. tendon, waste, etc.) are required to bring total to dissected side weight.

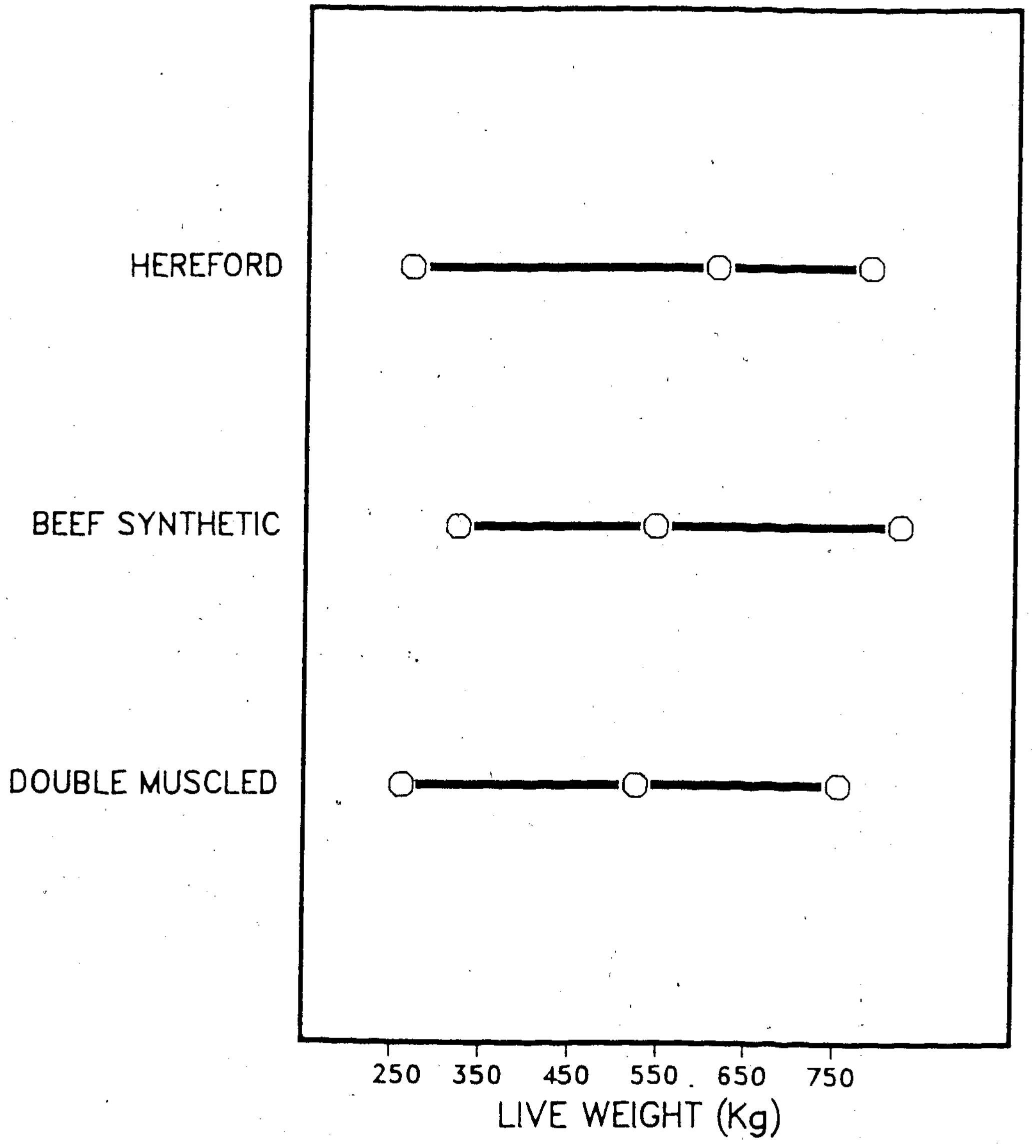


Figure I. 2. Range and mean of live weight at slaughter for each breed type.

STATISTICAL ANALYSIS

To assess genetic influence on growth patterns and carcass composition, the data were analysed by one-way analysis of covariance (Snedecor and Cochran, 1967). The allometric equation $Y = aX^b$ where a is a constant and b is the growth ratio (Huxley, 1924) formed the basis of the model. The statistical model was as follows:

$$\log Y_{ij} = A_0 + B_i + (b + (Bb)_i) \log X_{ij} + e_{ij},$$

Where Y_{ij} = the weight in kilograms of the component Y for the $_{ij}th$ animal; A_0 = the intercept; B_i = the effect of $_ith$ breed-group; X_{ij} = the weight in kilograms the control component for the $_{ij}th$ animal; b = the regression coefficient for Y on X; $(Bb)_i$ = adjustment to slope b due to $_ith$ breed-group and e_{ij} = error, assumed to be NID $(0 , \sigma^2 e)$.

Individual breed group regression coefficients were computed and compared and in cases where the regressions were homogeneous ($P > 0.05$) the common slope was used to adjust the breed-group means of the dependent variate (Y) to the geometric mean of the independent variate (X). Differences between adjusted means were tested for significance using Duncan's multiple range test (Steel and Torrie, 1980).

To study the influence of DSW and fat% in the side on muscle:bone ratio, the following power function was used: $Y = a\,C^{b_1}D^{b_2}$, where Y = muscle:bone ratio a = constant, C = DSW, D = fat%, b_1 = the regression coefficient between muscle:bone ratio and DSW with fat% held constant and b_2 = is the regression coefficient between muscle:bone ratio and fat% with DSW held constant, formed the basis of the model.

Step-wise discriminant analyses procedures were used to discriminate between the DM and normal (HE, SY) populations. The purpose of discriminant analysis is to establish functions based on quantitative measurements which will enable allocation of a new individual to the correct population even though it was only known that the individual was either one or another breed type (Kendall and Stuart, 1976). The general function used was:

$$I* = a_1x_1 + a_2x_2 + \ldots\ldots + a_nx_n$$

Where a_1, a_2, a_n are the weighting coefficients to be applied. The derivations of discriminant functions are summarized in Appendix 1.

RESULTS

In Table I.1 are presented unadjusted means and standard deviations for live weight (LW), hot carcass (HCW), dissected side weight (DSW), total side muscle (TSM), total side fat (TSF), subcutaneous fat (SCF), intermuscular fat (IMF), carcass cavity fat (CCF), total side bone (TSB), and various ratios involving these components.

Table I.2 gives results of analyses of covariance for weights of muscle, fat and bone. Although there were no significant breed differences between slopes of TSM on LW, the DM bulls had the highest growth coefficient followed by SY bulls, whereas the HE bulls had the lowest (Figure I.3). The rates of increase of TSM relative to that of DSW, bone plus fat (B+F) and TSB were significantly different among breed types. The breed differences in growth rate of TSM relative to TSB are shown graphically in Figure I.4. As DSW and TSB increased, the proportion of TSM remained relatively constant in SY and increased in DM. In HE, as DSW increased the proportion of TSM decreased and as TSB increased it remained relatively constant.

Comparisons of means adjusted to fixed LW showed DM to have 22.7% more muscle than HE ($P < 0.01$, Table 2).

Estimates of weights of TSM at minimum and maximum weight (12, 20 kg) of TSB, were calculated using individual breed regressions. At 12 kg TSB, DM had 11% and 1.1% more muscle than HE and SY respectively, while at 20 kg TSB, DM had 30.6% and 22.7% more muscle than HE and SY,

Table I.2. Growth Coefficients (*b*) and Adjusted Means of Major Tissues in Three Groups of Young Bulls

Dependent Variate (Y)	Independent Variate (X)	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV %	Adjusted Means'' Antilog (kg)			F-Values	
		b'	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
TSM	**Live weight**	**0.864**	0.06	1.051	0.06	**1.224**	0.10	1.072	0.06	12.80	88.50a	105.90b	108.55b	2.53	12.63**
	DSW	**0.841**	0.06	0.923	0.04	**1.070**	0.03	0.978	0.03	7.28	89.60	105.42	107.71	4.84*	—
	B+F	**0.226**	0.10	**0.667**	0.09	**0.733**	0.19	**0.481**	0.08	24.28	87.97	105.83	109.29	4.66*	—
	TSB	1.067	0.10	1.008	0.13	**1.386**	0.13	**1.197**	0.07	12.36	92.04	98.81	116.02	3.18*	—
TSF	**Live weight**	**1.517**	0.16	**1.633**	0.30	1.140	0.34	**1.386**	0.16	30.77	45.71a	29.79b	28.32b	0.88	12.23**
	DSW	**1.488**	0.13	**1.463**	0.20	0.907	0.27	1.189	0.14	30.56	46.77a	29.57b	27.88b	2.14	14.67**
	M+B	**1.536**	0.25	**1.366**	0.30	0.660	0.30	0.986	0.18	37.67	52.90a	28.04b	25.99b	2.47	19.31**
	TSM	**1.482**	0.22	**1.369**	0.30	0.619	0.28	0.944	0.17	37.67	53.49a	28.13b	25.63b	2.81	20.31**
SCF	**Live weight**	**1.757**	0.20	**2.037**	0.48	1.194	0.47	**1.591**	0.25	46.06	20.65a	10.00b	9.84b	1.08	14.16**
	DSW	**1.719**	0.17	**1.829**	0.35	0.964	0.37	**1.369**	0.15	45.79	21.19a	9.91b	9.67b	1.96	16.25**
	M+B	**1.762**	0.32	1.619	0.56	0.643	0.40	1.077	0.25	53.40	24.41a	9.34b	8.91b	2.13	20.40**
	TSM	**1.691**	0.32	1.645	0.53	0.605	0.38	1.037	0.24	53.30	24.71a	9.37b	8.77b	2.42	21.23**
IMF	**Live weight**	1.274	0.17	1.346	0.24	1.059	0.29	1.201	0.14	26.18	18.26a	15.55b	13.64b	0.40	5.20**
	DSW	1.259	0.14	1.218	0.19	0.823	0.24	1.029	0.12	26.07	18.63a	15.44b	13.45b	1.53	6.71**
	M+B	1.319	0.23	1.168	0.26	0.608	0.26	0.869	0.15	31.91	20.73a	14.75b	12.66b	2.20	11.25**
	TSM	1.280	0.23	1.165	0.25	0.567	0.25	0.831	0.15	31.95	20.93a	14.79b	12.51b	2.55	12.15**
TSB	**Live weight**	**0.754**	0.07	**0.842**	0.07	**0.867**	0.06	**0.828**	0.05	9.44	17.46a	18.99b	17.04a	0.43	6.42**
	DSW	**0.722**	0.07	**0.722**	0.10	**0.701**	0.06	**0.711**	0.04	9.18	17.70a	18.88b	16.88a	0.03	6.76**
	TSM	**0.823**	0.08	**0.782**	0.10	**0.836**	0.06	**0.703**	0.04	9.47	19.26a	18.26a	16.06b	1.83	17.40**

' Growth coefficients in bold type are significantly different from 1.0 at $P < 0.05$.

— Missing values mean covariance analysis was not legitimate.

'' Adjusted to geometric mean of live weight = 271 kg, dissected side weight (DSW) = 156.5 kg, muscle plus bone (M+B) = 118.5 kg, bone plus fat (B+F) = 52.8 kg, total side muscle (TSM) = 100.6 kg, total side bone (TSB) = 17.80 kg along the slope of common regression line.

Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.

* $P < 0.05$; ** $P < 0.01$

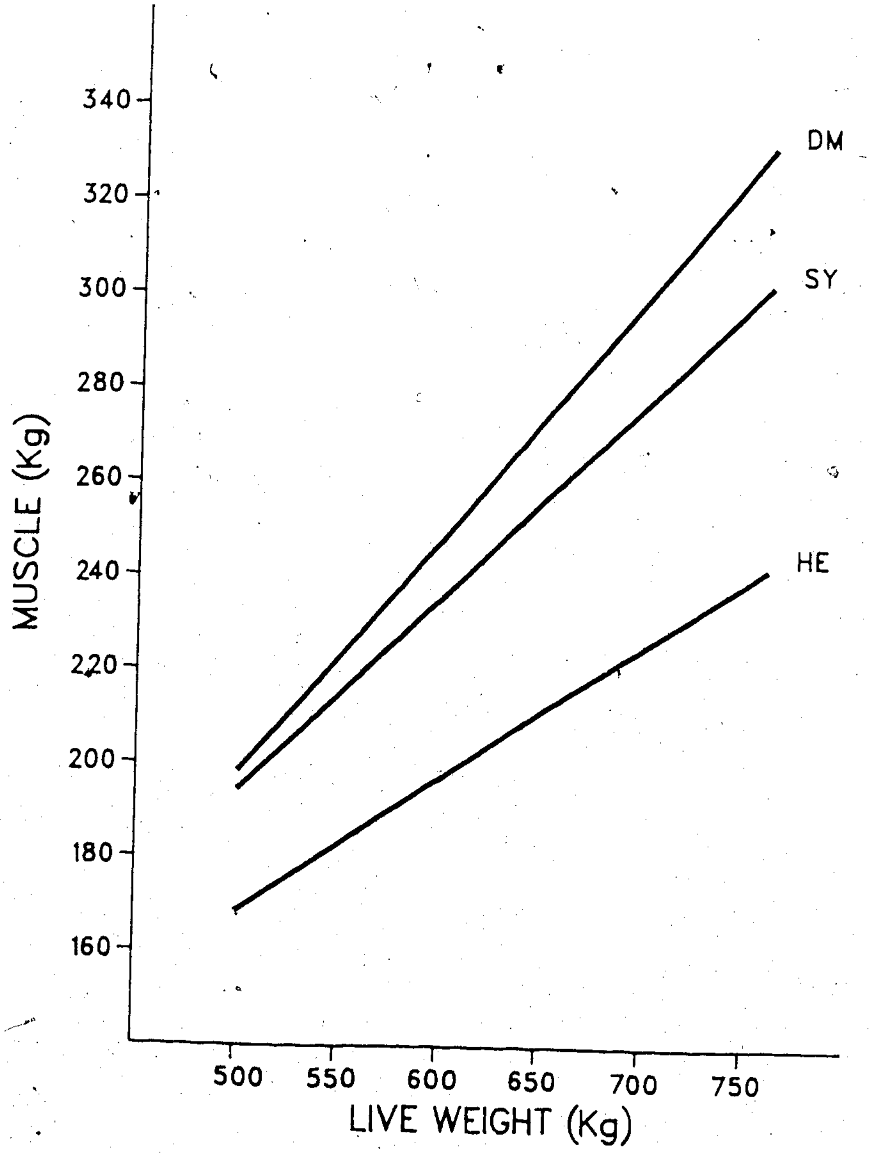


Figure I.3. Growth of muscle weight relative to live weight in three groups of young bulls.

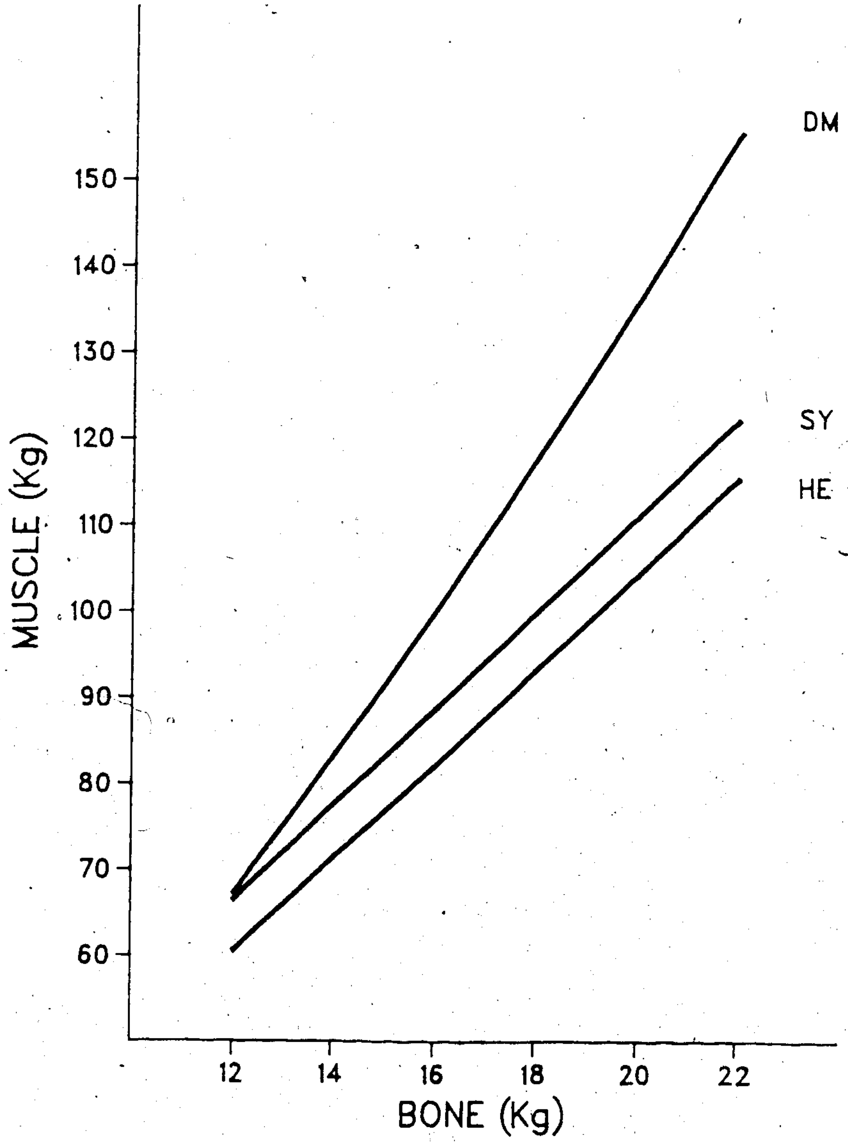


Figure I.4. Growth of muscle weight relative to bone weight in three groups of young bulls.

respectively.

Fat regressed on LW, DSW and TSM showed homogeneous growth coefficients among breed groups. Although there were no significant differences among slopes for any of the fat depots, the HE and SY had the higher values, while the DM had the lower ones. The common growth coefficients of TSF and SCF relative to LW were greater than 1 ($P < 0.05$), whereas the common growth coefficient of IMF was not different from 1 ($P > 0.05$).

At the same LW, DSW and TSM, the HE had more TSF, and more fat in each depot ($P < 0.01$) than SY and DM which did not differ ($P > 0.05$) from each other. At the same DSW, the DM had 60% as much TSF as the HE, 72% as much IMF but only 46% as much SCF (Table 2).

Breed types had similar less than unity slopes of TSB on LW, DSW or TSM.

At the same LW and DSW, DM had less TSB ($P < 0.01$) than SY, but did not differ significantly from HE in this respect, whereas at the same TSM, DM had much less TSB than either HE or SY which did not differ from each other.

The allometric equations for individual breed types were used to estimate values of TSM, TSF, and TSB and TSM:TSB at DSW of 70, 100, 130, 160, 190, and 220 kg (Table I.3). In HE and SY as DSW increased, the proportion of TSM and TSB decreased and the proportion of TSF increased; while in DM the proportion of muscle (TSM) increased, the proport[illegible]e decreased and the proportion of fat

Table I.3. Estimated* Carcass Composition and Muscle:Bone Ratios at Six Dissected Side Weights

Dissected side weight (kg)	Component+	Hereford		Beef Synthetic		Double Muscled	
		(kg)	%	(kg)	%	(kg)	%
70	Muscle	46.21	66.0	50.01	71.4	45.84	65.5
	Fat	13.76	19.7	9.17	13.1	13.26	18.9
	Bone	9.91	14.2	10.55	15.1	9.63	13.8
	Muscle:bone	4.66		4.74		4.76	
100	Muscle	62.37	62.4	69.50	69.5	67.14	67.1
	Fat	23.39	23.4	15.45	15.5	18.32	18.3
	Bone	12.82	12.8	13.65	13.7	12.36	12.4
	Muscle:bone	4.87		5.09		5.43	
130	Muscle	77.80	59.9	88.55	68.1	88.90	68.4
	Fat	34.56	26.6	22.68	17.5	23.25	17.9
	Bone	15.50	11.9	16.49	12.7	14.86	11.4
	Muscle:bone	5.02		5.37		5.98	
160	Muscle	92.61	57.9	107.25	67.0	111.02	69.4
	Fat	47.07	29.4	30.73	19.2	28.06	17.5
	Bone	18.00	11.3	19.16	12.0	17.18	10.7
	Muscle:bone	5.15		5.60		6.46	
190	Muscle	106.91	56.3	125.69	66.2	133.44	70.2
	Fat	60.78	32.0	39.52	20.8	32.80	17.3
	Bone	20.38	10.7	21.70	11.4	19.38	10.2
	Muscle:bone	5.25		5.79		6.89	
220	Muscle	121.06	55.0	143.90	65.4	156.10	71.0
	Fat	75.60	34.4	48.97	22.3	37.46	17.0
	Bone	22.66	10.3	24.11	11.0	21.48	9.8
	Muscle:bone	5.34		5.97		7.27	

* Derived from the appropriate regressions given in Table 2, weights then converted to percentages.

\+ The remaining components (i.e. tendon, waste, etc.) are required to bring totals to the dissected side weight (or to 100%).

remained relatively constant. At all side weights the estimated percentages of fat were higher and percentages of muscle were lower in HE than in the DM and SY. TSM:TSB ratios favoured the DM over HE and the SY were intermediate and the ratio increased with increasing side weight. At 220 kg DSW, the DM carcass had 36.0% and 21.8% larger muscle:bone ratios than HE and SY, respectively (Figure I.5).

The influence of carcass weight and fat percentage on muscle:bone ratio is shown in Table I.4. In this analysis, breed had a highly significant effect on muscle:bone ratio. There was a significant relationship between muscle:bone ratio and DSW, with fat% held constant, but there was no significant relationship between muscle:bone ratio and fat% at constant DSW. In this set of data, muscle:bone ratio was related to DSW and not to fat percentage.

Table I.5 presents a summary of the stepwise discriminant analysis between DM and HE and SY. The best discrimination function between DM and HE was based on SCF, TSM:IMF ratio and muscle:bone ratio and the analysis shows that the above mentioned traits are satisfactory discriminators for these data, providing complete discrimination between the two genotypes. The percentages of correct classification were 94.4% for HE and 100% for DM. No error was made in classifing DM using these objective slaughter criteria. The best discriminant function between DM and SY was based on TSB and muscle:bone ratio. The

Table I.4. Least Squares Means and Regression Coefficients of Muscle:Bone Ratio in the Equation:

$$\log Y_i = a + b_1 \log (DSW) + b_2 \log (Fat\%)$$

Source of Variation	Means Logarithmic ± S.E.	 Multiplicative	Level of Significance
Breed			**
HE	0.7145 ± 0.01	5.182a	
SY	0.7428 ± 0.01	5.531b	
DM	0.7990 ± 0.01	6.295c	
Regressions			
b_1	0.2805 ± 0.05	0.280	**
b_2	-0.0721 ± 0.05	-0.072	NS

** $P < 0.01$; NS, $P > 0.05$.

Table I.5. Statistics of Step-Wise Discriminant Analysis

Step	Variable In	Wilks' Lambda	Sig.	Rao's V	Sig.	Change In V	Sig.	Unstandarized Function	Standarized Function
Hereford and Double Muscled									
1	**SCF***	0.473	**	37.83	**	37.83	**	0.127	**0.974**
2	**M:B**	0.366	**	59.00	**	21.18	**	-0.925	**-0.766**
3	**TSM:IMF**	0.349	**	63.32	**	4.31	*	0.100	0.352
Constant								2.275	
Beef Synthetic and Double Muscled									
1	**TSB**	0.848	*	6.09	*	6.09	*		**-0.762**
2	**M:B**	0.726	**	12.80	**	6.72	**		**0.925**

* The symbols are defined in the text.

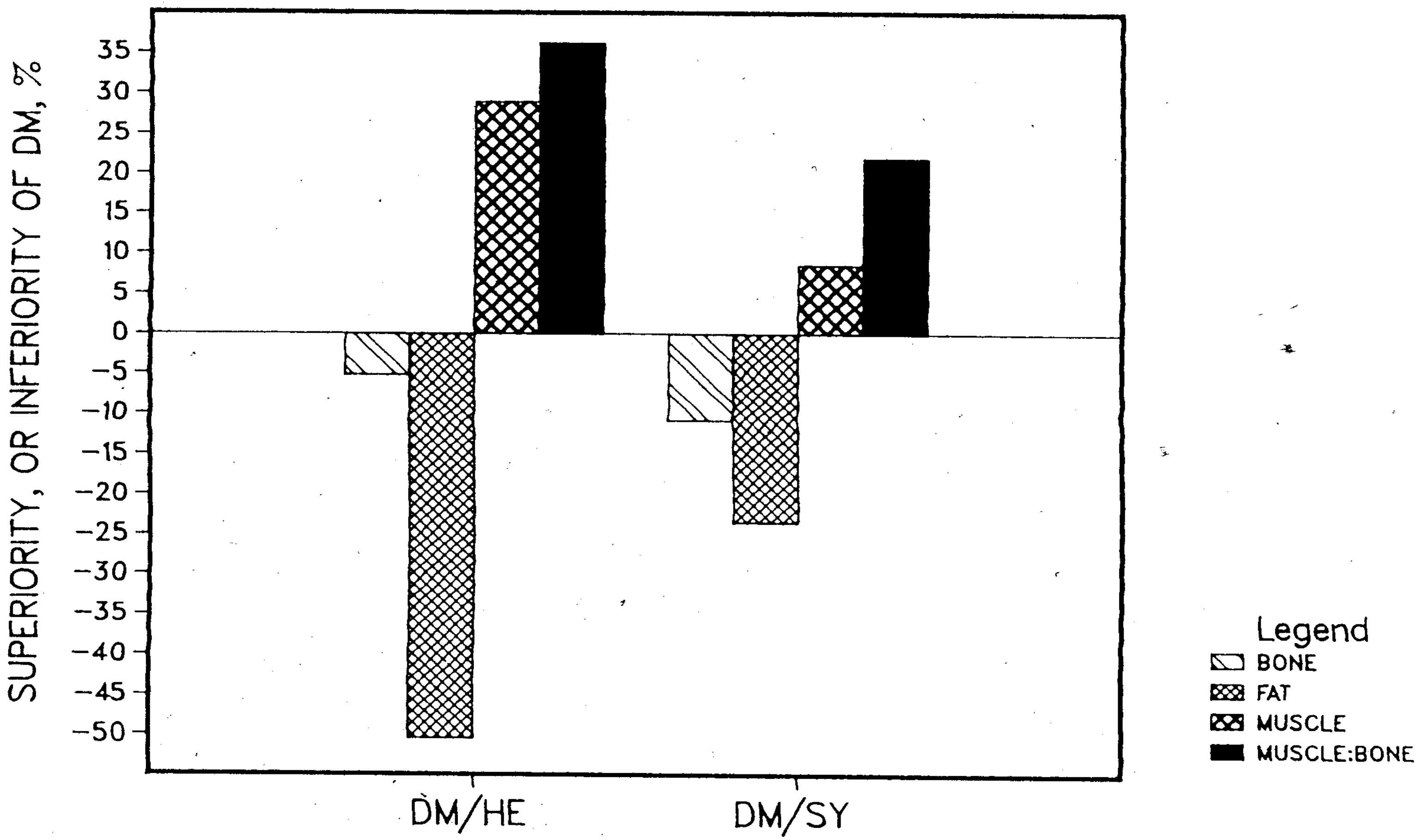


Figure. I. 5. Relative development of major carcass tissues in Double Muscled (DM) compared to Hereford (HE) and Beef Synthetic (SY) at constant dissected side weight of 220 kg.

percentage of correct classification was 72% for SY and 78% for DM.

DISCUSSION

GROWTH PATTERNS

The major carcass tissues (i.e. muscle, fat and bone) grow and develop at relatively different rates. This occurs in three overlapping phases with maximum bone growth preceding that of muscle, which in turn precedes fat deposition (Hammond, 1932). The common growth coefficients for the major carcass tissues in the present study indicate that bone increased in weight at a slower rate, muscle at the same rate and fat at a faster rate relative to live weight. The breed homogeneity of muscle, fat and bone on live weight is consistent with the results of Berg *et al.* (1978).

MUSCLE

Results of the present study showed that DM bulls differed significantly from HE and SY in the growth rate of TSM on DSW and TSB. The differences among breed types is attributed to differences in maturity (i.e. Hereford bulls fattening at lighter weight). Heterogeneity of TSM growth coefficient were also reported by Berg and Butterfield (1966) in trials involving four breed groups and Mukhoty and Berg (1974) with six breed groups. The latter authors used linear regression models and the former used log transformations. Berg *et al.* (1978) found no significant sire breed differences in the regressions of muscle on bone. However, they concluded that the apparent homogeneity of the allometric coefficients might have been due to the limited range of slaughter weights. Robelin *et al*. (1978) reported significant differences between Friesian and Charolais and Limousin breeds in the rate of muscle deposition relative to carcass weight.

The ratio of muscle growth to bone growth for different species and for different breeds, calculated from the literature, are shown in Table I.6. It is interesting to note that, the European breeds (i.e. Charolais, Limousin) or DM had higher coefficients for muscle growth relative to bone than those selected for 'traditional meat characteristics' (i.e. Hereford, Angus) which in turn had higher growth coefficients than dairy (i.e. Holstein) breeds. The results from the present study fall within the range of literature reports.

The present results showed that the pooled within-group coefficient of variation (a component of variance which is not explained by the regression of muscle on bone) was 13.4%. This relatively high coefficient suggests that there are other factors which might influence muscle growth or in other words muscle growth is somewhat independent of bone growth, which independency offers the possibility to examine the effect of breeds on muscle:bone ratio.

FAT

The DM bulls in the present study had non significantly lower relative growth rates for TSF, SCF and IMF than did the bulls in other breeds; the relatively low growth coefficients for fat in DM indicated a tendency to slower

Table I.6. The Regression Coefficient of Muscle⁺ on Bone

Species	Breed	Regression coefficient	Source
Cattle	Hereford	1.165	The present study
	Beef Synthetic	1.278	,,
	Double Muscled	1.526	,,
	Mixture	1.308	Tulloh (1964)
	Angus	1.222	Seebeck & Tulloh (1968)
	Mixture	1.190	Berg *et al.* (1978)
	Limousin	1.400	Robelin *et al.* (1978)
	Charolais	1.587	,,
	Friesian	1.165	,,
	Angus (H)	1.169	Fortin *et al.* (1981)
	Angus (L)	1.109	,,
	Holstein (H)	1.125	,,
	Holstein (L)	1.068	,,
	Mixture	1.388	Thompson & Barlow (1981)
Buffalo	Egyptian	1.440	Abdallah *et al.* (1981)
Pigs	Large White	1.230	Tulloh (1964)
	Pietrain	1.252	Davies (1974*a*)
	Large White	1.155	,,
	Landrace cross	1.377	Cole *et al.* (1976)
Sheep	S. Black face	1.360	Jackson (1967)
	Southdown	1.338	Fourie *et al.* (1970)
	Romney	1.260	,,
	Merino	1.264	Wynn & Thwaites (1981)

⁺ Derived from ratio of coefficients of muscle and bone on carcass weight. H = High energy; L = Low energy diet.

fattening. The lack of significant differences among regressions, might be due to the relatively high standard errors of the regression coefficients and is probably related to the high variability of fat. These results agree with those of Berg *et al*. (1978) who found the most muscular group (Blond d'Aquitaine) tended to have lower growth coefficients for fat. Significant differences among breeds in relative rate of fattening have been reported (Charles and Johnson, 1976 and Beranger and Robelin, 1977). Berg and Butterfield (1976) suggested that breed differences in carcass composition could result from breed differences in the time of onset of fattening as well as differences in the rate of fattening or both. In the present study the differences between DM and the other breed types seemed to be more influenced by time of onset of the fattening phase rather than the rate of fattening.

BONE

The present study showed that DM bulls tended to have somewhat similar growth coefficients to the more normal breed types for total bone in the side. The homogeneity of the growth coefficients for TSB implies there is no differential effect of the genotype on the relative growth of TSB. Thus any differences between adjusted means reflects either breed type differences established earlier in development than the start of the present experiment or differences in growth coefficients might not have been detected in the analysis used.

COMPOSITIONAL DIFFERENCES

MUSCLE

Muscle as a proportion of live weight or carcass weight varies with breed. According to Callow (1961) in all beef animals, muscular tissue is about one third of live weight. In the present study at the same LW muscular tissue as a percentage of LW was 32.7%, 39.1% and 40.1% for HE, SY and DM, respectively. In the HE group as LW increased, the proportion of muscle decreased, in the SY it remained relatively constant, while in the DM it increased (Figure I.6). The decrease in the proportion of muscle in HE is related to higher fat content and earlier fattening patterns. Muscular tissue as a proportion of live weight was proposed by Berg *et al*. (1978) as a net index for beef production. They reported significant differences among breeds in muscle weight relative to live weight and found that the Blond d'Aquitaine sired bulls had the highest proportion of muscle at 41% followed by the Limousin at 39%, whereas the Hereford had the lowest proportion at 35 per cent. These differences are comparable to the range of the results in the present study. The Blond d'Aquitaine sires used in the study of Berg *et al*. (1978) were considered to be Double Muscled.

In normal cattle, significant differences among breeds in the proportion of TSM in the side have been reported by Callow (1961) and Berg *et al*. (1978). At 125.2 kg side weight, in the present study, the Herefords bulls had an

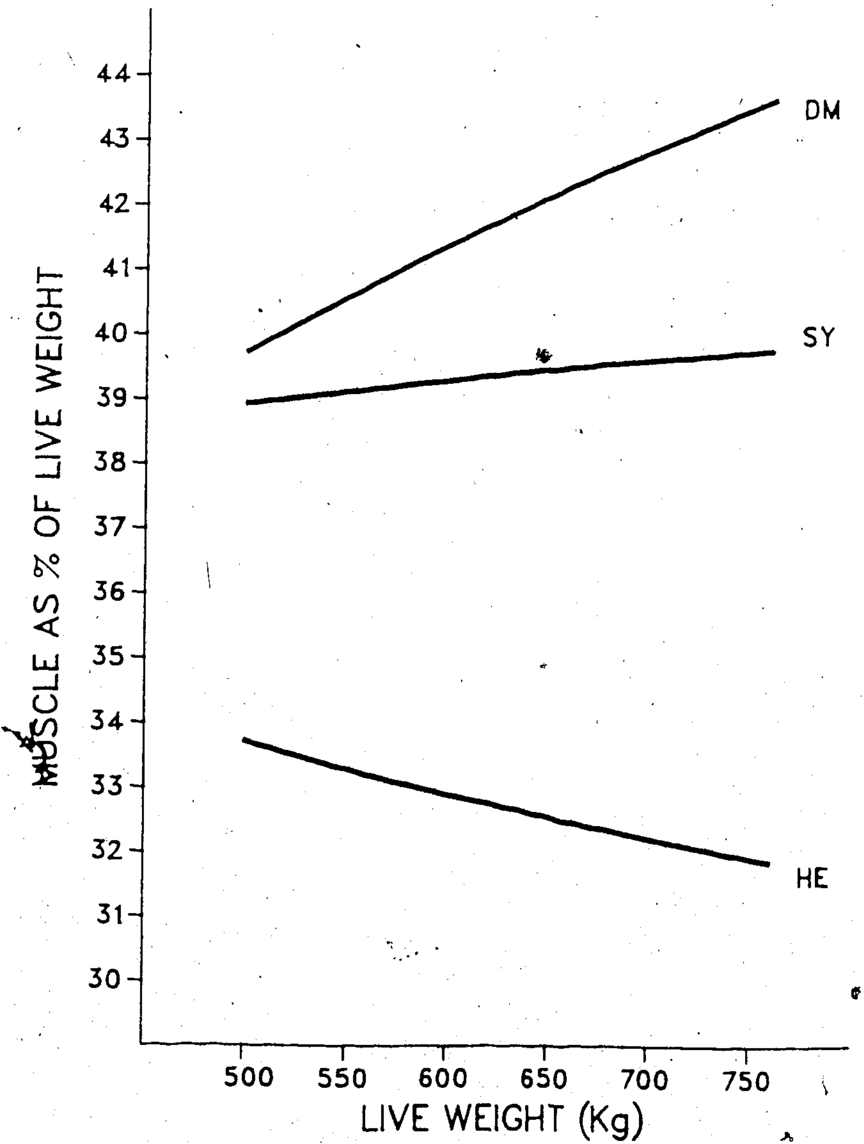


Figure I. 6. Muscle weight as % of live weight relative to live weight in three groups of young bulls.

estimated 60.2% muscle, the same as the value for the Herefords steers of Thompson and Barlow (1981*a*).

Many workers (Raimondi and Auxilia, 1973; Hanset *et al.*, 1977; Boccard 1981; Michaux *et al.*, 1983) have shown that Double Muscled carcasses are characterized by hyperdevelopment of muscle. Most of these studies reported that muscular tissue in Double Muscled animals represented about 80% of the cold carcass weight. At 220 kg DSW, the DM bulls in the present study had an estimated 71% muscle, whereas in the DM Maine-Anjou bulls of Dumont *et al.* (1982) the corresponding value was 79.9% in a side of 217 kg. Johnson (1981) reported muscle proportion as 73% in Double Muscled Santa Gertrudis steers.

The DM in the present study had somewhat less muscle as a percentage of carcass weight than some results cited. However, at heavier weights the present results are comparable to extremes reported, and we do have some cases in which muscle represented about 80% of carcass weight. As was stated in materials and methods our animals represented moderate to extreme manifestation of the 'Double Muscling' condition. Also the proportion of fat will influence the proportion of muscle in a carcass but has less influence when tissues are related to live weight or when muscle:bone ratios are compared. In these criteria our DM animals are quite comparable to others reported.

FAT

Many workers (Kidwell *et al*., 1952; Butterfield, 1966*a*; Johnson, 1981 and Dumont, 1982) have shown that compared with normal, DM had less fat and the effect of 'Double Muscling' on the hypodevelopment of fatty tissue was more pronounced on SCF than on IMF.

Results from the present study showed that at the same DSW, DM had significantly less TSF, less IMF and less SCF than HE, but did not differ significantly from SY in this respect. Results of discriminant analysis indicated that SCF can be used as a diagnostic discriminator between DM and HE carcasses.

Callow [illegible]1) suggested that the subcutaneous fat:intermus[illegible] ratio reflects the degree of intensity of selection [illegible]t qualities of species or breeds within species. Acco[illegible] to this concept the HE have been more intense[illegible] selected for 'traditional meat characteristics', while DM are [illegible] the other end of the spectrum being heavy in muscling and light in fat.

BONE

The effects of 'Double Muscling' on the amount of bone in the carcass are often not consistent between reports. Some workers (Pomeroy and Williams 1962; Rollins *et al*., 1969) have reported no significant difference between Double Muscled and normal cattle in the amount of bone in the carcass. Others (Butterfield, 1966*a*; Vissac, 1971 and Johnson, 198[illegible] have reported significant differences. In the present study, there were significant breed type differences ($P < 0.01$) in total side bone. At the same DSW, SY had more bone weight than DM and HE which did not differ significantly from each other, but at the same side muscle, DM had lower bone weight than both HE and SY, which were not significantly different. So it is clear that the difference depends on the basis of comparison (e.g. at constant live weight, side weight, fat-free carcass or TSM). Therefore it is very important that any statements about bone content in Double Muscled animals should be qualified by the basis on which comparisons were made.

MUSCLE:BONE RATIO

Davies (1974) suggested that between species, stage of maturity has a greater effect on muscle:bone ratio than body size. However, Berg and Butterfield (1966*a*) suggested that within breeds, carcass weight was the true determinant of muscle:bone ratio rather than fatness which agrees with the present study where fat had no effect on muscle:bone ratio when DSW was held constant.

Breed differences in muscle:bone ratio might be due to differences in muscle weight and dimensions, differences in bone weight and dimensions, differences in maturity, differences in intensity and direction of selection for muscling. Berg and Butterfield (1976) pointed out that breeds selected for thickness or for draft usage generally have higher muscle:bone ratios than those selected for dairy characteristics.

Results of the present study showed that DM had higher muscle:bone ratios than either HE or SY and that this ratio can be used as a diagnostic discriminating feature of the 'Double Muscling' condition. The high muscle:bone ratio in DM is due to muscle hypertrophy as well as a lesser development of the skeleton. Butterfield (1966*a*) found muscle:bone ratio of 5.2 for a Brahman hybrid Double Muscled steer. Dumont and Boccard (1967) reported a ratio of 6.8 in Double Muscled animals of 200 kg muscle weight. At 220 kg side weight, the DM bulls in the present study had an estimated 7.3 muscle:bone ratio, whereas in the DM Maine-Anjou bulls of Dumont *et al.* (1982) the corresponding value was 6.2 in a side of 217 kg.

Results of the present study showed that relative to DSW and TSB, DM had much higher growth rates for TSM than either HE or SY. DM was characterized by a high muscle:live weight ratio, a high proportion of muscle in the carcass, high muscle:bone and muscle:fat ratios and a low proportion of fat compared to more normal genotypes. Objective criteria to discriminate between HE and DM were **SCF, muscle:bone and TSM:IMF** ratios, and between SY and DM were **TSB and muscle:bone** ratio.

II. GROWTH AND DISTRIBUTION OF MUSCLE WEIGHT IN DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen Double Muscled (DM), 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls, serially slaughtered from approximately 250 to 800 kg live weight, were used to determine the influence of maturity type and 'Double Muscling' upon muscle growth patterns and distribution. The left side of each carcass was dissected into major carcass tissues and the weights of individual muscles were obtained and grouped into nine standard anatomical groups.

Relative to total side muscle (TSM), breed types tended to have similar growth coefficients for all muscle groups except muscles surrounding the spinal column where HE tended to have a higher growth coefficient than either DM or SY.

As TSM increased the proportion of muscle found in the proximal hindlimb, distal hindlimb and distal forelimb decreased ($b < 1$; $P < 0.05$), the proportion of muscle in abdominal wall and proximal forelimb remained relatively constant ($b = 1$; $P > 0.05$) and the proportion of muscle in thorax to forelimb, neck to forelimb and intrinsic muscles of neck and thorax increased ($b > 1$; $P < 0.05$).

At the same TSM, compared with the other breed types, DM tended to have more of their muscle in the hip and stifle region but less in the distal parts of both limbs and in the neck and thorax. The hyperdevelopment of the large

superficial muscles of the proximal part (thigh) and the hypodevelopment of the distal part in the hindlimb gives the DM animal the typical 'bottle thigh' appearance.

INTRODUCTION

The external appearance of any given animal is a function of muscle and bone quantity, distribution and dimensions and fat quantity and distribution. Double Muscled shape or external appearance is characterized by an appearance of hyperdevelopment of muscle in buttock, thigh, brachium, thorax and muscles responsible for weight support of the cranial end of the animal. Depending on the degree in muscular hypertrophy and the areas in which the enlargement of muscles occurred, different workers have described this phenomenon under several names such as Double Muscled, doppellender (which means in German duplicate or double), horse rump, bottle thigh, croupe de poulain, culard and 'viandeux' (beefy) and depending on the relative increase in muscle fibers and diameter, some workers described this condition as muscular hypertrophy or muscular hyperplasia.

Generally breed differences in muscle weight distribution have been found to be relatively small and probably of little economic importance. However, very heavy muscled breeds in pigs and cattle, and Continental beef breeds have relatively more of their muscle in the expensive parts of the carcass (reviewed by Berg and Walters, 1983).

Genetic improvement in muscle growth and distribution depends upon genetic diversity among and within breeds in these traits (Berg and Walters, 1983). Butterfield and Berg (1974) suggested that muscle weight distribution could be improved by breeding methods. They suggested that selection for 'Double Muscling' would alter muscle weight distribution in the more fleshy muscles. If there is genetic variation in muscle weight, it may be possible to increase the proportion in the regions of the expensive muscle groups through selective breeding.

Many studies have been reported on 'Double Muscling'. No studies on 'Double Muscling' involved a range in weight which would allow the study of relative growth patterns of muscle groups during growth and development and comparisons with more normal maturity types are very limited. Therefore this study was undertaken to examine the influence of maturity type and 'Double Muscling' on the relative growth patterns and distribution of anatomically defined muscle groups during growth and development. In Chapter I, comparisons of growth and development of the major carcass tissues using the same animals have been reported.

MATERIALS AND METHODS

The animals used for this investigation were the same as those described in Chapter I. Details of their feeding regimen, management and dissection procedure were described in Chapter I. All breed types had approximately the same average weight of total muscle (Figure II.1). The muscular tissue was dissected into 95 individual muscles, and after dissection the individual muscles were grouped into 'nine anatomical groups' based on their anatomical location (Butterfield and Berg, 1966) : G_1, proximal hindlimb; G_2, distal hindlimb; G_3, muscles surrounding spinal column; G_4, abdominal wall; G_5, proximal forelimb; G_6, distal forelimb; G_7, thorax to forelimb; G_8, neck to forelimb and G_9, intrinsic muscles of neck and thorax. Two groupings of expensive muscle were made. The sum of G_1 and G_3 was used as G_{10}, and the sum of G_1, G_3 and G_5 was used as G_{11}. The G_{10} and G_{11} muscles represent high priced cuts in most countries. Three other groups were made according to the articulations over which they passed. The sum of the *m. rhomboideus, m. trapezius, m. omotransversarius, m. brachiocephalicus, m. latissimus dorsi, mm. serratus ventralis cervicalis et thoracis, m. pectoralis profundus, m. pectoralis superficialis* was used as total pectoral girdle. The sum of the *m. biceps femoris, m. semitendinosus, m. semimembranosus and m. rectus femoris* was used as hip and stifle. The sum of *m. tensor fasciae antebrachii, m. triceps brachii (caput longum)* and *m. biceps brachii* was used as total shoulder and elbow. The sum of the individual muscles was used as total side muscle (TSM).

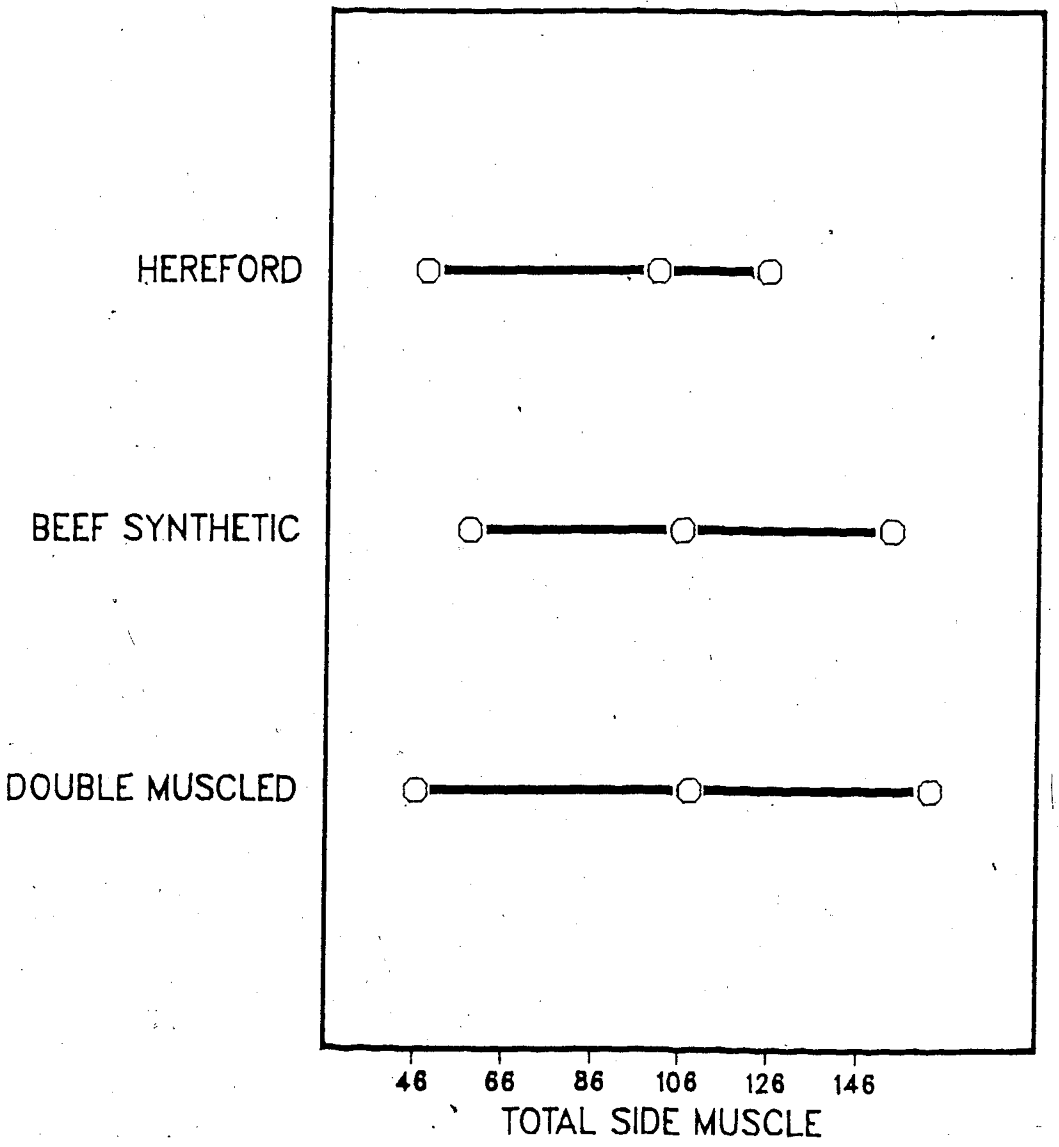


Figure II.1. Range and mean of total side muscle weight for each breed type.

STATISTICAL ANALYSIS

The data were analyzed by one way analysis of covariance (Snedecor and Cochran, 1967), according to the following model.

$$\log Y_{ij} = A_0 + G_i + b \log X_{ij} + (Gb)_i \log X_{ij} + e_{ij},$$

where:

Y_{ij} = weight (g) of a group of muscles of the $_{ij}th$ animal;
A_0 = the intercept;
G_i = fixed effect of the $_{i}th$ breed group;
X_{ij} = total weight (g) of the total side muscle of the $_{ij}th$ animal;
b = regression coefficient of Y on X;
$(Gb)_i$ = interactions effect (breed x regression coefficient);
e_{ij} = error, assumed to be normally and independently distributed (0, $\sigma^2 e$).

Individual breed type regression coefficients were computed and compared and in cases where the slopes were homogeneous (P > 0.05) the common regression coefficient was used for adjustment. However, if among slopes differences were significant, adjusted means were computed using the appropriate breed type regression but means were not statistically tested for significance. Duncan's multiple range test (Steel and Torrie, 1980) was used to test for significant differences between adjusted means.

The residual coefficient of variation (RCV%) was calculated as: RCV% = $100 (10^{S_{y \cdot x}} - 1)$. Where $S_{y \cdot x}$ is the square root of the error variance (standard error) and $10^{S_{y \cdot x}}$ = antilogarithm of standard error.

RESULTS

Presented in Table II.1 are unadjusted means and standard deviation for weight of muscle groups as well as DSW and TSM.

Relative to TSM, breed types did not differ in growth rate of muscle groups except G_3 (Table II.2). As TSM increased, the proportion of muscles in G_3 remained relatively constant in HE, while it decreased in DM and SY (Figure II.2). As TSM increased the proportion of muscles in G_1, G_2, and G_6 decreased ($b < 1$; $P < 0.05$), the proportion of muscle in G_4, and G_5 remained relatively constant ($b = 1$; $P > 0.05$) and the proportion of muscle in G_7, G_8 and G_9 increased ($b > 1$; $P < 0.05$). Although there were no differences ($P > 0.05$) among slopes for G_9 the HE and SY had high values while the DM had low (Figure II.3). The proportion of 'expensive groups' (e.g. G_1, G_{10}, G_{11}) decreased ($b < 1$; $P < 0.05$) as TSM increased. In Figures II.4 and II.5 are illustrated changes in growth patterns of proximal hindlimb (G_1) and in hip and stifle. As TSM increased the proportion of muscle in these groups decreased, but the rate of decrease in HE and SY (though not significant) tended to be greater than in DM.

Differences existed between DM and HE and SY in muscle weight distribution at standard muscle weight (Table II.2 and Figure II.6). At the same TSM, DM had more muscle in G_5 and in G_8 and less muscle in G_6 than SY. HE and SY had more muscle in G_2 and G_9 than DM. SY had less muscle in G_4 than

Table II.1. Unadjusted Means (kg) and Standard Deviations (S.D.)
of the Weights of Muscle Groups, DSW and TSM by Breed Group

Muscle[+] Groups	Hereford		Beef Synthetic		Double Muscled		Overall	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
G_1	28.14	4.96	30.07	6.89	30.89	11.45	29.70	8.20
G_2	3.90	0.71	4.14	0.84	3.85	1.20	3.96	0.96
G_3	12.36	2.44	12.90	2.97	13.10	4.30	12.78	3.28
G_4	10.19	2.15	10.03	2.49	10.98	4.14	10.40	3.02
G_5	12.47	2.28	12.92	3.10	13.40	4.96	12.93	3.58
G_6	2.20	0.37	2.31	0.47	2.21	0.66	2.24	0.51
G_7	10.46	2.00	11.18	3.02	11.52	4.56	11.06	3.33
G_8	6.04	1.27	6.41	1.86	6.81	2.89	6.42	2.10
G_9	12.19	2.58	13.04	3.84	12.35	4.82	12.53	3.81
G_{10}	40.50	7.36	42.96	9.82	43.99	15.62	42.48	11.34
G_{11}	52.97	9.57	55.88	12.89	57.39	20.53	55.41	14.88
DSW	176.4	34.9	158.6	41.6	154.2	49.8	163.1	42.8
TSM	100.3	18.4	106.4	25.4	107.7	39.2	104.8	28.9

[+] The symbols are defined in the text

Table II.2. Growth Coefficients *(b)* and Adjusted Means for Weights of Muscle Groups Relative to Total Side Muscle

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means** antilog (g)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
G_1	**0.887**	0.05	**0.915**	0.04	0.943	0.04	**0.927**	0.02	5.3	28255	28575	28917	0.39	1.62
G_2	**0.832**	0.07	**0.729**	0.07	**0.778**	0.04	**0.776**	0.03	7.2	3903a	3980a	3681b	0.52	6.37**
G_3	1.054	0.04	**0.926**	0.03	**0.911**	0.03	**0.939**	0.02	4.5	12339	12247	12373	3.99*	—
G_4	1.063	0.10	0.972	0.07	**1.082**	0.06	1.053	0.04	9.1	10171a	9460b	10148a	0.64	4.10*
G_5	0.985	0.04	1.002	0.03	1.014	0.03	1.006	0.02	3.7	12512a	12205b	12477a	0.20	4.40*
G_6	**0.841**	0.05	**0.760**	0.07	**0.788**	0.04	**0.791**	0.03	6.4	2203a	2217a	2116b	0.40	3.71*
G_7	1.053	0.04	**1.160**	0.05	**1.088**	0.03	**1.099**	0.02	5.3	10493	10437	10613	1.19	1.85
G_8	**1.179**	0.05	**1.224**	0.05	**1.217**	0.04	**1.212**	0.02	5.5	6042ab	5934a	6147b	0.19	3.23*
G_9	**1.187**	0.08	**1.242**	0.08	**1.107**	0.07	**1.152**	0.04	9.6	12154a	12070a	11337b	0.95	3.66*
G_{10}	**0.937**	0.02	**0.920**	0.03	**0.933**	0.03	**0.931**	0.02	3.8	40610	40831	41330	0.06	1.26
G_{11}	**0.949**	0.02	**0.937**	0.03	**0.950**	0.02	**0.947**	0.01	2.8	53134	53046	53832	0.10	1.81
Pectoral Girdle	**1.082**	0.04	**1.182**	0.04	**1.144**	0.02	**1.142**	0.02	3.6	18224ab	17895b	18451a	1.93	5.77**
Shoulder and elbow	1.039	0.05	**1.093**	0.03	**1.079**	0.03	**1.075**	0.02	4.9	4044ab	4003b	4146a	0.32	5.39**
Hip and Stifle	0.893	0.05	0.954	0.05	0.963	0.03	0.949	0.03	6.2	15182a	15305a	15888b	0.44	3.50*

* Growth coefficients in bold type are significantly different from 1 at $P < 0.05$.
** Adjusted to geometric mean total side muscle = 100.6 kg along the slope of common regression line.
Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.
— Missing values, mean covariance analysis was not legitimate.
* $P < 0.05$; ** $P < 0.01$.

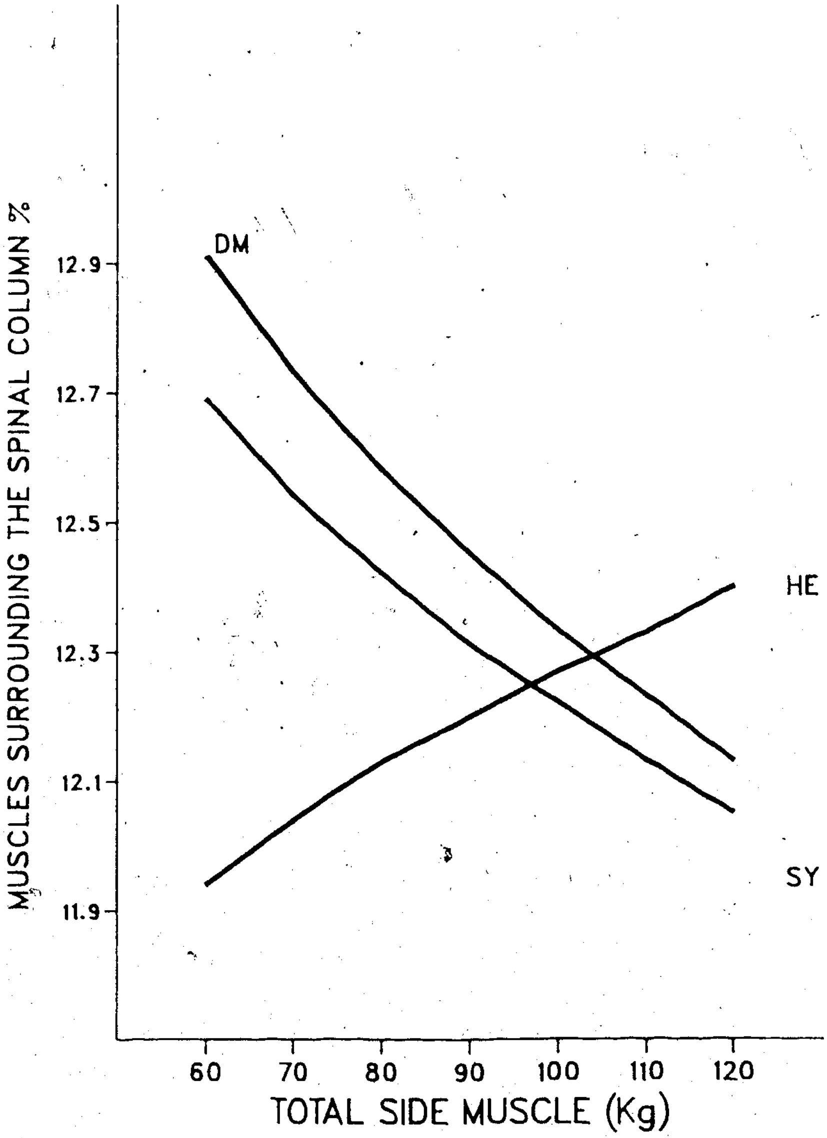


Figure II.2. Growth patterns of muscles surrounding the spinal column in three groups of young bulls.

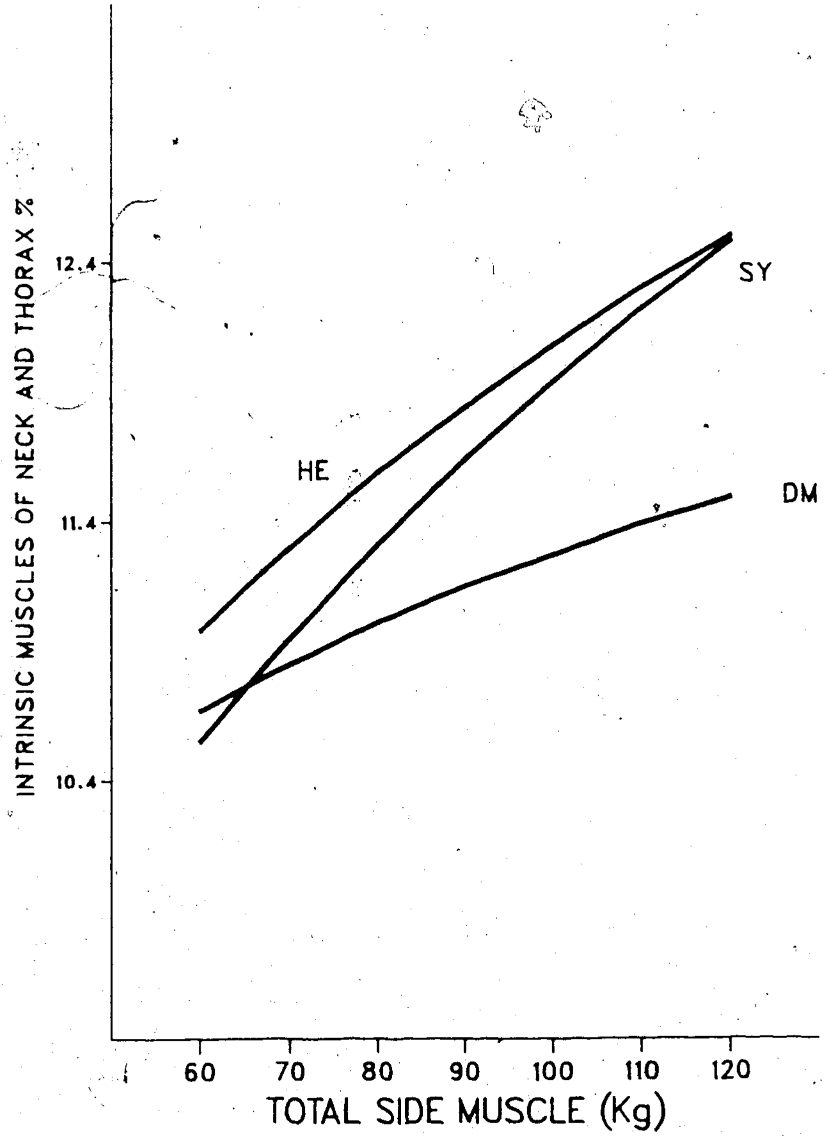


Figure II. 3. Growth patterns of intrinsic muscles of the neck and thorax in three groups of young bulls.

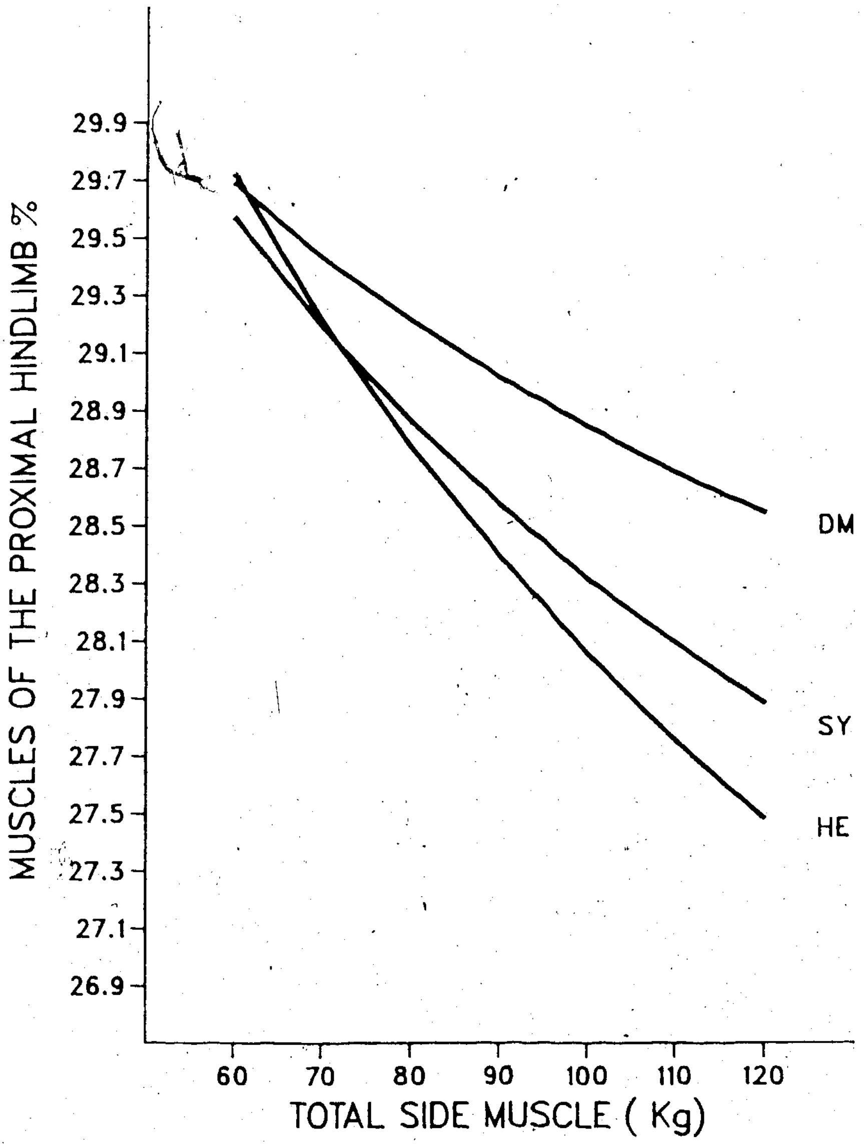


Figure II. 4. Growth patterns of muscles of the proximal hindlimb in three groups of young bulls.

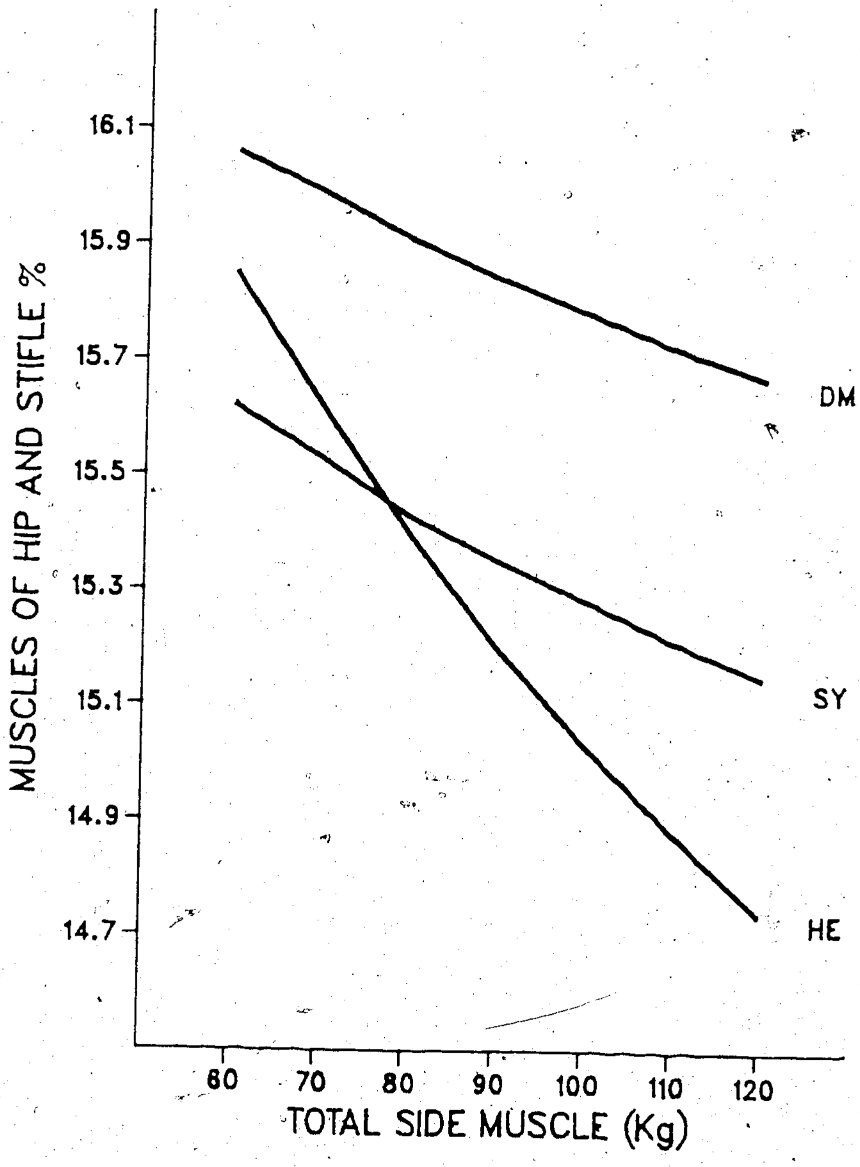


Figure II. 5. Growth patterns of muscles of the hip and stifle in three groups of young bulls.

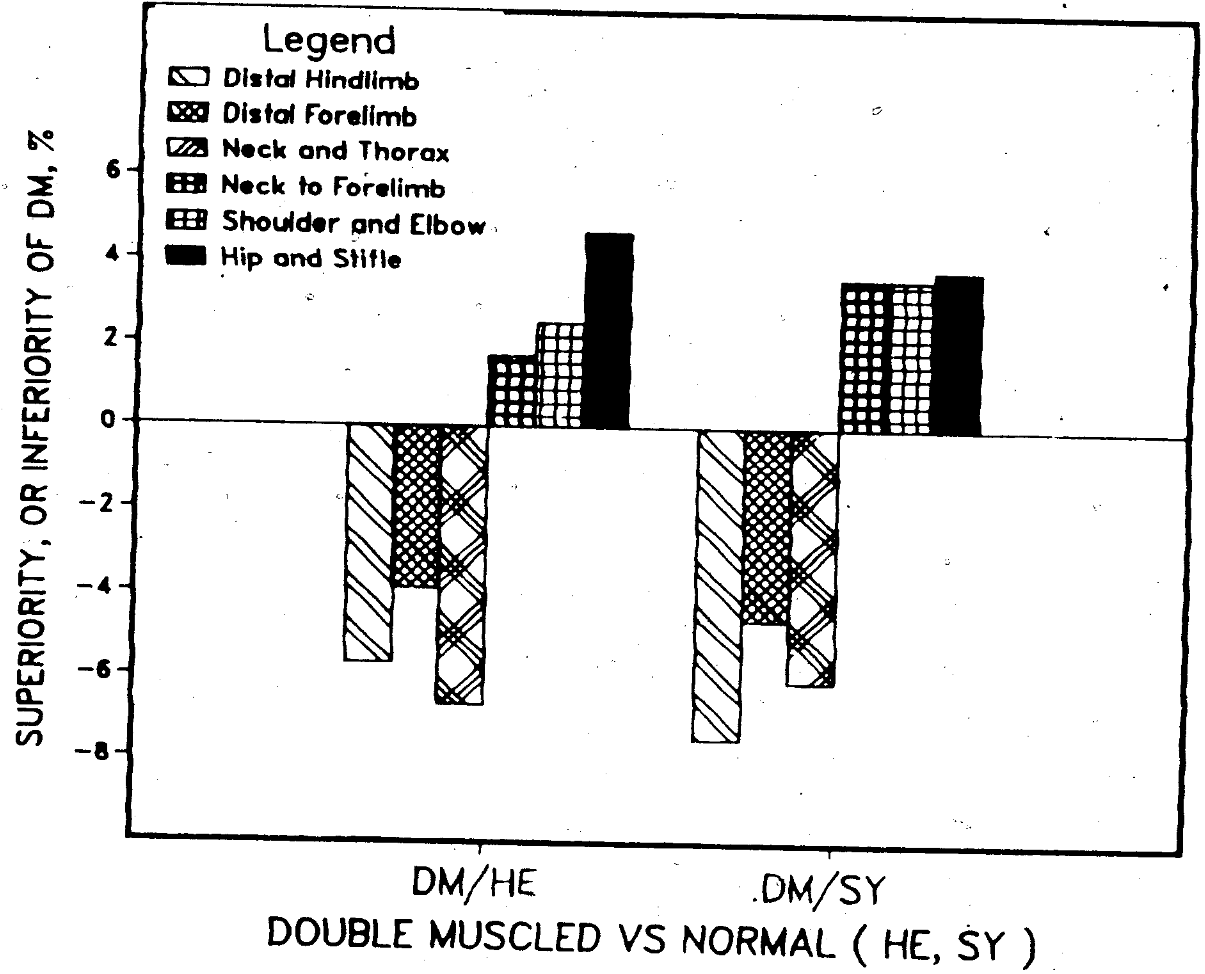


Figure II. 6. Relative development of muscle groups in Double Muscled (DM) compared with Hereford (HE) and Beef Synthetic (SY).

DM and HE. No differences ($P > 0.05$) among breed types were found for any other muscle group.

Double Muscled animals exceeded the other breed types in percentage of muscle in the hip and stifle region. DM had more muscle in the pectoral girdle and the shoulder and elbow than SY but did not differ from the HE in these regions. DM had a higher proportion of muscle in the 'expensive muscle groups' (e.g. G_{10}, G_{11} , $P > 0.05$).

Since breed types differed in growth coefficients for G_3, estimates of weights of muscles of G_3 at 60 and 120 kg of TSM were calculated using the individual breed regressions. At 60 kg TSM, DM had 8.1% and 1.7% more muscle in G_3 than HE and SY, respectively, while at 120 kg TSM, DM had 2% less than HE and 0.6% more than SY for this muscle group.

The highest RCV%'s were found in G_9 and G_4 while the lowest ones were found in G_{10} and G_{11} (Table II.2). Generally the RCV% for the large standard muscle groups (e.g. G_1, G_{10}, G_{11}) were lower than for smaller ones (e.g. G_2, G_6). The variability among anatomical regions was relatively low, the variability within certain anatomical regions was relatively high.

In Table II.3 ratios of weights of muscle groups from DM *vs* HE and SY are presented. At the same TSM, DM showed 1 and 2% hypertrophy for G_1, 1 and 2% for G_7, 2 and 4% for G_8, 1 and 3% for muscles of shoulder and elbow and 4 and 5% for muscles of hip and stifle, whereas they showed 6 and 7%

Table II.3. Ratios of Muscle Group Weights from DM *vs.* HE or SY Based on Unadjusted Means, Means Adjusted to the Same DSW, M+B and TSM

Muscle Groups	Ratios (unadjusted means)		Ratios (same DSW)		Ratios (same M+B)		Ratios (same TSM)	
	DM/HE	DM/SY	DM/HE	DM/SY	DM/HE	DM/SY	DM/HE	DM/SY
G_1	1.098	1.027	1.212	1.032	1.049	1.029	1.023	1.012
G_2	0.988	0.930	1.087	0.939	0.964	0.940	0.943	0.925
G_3	1.060	1.016	1.193	1.031	1.028	1.028	1.003	1.010
G_4	1.078	1.095	1.214	1.096	1.023	1.091	0.998	1.073
G_5	1.075	1.038	1.381	1.200	1.024	1.041	0.997	1.022
G_6	1.006	0.958	1.109	0.970	0.982	0.968	0.961	0.954
G_7	1.101	1.030	1.241	1.042	1.042	1.038	1.011	1.017
G_8	1.126	1.061	1.274	1.065	1.050	1.059	1.017	1.036
G_9	1.014	0.947	1.157	0.964	0.962	0.960	0.933	0.939
G_{10}	1.086	1.024	1.207	1.032	1.043	1.030	1.018	1.012
G_{11}	1.083	1.027	1.205	1.035	1.039	1.033	1.013	1.015

+ The symbols are defined in the text

hypotrophy for muscles in G_2, 4% for muscles of G_6 and 6 and 7% for muscles of the neck and thorax (G_9). The effect of 'Double Muscling' on the rest of the muscle groups was not consistent, since the DM was similar in percentage to one or the other breed types in all cases.

Also in Table 3 are given the ratios of muscle group weights of DM to HE and SY derived from means adjusted to fixed dissected side weight (DSW), and muscle plus bone weight (M+B). At the same DSW, compared to HE, all muscle groups in DM showed hypertrophy, whereas when comparison was made at the same M+B or TSM, some muscle groups showed hypertrophy, others showed either hypotrophy or no difference. At the same DSW, compared to HE, DM had 21% more muscle weight in G_1, 27% more muscle weight in G_8 and 38% more in G_5. The hyperdevelopment of muscle in DM was most conspicuous when they were compared at the same DSW, but when they were compared at the same TSM differences were minor.

DISCUSSION

MUSCLE GROWTH PATTERNS.

Each muscle or group of muscles grows and develops relative to functional demands. In general the main functions of the muscles are movement (i.e. locomotion, grasping, striking and lifting), posture and heat production. Movement and stature functions are manifest by flexion, extension, abduction, adduction, rotation, levitation, depression, tension, protraction and retraction. The main function of the hindlimb is propulsion of the body or pushing the body forwards, while the main function of the forelimb is to support the body rather than propel it. The muscles and bones in the pelvic girdle and vertebral column form a 'girder' for the support of the whole body; the back as a whole acts as a loaded beam (Young and Hobbs, 1975). The main function of the abdominal muscles is to hold and support the viscera acting as a sling attached to the ribs, lumbar vertebrae and pelvic girdle (Young and Hobbs, 1975). Also these muscles aid in respiration.

Berg and Butterfield (1976) showed that individual muscles and muscle groups, undergo a period of diverse growth rate immediately after birth, until the birth weight of the musculature has approximately doubled, after that time they tended to grow at a similar proportional rate and then a further phase of change in muscle weights occurs during sexual maturing. Also Bergstrom (1978) pointed out that the most important changes in growth intensity of muscles takes place in the very young. In the present study, which did not include the early stages of growth, breed types did not differ significantly in the relative growth rate of 8 out of the 9 standard muscle groups. The homogeneity of the growth coefficients for muscle groups, implies there was no differential effect of the genotype on the relative growth rate of these muscle groups. The common growth coefficients indicated that muscles in the proximal hindlimb and the distal parts of both limbs increased in weight at a slower rate, abdominal muscles and proximal forelimb muscles at the same rate, and muscles of the thorax and neck at a faster rate relative to total muscle. These results are compatible with those of Butterfield and Berg (1966*b*) and Andersen (1975).

The common growth coefficients of muscle groups revealed an increasing disto-proximal gradient along the limbs, and revealed an increasing posterio-anterior (caudal to cranial) gradient along the trunk. These results are in general agreement with Butterfield and Berg (1966*b*) and Berg *et al*. (1978). In pigs Davies (1974*b*) found that there was a disto-proximal gradient of increasing muscle growth in the limbs and a cranio-caudal gradient in the trunk.

The lowest growth coefficients were found in the distal muscles of fore and hind limbs. The muscles within these anatomical regions are essential for locomotion, so it seems logical these muscles attained most of their growth in the prenatal phases and early postnatal phases of growth. These results are in agreement with Butterfield and Berg (1966*b*), Bergstrom (1978) and Butterfield *et al*. (1983).

The highest growth coefficients were found in the thorax and neck region. The late maturity of thorax muscles could be related to the weight support of the cranial end of the animal, while the late maturity of neck muscles could be related to sexual maturity of the animal. These results are in agreement with Butterfield and Berg (1966*b*), Andersen (1975) and Butterfield *et al*. (1983).

Significant breed differences in the relative growth rate of muscles surrounding the spinal column, have been reported in sheep by Jury *et al*. (1977), in pigs by Davies (1974) and in cattle (the present study). In young animals this muscle group seems to be responsible for weight support and thus it tends to grow at a faster rate than total muscle immediately after birth. Supporting this assumption, Jury *et al*. (1977) reported that in sheep the muscles surrounding the spinal column grew faster than total muscle at low weights of total muscle, but tended to grow at a slower rate than total muscle at heavy total muscle weight. Similarly Butterfield and Berg (1966*b*) showed that spinal muscles tended to grow at a faster rate than total muscle immediately after birth and tended to grow at the same or a slower rate thereafter. In the present study which does not include the early post-natal stage, spinal muscles tended to grow at a slower rate than TSM in SY and DM. The early maturity of these muscles in SY and DM, is in general agreement with Robelin *et al*. (1977). Also, it can be argued that differences in growth rate of spinal muscle might be related to mature size, i.e. it seems more likely that heavy, later maturing beef breeds tend to have slightly lower growth coefficients for these muscles as noted by Berg and Butterfield (1976). Robelin *et al*. (1978) found that the growth coefficient for this group in Limousin bulls was 0.88. Butterfield and Berg (1966*b*) and Andersen (1975) reported that spinal muscles tended to grow at the same rate as total muscle.

Studies have shown that in prenatal phases of growth, abdominal muscles tended to grow at a slower rate than total muscle (Johnson, 1974), while in postnatal phases of growth they had either high growth coefficients (Butterfield and Berg, 1966*b*) or average growth coefficients (Andersen, 1975; Butterfield *et al*., 1983 and the present study). Generally in bulls, this muscle group seems to grow at the same rate as TSM since there is less functional demand for faster growth. In steers Seebeck and Tulloh (1968) reported abdominal muscles as late developing, while in bulls, Robelin (1978) found it an average maturing group.

In females, abdominal wall muscles in (G_4) seem to grow at a relatively faster rate than in bulls. Lodge and Heap (1967) working with pigs reported that during pregnancy muscles of the abdomen increased in weight. Gray (1968) pointed out that, if the body is long and heavy very considerable effort is required by the abdominal muscles to keep the body from sagging ventrally between the shoulders and hips. Anthony (1967) reported that muscles of the abdomen play an important postural function by pulling the pelvis dorsally, thereby flattening the lumbar curve of the spine. Lohse *et al*. (1971) pointed out that the growth of muscles in G_4 was dependent on size and weight of the contents of the abdominal cavity. Murray *et al*. (1974) found that muscles in G_4 increased at a slower rate on a high-medium (HM) and low (L) plane of nutrition than on a high (H) plane. Berg and Butterfield (1976) suggested that the growth of muscle in G_4 is dependent on functional stimuli of weight of gut contents. Badoux (1975) pointed out that the growth of the abdominal muscles might be related to the construction of the body axis.

The decrease in proportion of 'expensive groups' as total side muscle increased, supports the commonly known fact that muscle weight distribution becomes less favourable from a meat production point of view as a carcass increases in weight and/or becomes fatter (Berg *et al*., 1978 and Robelin, 1978).

MUSCLE WEIGHT DISTRIBUTION

Muscle weight distribution as used here refers to the proportions of anatomically distinct muscle groups in relation to the total musculature. Comparisons of muscle weight distribution has been made at the same weight of TSM. However it is necessary to consider possible differences in maturity and mature weight of different breed types at the same TSM. The breed type which has reached a greater degree of maturity at a standard TSM will have a relatively higher proportion of late developing muscle groups. In the present study breed types differed significantly in adjusted mean weights of 7 of the 9 muscle groups. Compared with the more normal breed types, DM tended to have more of their muscle in the hip and stifle region but less of their muscle in the distal parts of both limbs and in neck and thorax. Somewhat similar findings have been reported by Boccard and Dumont (1974), Johnson (1981) and Dumont *et al.* (1982).

As was mentioned earlier breed types differed significantly in the relative growth rate of muscles surrounding the spinal column. This difference implies that the adjusted means of this group of muscles are conditional on the weight of TSM. At lighter weights of TSM, DM had more spinal muscle than HE, but at heavier weights of TSM, HE was heavier for this muscle group. Johnson (1981) found that Double Muscled Santa Gertrudis steers had less spinal muscle than Brangus and heterogenous crosses of Hereford, Angus, Friesian and Charolais.

The differences among breed types in abdominal wall muscles reported in this study may be due to differences in the way the weight is distributed over the body; in a well balanced animal little strain falls on the abdominal region and the abdominal muscles are thin (Young and Hobbs, 1975). Differences in visceral content or differences in intramuscular fat also could influence this group. Berg and Butterfield (1976) reported that domestication had a profound effect on muscle weight distribution with domestics characterized by greater proportion of muscle of the abdominal wall. Examining the individual muscles within this group in the present study showed that the only significant differences between breed types were found in *m. cutaneus trunci*, that of the DM being heavier by 5.6% and 20.8% than HE and SY, respectively. Therefore, the differences observed in the abdominal group seemed to be due to SY having proportionately less *m. cutaneus trunci*.

The differences in intrinsic muscles of neck and thorax may be due to differences in the stage of maturity, HE and SY being earlier maturing than DM. This group contains most of the muscles responsible for sexual features (e.g. crest formation) and this group also contains some muscles which act to elevate and extend the head. The hypodevelopment of the muscles within this group in DM, could be related to sexual immaturity and/or to the relatively small head of these animals. Within this group, DM had proportionately less weight in the muscles associated with respiration (i.e. *m. intercostales interni* and *m. intercostales externi*). Similar findings have been reported by Boccard and Dumont (1974).

In the present study at the same dissected side weight, compared with the more normal breed types, there was general but not uniform hypertrophy, being greater in proximal limb muscl[illegible] in distal limb muscles. However, when comp[illegible]e at the same total side muscle, there wa[illegible]rtrophy in different anatomical regions. Muscular hypertrophy revealed an increasing disto-proximal gradient along the limbs, in agreement with Butterfield (1966*a*), Rollins *et al*. (1969) and Vissac (1972). In the hindlimb the contrast between the hyperdevelopment of the large superficial muscles of the proximal part (thigh) and the hypodevelopment of the distal part, gives the DM animal the typical 'bottle thigh' appearance which agrees with Dumont *et al*. (1982). The present study showed 'Double Muscling' had a greater hypertrophic effect on muscles of the hindlimb than the forelimb which agrees with Vissac (1968) and Boccard and Dumont (1974) who studied 'Double Muscling' in Continental breeds. Rollins *et al*. (1969) studying 'Double Muscling' in Angus did not find a similar effect.

In summary, relative to total side muscle, DM did not differ from the more normal breed types in the rate of muscle deposition in all muscle groups except those surrounding the spinal column. At the same total side muscle, in DM carcasses there were shifts in muscle weight distribution towards the more fleshy, expensive muscles. DM had proportionately less muscle weight in the distal parts of both limbs, and in neck muscles. Differences were more pronounced when comparisons were made at the same dissected side weight than when comparisons were made at the same total side muscle weight. This is a reflection of the generally higher proportion of muscle in the carcass of DM's compared with more normal breed types (Chapter I).

III. GROWTH AND DISTRIBUTION OF THE WEIGHT OF INDIVIDUAL MUSCLES IN DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen Double Muscled (DM), 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls, serially slaughtered from approximately 250 to 800 kg live weight, were used to examine the influence of maturity type and Double Muscling on individual muscle growth patterns and distribution.

Breed types differed significantly in the relative growth rate of 5 of the 95 muscles. Individual muscles grew and developed at relatively different rates with muscles associated with locomotion being early developing followed by those associated with structure or posture and finally those which respond to sexual maturation or luxury muscles which were late developing. Individual muscle growth patterns revealed an increasing disto-proximal gradient along the limbs and an increasing caudo-cranial gradient along the whole body. However, within any anatomical region considerable variation with well defined growth gradients were found for individual muscles. In the proximal region of both limbs increasing medio-lateral growth gradients were apparent.

Breed types differed significantly in adjusted mean weights of 33 of the 95 muscles. When comparison was made at the same total side muscle, DM showed a range of hypertrophy of +28% to -28% when compared to the more normal breed

types.

Muscular hypertrophy followed a disto-proximal gradient along the limbs and an inner-outer gradient across the muscle layers with the superficial and bulkiest muscles being the most hypertrophied. At the same total side muscle, DM had heavier expensive or luxury muscles than normal cattle.

INTRODUCTION

Cattle exhibiting extreme muscular appearance are characterized by spectacular bulging conformation most visible in the posterior part of the proximal hindlimb and in the brachium where muscles appear extremely enlarged. The general nature of animals displaying muscular hypertrophy was described in chapter I.

Studies with Double Muscled cattle leave uncertainties about the effect of double muscling on muscle weight distribution. Pomeroy and Williams, 1962, Butterfield, 1966*a*, Oliver and Cartwright, 1968 and Lohmán *et al*., 1971 found no differences between Double Muscled and normal animals in muscle weight distribution. On the other hand, Vissac, 1968; Rollin *et al*., 1969; Hanset and Ansay, 1972; Dumont *et al*., 1982 and Michaux *et al*., 1983 demonstrated differences in muscle weight distribution in Double Muscled cattle when compared to normal cattle.

Although muscle weight distribution of Double Muscled animals is well documented at specific ages and live weights, there are no reports where serial slaughter over a wide range of live weights has been used to study the influence of 'Double Muscling' on growth patterns and distribution of individual muscles could be characterized and compared to other genotypes. Chapter II dealt with anatomical muscle groupings and in the present Chapter growth patterns and distribution of individual muscles of Double Muscled animals are examined and compared to more normal breed types.

MATERIALS AND METHODS

Details of the animals, and of their feeding regimen, management and dissection procedure were described in Chapter I.

The left side of each carcass was dissected into muscle, bone and fat (Butterfield and May, 1966). The muscular tissue was dissected into 95 individual muscles. For convenience the individual muscles were grouped into nine anatomical groups based on their anatomical location (Chapter II). The sum of the individual muscles was used as total side muscle (TSM).

STATISTICAL ANALYSIS

The data were analyzed by one way analysis of covariance (Snedecor and Cochran, 1967), according to the following model.

$$\log Y_{ij} = A_0 + G_i + b \log X_{ij} + (Gb)_i \log X_{ij} + e_{ij},$$

where:

Y_{ij} = weight (g) of individual muscle of the $_{ij}th$ animal;

A_0 = the intercept;

G_i = fixed effect of the $_{i}th$ breed type;

X_{ij} = total weight (g) of the total side muscle of the $_{ij}th$ animal;

b = regression coefficient of Y on X;

$(Gb)_i$ = interactions effect (breed x regression coefficient)

e_{ij} = error, assumed to be $NID (0, \sigma^2 e)$.

Individual breed type regression coefficients were computed and compared and in cases where the slopes were homogeneous ($P > 0.05$) the common regression coefficient was used for adjustment. However, if among slope differences were significant, adjusted means were computed using the appropriate breed type regression but were not statistically tested for signficance. Duncan's multiple range test (Steel and Torrie, 1980) was used to test the significant differences between adjusted means.

The residual coefficient of variation (RCV%) was calculated as: RCV% = $100 \left(10^{S_{y \cdot x}} - 1 \right)$. Where $S_{y \cdot x}$ is the square root of the error variance (standard error) and $10^{S_{y \cdot x}}$ = antilogarithm of standard error.

RESULTS

In Table III.1 are presented unadjusted means and standard deviations for dissected side weight (DSW), total side muscle (TSM) and the proportion of muscle in the side for each breed type.

Growth coefficients and adjusted means are presented in Table III.2 for individual muscles within anatomical groupings for each breed type. One muscle within the proximal hindlimb group (*m. tensor fasciae latae*) tended to grow faster than TSM, while other muscles tended to grow at the same rate or at a slower rate than TSM. DM bulls had a higher growth coefficient than did the bulls in the other breed types for *m. sartorius* while all breed types tended to have somewhat similar growth coefficients for all other muscles within this group.

Almost all the extensor and flexor muscles of the distal hindlimb had low growth coefficients and there were no breed type differences in growth coefficients for any of the muscles of this group.

Along the dorsal line most muscles had either low or average growth coefficients. HE had a higher growth coefficient for *m. longissimus thoracis et lumborum* (formerly *m. longissimus dorsi*) than either SY or DM (1.070 *vs* 0.910 and 0.920 respectively).

Within the abdominal group, only 2 muscles tended to grow faster than TSM ($b > 1$; $P < 0.05$), while the remainder had average growth coefficients. Breed types

Table III.1. Unadjusted Means and Standard Deviations of Side Weight, Total Side Muscle Weight and Muscle Weight as % of Side Weight by Breed Type

	Hereford		Beef Synthetic		Double Muscled	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Side weight (kg)⁺	176.4	34.9	158.6	41.6	154.2	49.8
Total side muscle (kg)	100.3	18.4	106.4	25.4	107.7	39.2
Muscle in side (%)	57.3	4.2	67.5	3.5	69.2	6.2

⁺Excluding kidney knob and channel fat.

S.D = standard deviation

Table III.2. Estimates of Growth Coefficients *(b)* and Adjusted Means for Weights of Individual Muscle Relative to Total Side Muscle

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted antilog Means (g)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Group 1. Muscles of the proximal hindlimb														
M. tensor fasciae latae	1.031	0.08	1.016	0.06	**1.175**	0.06	**1.113**	0.04	8.14	1255a	1250a	1328b	2.12	3.78*
M. biceps femoris	0.972	0.05	1.048	0.05	0.994	0.05	1.002	0.03	6.05	6503	6520	6704	0.44	2.13
M. gluteus medius	**0.838**	0.07	0.895	0.18	0.944	0.04	0.914	0.05	11.94	3259	3163	3359	0.27	1.36
M. vastus lateralis	**0.878**	0.05	0.897	0.18	0.923	0.07	**0.909**	0.04	12.74	2074	2213	2067	0.05	1.82
M. gluteus accessorius	0.802	0.16	1.000	0.17	0.840	0.10	0.871	0.07	16.12	247	236	225	0.47	1.61
M. rectus femoris	**0.779**	0.08	**0.729**	0.07	0.913	0.06	**0.847**	0.04	8.68	1745	1760	1799	2.20	1.10
M. semitendinosus	1.012	0.09	0.936	0.07	1.021	0.05	1.000	0.04	7.81	2494a	2470a	2633b	0.47	3.82*
M. gracilis	0.966	0.09	0.946	0.07	0.994	0.04	0.978	0.03	7.24	1155a	1206ab	1233b	0.18	4.25**
M. semimembranosus	**0.762**	0.09	0.922	0.07	0.909	0.05	**0.886**	0.04	8.43	4421a	4538a	4737b	1.12	3.43*
M. adductor femoris	1.020	0.06	**0.805**	0.06	**0.850**	0.07	**0.869**	0.04	8.65	1448	1425	1387	1.69	1.69
M. pectineus	**0.719**	0.13	0.847	0.17	0.981	0.07	0.904	0.07	14.47	513	505	500	1.18	0.27
M. sartorius	**0.797**	0.08	**0.745**	0.08	1.119	0.08	0.976	0.05	12.76	323	343	362	5.19*	——
M. quadratus femoris	0.692	0.19	0.673	0.21	0.584	0.12	**0.624**	0.09	19.66	52a	51a	42b	0.14	6.09**
Mm. obturatorii externus et interus	1.043	0.14	0.921	0.11	**0.755**	0.06	**0.844**	0.05	11.94	423	462	428	2.29	3.14
M. vastus medialis	0.898	0.10	**0.758**	0.11	**0.669**	0.06	**0.730**	0.09	12.38	631a	626a	560b	1.15	5.37**
M. articularis genu	**0.074**	0.54	0.815	0.52	0.565	0.30	0.511	0.23	51.57	32a	31a	23b	0.74	6.52**

Continued

Table III.2. *Contd.*

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means antilog (g)			F-Values	
	b	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
M. iliacus	**0.752**	0.11	**0.649**	0.09	**0.773**	0.05	**0.740**	0.05	10.63	661ab	704a	623b	0.54	6.24**
M. gluteus profundus	0.798	0.17	0.851	0.08	**0.720**	0.06	**0.764**	0.05	11.54	321a	324a	274b	0.55	12.20**
M. gemellus	0.829	0.24	**0.401**	0.33	**0.627**	0.10	**0.610**	0.12	25.83	56a	62a	47b	0.66	5.31**
M. vastus intermedius	**0.685**	0.14	**0.788**	0.10	**0.670**	0.08	**0.700**	0.07	13.54	571a	522ab	480b	0.30	4.56**
Group 2 Muscles of the distal hindlimb														
M. gastrocnemius	**0.846**	0.07	**0.767**	0.07	**0.773**	0.05	**0.785**	0.04	8.21	1615a	1756b	1642a	0.30	5.71**
Mm. extensores	**0.854**	0.07	**0.720**	0.09	**0.855**	0.04	**0.823**	0.04	7.84	610a	560b	509c	1.28	23.89**
M. peroneus longus	**0.635**	0.17	**0.470**	0.16	**0.630**	0.17	**0.594**	0.13	27.96	90	99	93	0.14	0.60
M. extensor digitorum lateralis	**0.535**	0.22	**0.129**	0.28	**0.485**	0.26	**0.411**	0.15	34.83	98a	157b	123a	0.47	8.44**
M. tibialis cranialis	**0.361**	0.30	1.214	0.34	0.864	0.25	0.858	0.18	39.20	120	101	93	1.14	1.98
M. tibialis caudalis	1.307	0.41	0.703	0.35	0.913	0.19	0.933	0.16	35.58	111a	76b	84b	0.69	5.51**
M. popliteus	**0.738**	0.12	**0.755**	0.11	**0.663**	0.06	**0.697**	0.05	11.44	221	217	208	0.31	1.52
M. flexor digitorum longus	0.988	0.16	**0.760**	0.11	**0.800**	0.09	**0.824**	0.07	16.95	178	172	187	0.49	1.15
M. flexor digitorum superficialis	**0.804**	0.09	**0.793**	0.09	**0.721**	0.08	**0.752**	0.06	14.12	333a	346a	294b	0.17	6.64**
M. flexor hallucis longus	**0.842**	0.07	**0.647**	0.11	**0.804**	0.06	**0.774**	0.05	10.43	493a	469a	411b	1.14	15.09**

Continued

Table III.2. *Contd.*

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means antilog (g)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Group 3. Muscles surrounding the spinal column														
M. psoas major	**0.852**	0.06	**0.796**	0.08	0.950	0.05	**0.897**	0.04	8.01	1446a	1422a	1520b	1.67	3.92*
M. quadratus lumborum	1.237	0.17	0.980	0.20	**0.690**	0.12	0.853	0.09	19.98	143	131	129	2.93	1.43
M. iliocostalis thoracis	1.140	0.13	1.038	0.12	0.830	0.09	0.932	0.06	13.97	512a	534a	438b	2.10	10.27**
M. longissimus thoracis et lumborum	1.070	0.04	**0.910**	0.04	**0.920**	0.03	**0.944**	0.02	4.83	6459	6483	6576	3.91*	——
M. multifidus thoracis et lumborum	1.002	0.17	0.929	0.22	**0.626**	0.15	**0.762**	0.10	22.41	1189	1023	1115	1.34	2.05
M. longissimus cervicis	1.022	0.33	1.0495	0.27	1.280	0.14	1.181	0.12	27.28	327a	414b	345a	0.45	3.80*
M. spinalis cervicis et thoracis	**1.144**	0.06	**1.115**	0.05	1.005	0.08	1.055	0.04	9.41	1935	1889	1865	0.99	1.21
M. psoas minor	1.166	0.19	0.809	0.14	0.815	0.08	0.874	0.07	16.12	286	287	300	1.70	0.58
Group 4. Muscles of the abdominal wall														
M. cutaneus trunci	1.105	0.12	0.839	0.17	1.165	0.19	1.078	0.10	21.76	1815a	1586b	1916c	0.90	3.66*
M. serratus dorsalis caudalis	1.033	0.32	0.969	0.16	**1.469**	0.15	**1.276**	0.11	24.96	153	151	175	2.19	1.92
M. obliquus externus abdominis	1.065	0.20	0.958	0.09	**1.241**	0.07	**1.144**	0.07	14.53	2539	2359	2561	1.71	1.98
M. retractor costae	1.548	0.81	0.256	0.50	1.190	0.34	**1.035**	0.28	62.68	85	96	75	1.24	0.71
M. obliquus internus abdominis	0.923	0.25	1.079	0.08	0.923	0.04	**0.959**	0.07	14.65	1790	1721	1769	0.47	0.48
M. transversus abdominis	1.012	0.32	0.889	0.09	0.862	0.14	**0.894**	0.10	22.15	1322	1286	1294	0.14	0.15
M. rectus abdominis	1.121	0.08	1.089	0.07	0.975	0.06	**1.027**	0.04	9.07	2335	2214	2210	1.19	2.66

Continued

Table III.2. *Contd.*

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means antilog (g)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	**b**	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Group 5. Muscles of the proximal forelimb														
M. deltoideus	1.077	0.10	1.156	0.07	0.832	0.14	**0.950**	0.07	15.97	585	524	555	2.05	2.33
M. infraspinatus	1.020	0.09	0.932	0.06	0.991	0.03	**0.982**	0.03	6.39	1911a	1819b	1808b	0.51	4.91*
M. triceps brachii (Caput laterale)	0.893	0.09	**0.848**	0.07	0.936	0.04	**0.908**	0.04	7.67	618a	580b	60[illegible]	0.54	3.73*
M. teres minor	0.961	0.20	0.683	0.20	**0.608**	0.11	**0.687**	0.09	19.40	190a	192a	161b	1.07	4.74*
M. triceps brachii (Caput longum)	1.056	0.06	**1.112**	0.03	**1.083**	0.03	**1.085**	0.02	4.43	3282ab	3267b	3376a	0.39	4.66*
M. tensor fasciae antebrachii	0.988	0.08	1.162	0.12	**1.202**	0.08	**1.155**	0.05	11.67	199ab	187b	207a	1.09	3.80*
M. supraspinatus	0.921	0.09	**0.766**	0.05	0.961	0.04	**0.909**	0.03	7.10	1295	1336	1344	3.33*	--
M. biceps brachii	0.955	0.06	0.977	0.10	0.946	0.15	0.955	0.07	15.87	559	546	546	0.01	0.36
M. teres major	1.036	0.12	1.162	0.14	1.065	0.05	1.083	0.05	11.72	397	414	432	0.34	2.68
M. brachialis	**0.821**	0.07	**0.786**	0.08	**0.856**	0.04	**0.833**	0.03	7.06	390a	410b	373a	0.40	9.09**
M. coracobrachialis	1.096	0.27	**0.535**	0.20	**0.581**	0.14	**0.660**	0.11	25.31	106	113	105	1.55	0.46
M. subscapularis	1.020	0.09	0.995	0.08	0.904	0.06	**0.945**	0.04	9.24	1162	1172	1138	0.72	0.95
M. triceps brachii (Caput mediale)	0.641	0.21	0.870	0.28	0.809	0.18	**0.794**	0.12	26.60	106	93	90	0.18	2.05

Continued

Table III.2. *Contd.*

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means antilog (g)			F-Values	
	b	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM.	Among slopes	Among adjusted means
Group 6. Muscles of the distal forelimb														
M. extensor carpi radialis	0.930	0.08	**0.868**	0.05	0.938	0.05	**0.920**	0.03	7.28	686	673	673	0.37	0.99
M. extensor digitorum tertii	0.988	0.07	**0.677**	0.15	**0.727**	0.07	**0.761**	0.06	12.27	100	99	101	1.87	0.29
M. extensor digitorum communis	**0.749**	0.11	0.889	0.18	**0.749**	0.07	**0.782**	0.07	15.27	76a	75a	66b	0.36	5.17**
M. extensor digitorum lateralis	0.854	0.22	**0.570**	0.18	**0.639**	0.14	**0.661**	0.09	20.70	115	107	109	0.48	0.73
M. ulnaris lateralis	0.784	0.21	0.840	0.11	0.957	0.14	0.899	0.09	18.88	219	228	201	0.33	2.26
M. abductor pollicis longus	0.828	0.42	0.727	0.26	**0.575**	0.18	**0.655**	0.14	31.71	22	27	23	0.24	1.58
M. flexor carpi radialis	0.962	0.11	**0.788**	0.10	**0.813**	0.07	**0.833**	0.05	11.09	100	99	92	0.70	3.08
M. flexor carpi ulnaris	0.918	0.14	0.746	0.31	0.876	0.20	**0.853**	0.12	27.42	96	102	97	0.11	0.25
M. flexor digitorum profundus	**0.763**	0.11	0.869	0.18	**0.696**	0.08	**0.748**	0.07	15.58	362a	422a	329b	0.49	11.66**
M. anconeus	0.902	0.15	**0.664**	0.15	**0.492**	0.16	**0.604**	0.12	27.34	92a	74b	72b	0.75	4.35*
M. flexor digitorum sublimis	**0.678**	0.16	**0.411**	0.26	**0.566**	0.12	**0.549**	0.10	23.07	316	284	325	0.33	1.70

Continued

Table III.2. *Contd.*

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means antilog (g)			F-Values	
	b	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Group 7. Muscles connecting the thorax to the forelimb														
M. trapezius thoracis	0.835	0.10	**0.538**	0.18	1.152	0.17	0.840	0.10	25.53	908	873	896	4.22*	—
M. latissimus dorsi	1.116	0.08	**1.378**	0.12	**1.174**	0.06	**1.211**	0.05	10.43	2313	2359	2445	2.04	1.76
M. serratus ventralis thoracis	**1.085**	0.04	1.098	0.07	1.007	0.05	1.042	0.03	6.87	1396	1445	1395	0.91	2.67
M. pectoralis profundus	0.924	0.08	0.761	0.18	1.080	0.06	0.978	0.06	13.31	4051	3698	4025	2.53	2.78
M. pectoralis superficialis	**1.278**	0.10	**1.461**	0.21	0.962	0.10	1.133	0.08	17.85	1783	1895	1753	3.87*	—
Group 8. Muscles connecting the neck to the forelimb														
M. trapezius cervicalis	1.250	0.14	1.236	0.26	**1.481**	0.11	**1.384**	0.09	20.65	779	667	759	0.77	3.12
M. omotransversarius	**1.247**	0.11	**1.291**	0.12	**1.275**	0.08	**1.274**	0.06	13.35	644	672	704	0.02	2.32
M. rhomboideus	**1.229**	0.08	**1.254**	0.08	**1.365**	0.07	**1.315**	0.04	9.52	1728a	1739a	1845b	0.96	3.28*
M. serratus ventralis cervicis	**1.124**	0.05	**1.212**	0.05	1.044	0.05	**1.097**	0.03	6.59	2879	2818	2799	2.88	2.28
M. brachiocephalicus	0.938	0.18	1.197	0.15	**1.232**	0.06	**1.172**	0.07	14.67	1662	1499	1658	1.33	3.13
Group 9. Intrinsic muscles of the neck and thorax														
M. intercostales (externi et interni)	0.963	0.14	0.927	0.16	0.842	0.08	0.883	0.07	14.58	3185a	3276a	2881b	0.28	4.04*
M. serratus dorsalis cranialis	**1.365**	0.17	**1.447**	0.20	**1.498**	0.07	**1.470**	0.12	25.92	157	179b	180	0.08	1.74

Continued

Table III.2. *Contd.*

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means antilog (g)			F-Values	
	b'	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
M. scalenus dorsalis	**1.412**	0.19	**1.751**	0.15	**1.633**	0.09	**1.622**	0.10	21.82	239a	265ab	306b	0.57	5.85**
M. splenius	1.482	0.11	1.746	0.21	**1.646**	0.19	**1.641**	0.08	18.20	1465	1391	1314	0.59	2.28
M. intertransversarius longus	**1.655**	0.30	1.249	0.26	1.180	0.18	**1.278**	0.13	29.21	421	498	450	0.86	1.62
M. longus capitis	1.327	0.25	1.119	0.26	1.068	0.21	1.125	0.13	29.03	252	227	269	0.25	1.56
M. longissimus capitis et atlantis	**1.692**	0.30	**1.555**	0.23	**1.395**	0.13	**1.484**	0.12	25.84	502	552	473	0.47	1.80
M. intertransversarius cervicis (dorsalis et ventralis)	0.958	0.20	1.209	0.32	1.030	0.13	1.059	0.12	25.34	824a	664b	781ab	0.27	3.59*
M. complexus	**1.323**	0.12	**1.423**	0.18	**1.182**	0.08	**1.263**	0.07	15.50	2354	2262	2102	1.04	2.66
M. obliquus capitis caudalis	0.926	0.08	1.064	0.12	**0.804**	0.07	**0.886**	0.05	11.51	683a	662a	585b	2.20	9.43**
M. rectus thoracis	0.954	0.14	**0.623**	0.17	1.023	0.14	0.848	0.09	23.00	116	114	130	2.23	1.70
M. transversus thoracis	0.768	0.44	**0.888**	0.20	0.864	0.18	0.853	0.14	31.09	195	201	196	0.04	0.07
M. cervicohyoideus	1.147	0.25	**2.130**	0.24	**1.459**	0.20	**1.561**	0.16	34.82	46	38	48	2.32	2.48
M. scalenus ventralis	**1.325**	0.15	1.182	0.24	**1.457**	0.20	**1.370**	0.13	28.96	462	426	394	0.37	1.48
M. longus colli	**1.213**	0.09	**1.243**	0.11	0.848	0.11	1.003	0.08	18.31	736	763	694	2.72	1.34
M. multifidus cervicis	1.085	0.14	1.084	0.23	**0.741**	0.12	0.881	0.10	23.01	366	327	333	1.30	1.22

'Growth coefficients in bold type are significantly different from 1 at $P < 0.05$.
Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.
Adjusted to geometric mean total side muscle (TSM) = 100.6 kg along the slope of common regression line.
HE, Hereford; SY, Beef. Synthetic; DM, Double Muscled.
—— Missing values means covariance analysis was not legitimate.
* $P < 0.05$; ** $P < 0.01$

tended to have somewhat similar growth coefficients for all abdominal muscles.

Two muscles in the proximal forelimb (*m. tensor fasciae antebrachii* and *m. triceps brachii* (*Caput longum*)) tended to grow faster than TSM, while other muscles tended to grow at the same rate or at a slower rate than TSM. DM and normal cattle tended to have somewhat similar growth rates for all muscles within this group other than *m. supraspinatus* for which DM had a higher growth rate than the more normal breed types.

Most muscles in the distal forelimb had low growth coefficients and breed types did not differ in this respect.

In the cranial end of the animal, all muscles within the neck attached to the forelimb had high growth coefficients, while those of the thorax to the forelimb and the intrinsic muscles of neck and thorax had either very high or average growth coefficients. Breed types differed significantly in growth rate of *m. trapezius thoracis*, of which DM had a higher growth coefficient than both HE and SY. SY had significantly higher growth coefficient for *m. pectoralis superficialis* than DM and HE (1.461 *vs* 0.962 and 1.278 respectively). No significant ($P > 0.05$) differences between breed types were found for any other muscle within these regions.

The residual coefficients of variation for individual muscles are presented in Table III.2. Generally, the large muscles were less variable than the small ones.

Breed types differed significantly in adjusted mean weights of 33 of the 95 muscles (Table III.2).

In Table 3 ratios of weights of muscles adjusted to the same TSM from DM *vs* HE and SY are presented. In DM some muscles showed hypertrophy and others hypotrophy which is inevitable when comparison is made at a standard TSM. Degree of muscular hypertrophy in DM depended on whether they were compared with HE or SY. When compared with HE, DM ranged from +28% (*m. scalenus dorsalis*) to -28% (*m. articularis genu*). Compared with SY, DM ranged from +21% for *m. cutaneus trunci* to -24% for *m. gemellus*.

Compared with phenotypically more normal cattle, DM had quite different muscle weight distribution. In muscular hypertrophied animals 10 muscles constituting approximately 19% of TSM were grossly hypertrophied, 23 muscles constituting approximately 13% of TSM showed hypotrophy and the remaining 62 muscles (constituting 68% of TSM) were not significantly different (Tables III.2 and III.3). At the same TSM, DM had significantly higher proportions than HE and SY for *m. tensor fasciae latae*, *m. semitendinosus*, *m. semimembranosus*, *m. cutaneus trunci* *m. rhomboideus*. **DM** had a higher proportion of *m. gracilis* and *m. scalenus dorsalis* than HE but did not differ (P > 0.05) from SY for this muscle. DM had significantly higher proportion than SY of *m. psoas major*, *m. triceps brachii* (*caput longum*) and *m. tensor fasciae antebrachii* but did not differ significantly from HE for these muscles.

Table III.3. Ratios of Weight of Muscles from DM *VS* HE or SY at Equal Total Side Muscle

	Ratios[+]	
	DM/HE	DM/SY
Group 1. Muscles of the proximal hindlimb		
M. tensor fasciae latae	1.058*	1.062*
M. biceps femoris	1.031	1.028
M. gluteus medius	1.031	1.062
M. vastus lateralis	0.997	0.934
M. gluteus accessorius	0.911	0.953
M. rectus femoris	1.031	1.022
M. semitendinosus	1.056*	1.066*
M. gracilis	1.068*	1.023
M. semimembranosus	1.071*	1.044*
M. adductor femoris	0.958	0.973
M. pectineus	0.975	0.990
M. sartorius	1.120	1.055
M. quadratus femoris	0.808**	0.824**
Mm. obturatorii externus et interus	1.012	0.926
M. vastus medialis	0.887**	0.895**
M. articularis genu	0.719**	0.722**

Continued

Table III.3. *Contd.*

	Ratios⁺	
	DM/HE	DM/SY
M. iliacus	0.943	0.885**
M. gluteus profundus	0.846**	0.846**
M. gemellus	0.839**	0.758**
M. vastus intermedius	0.841**	0.920
Group 2 Muscles of the distal hindlimb		
M. gastrocnemius	1.017	0.935*
Mm. extensores	0.834**	0.909**
M. peroneus longus	1.033	0.939
M. extensor digitorum lateralis	1.250	0.847**
M. tibialis cranialis	0.775	0.921
M. tibialis caudalis	0.757*	1.105
M. popliteus	0.941	0.959
M. flexor digitorum longus	1.051	1.087
M. flexor digitorum superficialis	0.883**	0.850**
M. flexor hallucis longus	0.834**	0.876**

Continued

Table III.3. *Contd.*

	Ratios⁺	
	DM/HE	DM/SY
Group 3. Muscles surrounding the spinal column		
M. psoas major	1.052*	1.067*
M. quadratus lumborum	0.902	0.985
M. iliocostalis thoracis	0.855**	0.820**
M. longissimus thoracis et lumborum	1.018	1.014
M. multifidus thoracis et lumborum	0.938	1.090
M. longissimus cervicis	1.055	0.833*
M. spinalis cervicis et thoracis	0.964	0.987
M. psoas minor	1.049	1.045
Group 4. Muscles of the abdominal wall		
M. cutaneus trunci	1.056	1.208*
M. serratus dorsalis caudalis	1.144	1.159
M. obliquus externus abdominis	[illegible]009	1.086
M. retractor costae	0.882	0.781
M. obliquus internus abdominis	0.988	1.028
M. transversus abdominis	0.979	1.006
M. rectus abdominis	0.946	0.998

Continued

Table III.3. *Contd.*

	Ratios⁺	
	DM/HE	DM/SY
Group 5. Muscles of the proximal forelimb		
M. deltoideus	0.949	1.059
M. infraspinatus	0.946*	0.994
M. triceps brachii (Caput laterale)	0.977	1.041
M. teres minor	0.847*	0.839*
M. triceps brachii (Caput longum)	1.029	1.033*
M. tensor fasciae antebrachii	1.040	1.107*
M. supraspinatus	1.038	1.006
M. biceps brachii	0.977	1.000
M. teres major	1.088	1.043
M. brachialis	0.956	0.910**
M. coracobrachialis	0.991	1.076
M. subscapularis	0.979	0.971
M. triceps brachii (Caput mediale)	0.849	0.968

Continued

Table III.3. *Contd.*

	Ratios⁺	
	DM/HE	DM/SY
Group 6. Muscles of the distal forelimb		
M. extensor carpi radialis	0.981	1.000
M. extensor digitorum tertii	1.01	1.02
M. extensor digitorum communis	0.868**	0.880**
M. extensor digitorum lateralis	0.948	1.019
M. ulnaris lateralis	0.918	0.882
M. abductor pollicis longus	1.045	0.852
M. flexor carpi radialis	0.920	0.929
M. flexor carpi ulnaris	1.010	0.951
M. flexor digitorum profundus	0.909**	0.780**
M. anconeus	0.783*	0.973
M. flexor digitorum sublimis	1.028	1.144

Continued

Table III.3. *Contd.*

	Ratios⁺	
	DM/HE	DM/SY
Group 7. Muscles connecting the thorax to the forelimb		
M. trapezius thoracis	0.987	1.026
M. latissimus dorsi	1.057	1.036
M. serratus ventralis thoracis	0.999	0.965
M. pectoralis profundus	0.994	1.088
Mm. pectoralis superficialis	0.983	0.925
Group 8. Muscles connecting the neck to the forelimb		
M. trapezius cervicalis	0.974	1.138
M. omotransversarius	1.093	1.048
M. rhomboideus	1.068*	1.061*
M. serratus ventralis cervicis	0.972	0.993
M. brachiocephalicus	0.998	1.106
Group 9. Intrinsic muscles of the neck and thorax		
M. intercostales (externi et interni)	0.905*	0.879*
M. serratus dorsalis cranialis	1.146	1.006

Continued

Table III.3. *Contd.*

	Ratios[+]	
	DM/HE	DM/SY
M. scalenus dorsalis	1.280**	1.155
M. splenius	0.897	0.945
M. intertransversarius longus	1.069	0.904
M. longus capitis	1.067	1.185
M. longissimus capitis et atlantis	0.942	0.857
M. intertransversarius cervicis (dorsalis et ventralis)	0.948	1.176
M. complexus	0.893	0.929
M. obliquus capitis caudalis	0.857**	0.884**
M. rectus thoracis	1.121	1.140
M. transversus thoracis	1.005	0.975
M. cervicohyoideus	1.043	1.263
M. scalenus ventralis	0.853	0.925
M. longus colli	0.943	0.910
M. multifidus cervicis	0.910	1.018

* $P < 0.05$; ** $P < 0.01$.

[+] Weight of muscle in DM shown as ratio of weight in HE and SY.

DISCUSSION

MUSCLE GROWTH PATTERNS

Hammond (1932) pointed out that the growth of the individual muscles varied with age and he suggested that these variations in growth might be due to changes in the relative points of attachment as a consequence of differential rate of growth in the bone. Berg and Butterfield (1976) concluded that individual muscles and muscle groups, undergo a period of diverse growth rate immediately after birth, until the birth weight of the musculature has doubled, after that time they tended to grow at a similar proportional rate and then a further phase of change in muscle growth occurs following puberty. It should be mentioned that the values of growth coefficients (*b*) depend upon the range of slaughter weights and the stage of maturity. Data used in this study do not embrace the early post-natal stage, thus, growth patterns of muscles reported in this study might be quite different from those which included this stage.

Growth rate of various muscles in the proximal hindlimb varied considerably from a high of b = 1.113 for *m. tensor fasciae latae* to a low of b = 0.511 for *m. articularis genu*. The common growth coefficients of muscles of the proximal hindlimb revealed an increasing medio-lateral growth gradient. DM had a higher relative rate of muscle growth for *m. sartorius* than HE and SY. Hammond (1932) reported that the greatest difference between large and small breeds in development of the thigh muscles lay in *m. sartorius* of which the Suffolk exceeded both Southdown and Welsh breeds.

Within the shoulder muscles the growth coefficients revealed increasing medio-lateral growth gradients. The highest growth coefficients were found in *m. tensor fasciae antebrachii* and *m. triceps brachii* (*caput longum*) and the lowest was found in *m. triceps brachii* (*caput mediale*). Within this group the only significant differences among breed types was in *m. supraspinatus*, which tended to grow at a slower rate in SY and similar rate to TSM in HE and DM. Butterfield and Berg (1966*a*) reported that *m. supraspinatus* had a low growth coefficient while Lohse *et al.* (1971) working with sheep, reported an average-low growth coefficient. Davies (1974) reported that at the same total muscle, Large White pigs had a significantly higher growth coefficient for *m. supraspinatus* than Pietrain (double muscled). Also, Jury *et al.* (1977) reported significant breed differences in the relative growth rate of the *m. supraspinatus* in sheep. ✓

Significant breed differences in the relative growth rate of *m. longissimus thoracis et lumborum*, have been reported in sheep by Jury *et al.* (1977), in pigs by Davies (1974) and in cattle (the present study). Breed differences in growth rate of this muscle could be related to differences in the shape of the lumbar vertebrae, differences in the way the weight is distributed over the body or differences in mature size and stage of maturity. In young animals this muscle seems to be responsible for weight support and thus it tends to grow at a faster rate than total muscle immediately after birth. Supporting this assumption, Jury *et al*. (1977) reported that in sheep the muscles surrounding the spinal column grew faster than total muscle at low weights of TSM, but tended to grow at a slower rate than total muscle at heavy total muscle weight. Similarly (Butterfield and Berg, 1966*a*; Jury *et al*., 1977) showed that *m. longissimus thoracis et lumborum* tended to grow at a faster rate than total muscle immediately after birth and tended to grow at the same rate or a slower rate thereafter. In the present study which does not include the early post-natal stage, it tended to grow at a slower rate than TSM in SY and DM. Similar findings have been reported by Butterfield *et al*.(1983) with sheep.

In prenatal phases of growth, abdominal muscles tend to grow at a slower rate than total muscle (Johnson, 1974), while in postnatal phases of growth they have either high growth coefficients (Butterfield and Berg, 1966*a*) or average growth coefficients (Andersen, 1975; Butterfield *et al*., 1983 and the present study).

Almost, all muscles of the distal limbs had low growth coefficients. The relatively low growth coefficients for these muscles could be related to their anatomical locations or to their higher proportion of connective tissue relative to muscle fibers. These results are similar to those of Andersen (1975) and Butterfield *et al*. (1983). Berg and

Butterfield (1976) suggested that the anatomical location of the muscles within the carcass is the major factor determining their growth potential. They reported that the extensors and flexors were tightly bound by connective tissue which would impede their growth, consequently they had low growth rates.

Results of the present study showed that the highest growth coefficients were located in the cranial end of the animal. However, within these anatomical regions there was considerable variation in the relative growth rate for individual muscles. These results are consistent with the reports of Butterfield *et al.* (1983). In HE and SY, *m. pectoralis superficialis* tended to grow at a faster rate than TSM, while in DM, it tended to grow at the same rate which might be related to greater fat deposition in HE and SY. The high growth coefficients for this muscle in HE and SY are in agreement with Jury *et al.* (1977), while the average growth coefficient in DM is in agreement with Berg and Butterfield (1976). However, Lohse *et al.* (1971) reported that the above mentioned muscle grew at a relatively slower rate than total muscle in sheep. Jury *et al.* (1977) reported significant breed differences in the relative growth rate of this muscle in sheep.

Relative to TSM, DM and SY bulls had nonsignificantly higher growth rate for *m. splenius* than did the HE bulls perhaps reflecting the later maturing patterns for the former breed types. *M. splenius* (crest formation) was shown by Brannang (1971) to be the muscle in the whole carcass most inhibited by castration.

The present study showed that individual muscles grew and developed at relatively different rates with muscles associated with locomotion being early developing followed by those associated with structure or posture and finally those which are influenced by sexual differentiation or luxury muscles which were late developing. The lowest growth coefficients were found in the muscles of the distal parts of both limbs and those located very deeply within the carcass or those containing a higher proportion of connective tissue, whereas the highest growth coefficients were found in the superficial muscles or in the more fleshy, and bulky muscles and in the cranial end of the animal.

MUSCLE WEIGHT DISTRIBUTION

Muscle weight distribution as used here refers to the proportions of anatomically distinct muscles or muscle groups in relation to the total musculature. Comparisons of muscle weight distribution have been made at the same weight of TSM. However it is necessary to consider possible differences in maturity and mature weight of different breed types at the same TSM. The breed type which has reached a greater degree of maturity at a standard TSM will have a relatively higher proportion of late developing muscles. However, with 'Double Muscling' other factors besides that of rate of maturity may affect the proportions of muscles.

Studies have shown that compared with normal, at the same live weight or carcass weight, DM had more muscle in the carcass and heavier muscles, based on these observation Oliver and Cartwright (1968) reported that in DM all the muscles were hypertrophied and the proportion of one muscle to another was similar in DM and normal (i.e. generalized hypertrophy). In a previous chapter it was found that at the same dissected side weight, compared with more normal breed types, there was general but not uniform hypertrophy, being greater in proximal limbs and lower in distal limbs. However, when comparisons were made at the same TSM, there was differential hypertrophy in different anatomical regions. So it is clear that the term generalized hypertrophy or localized and differential hypertrophy depends on the basis of comparison (e.g. at constant live weight, side weight or total muscle weight). Therefore it is very important that any statements about the effect of 'Double Muscling' on muscle development should be qualified by the basis on which comparisons are made.

The present study showed that 'Double Muscling' affects the various muscles in a differential manner related to their maturity, size, dimensions, number of joints crossed by a muscle, anatomical location within the carcass, and of their muscle fiber or connective tissue content. In Figures III.1 and III.2 are illustrated relative development of those muscles differing significantly in DM compared to HE and SY at equal total side muscle. It can seen that the

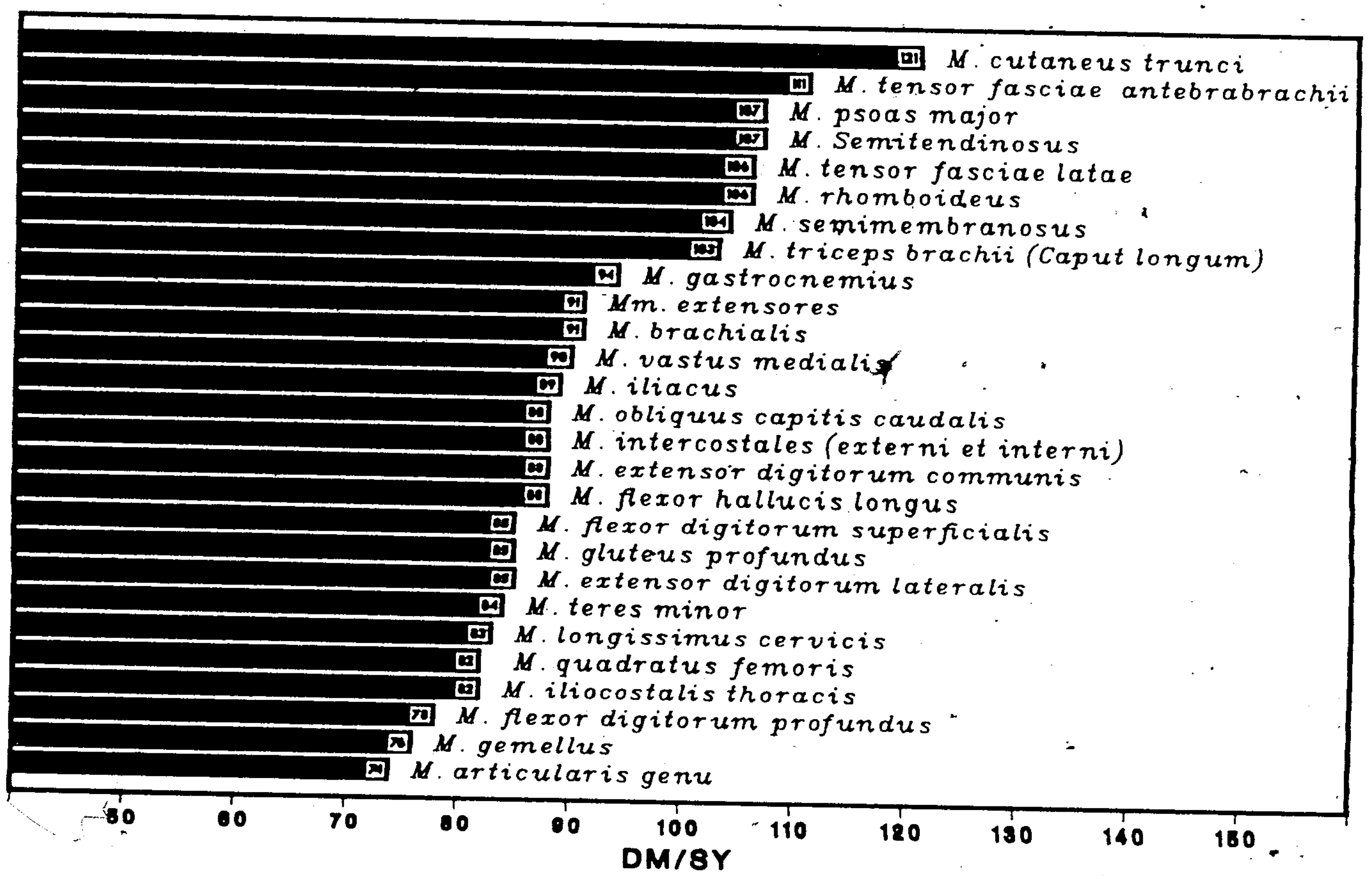


Figure III.1. Relative development of muscles in Double Muscled (DM) compared with Beef Synthetic (SY) at the total muscle weight. (Muscles with ratios

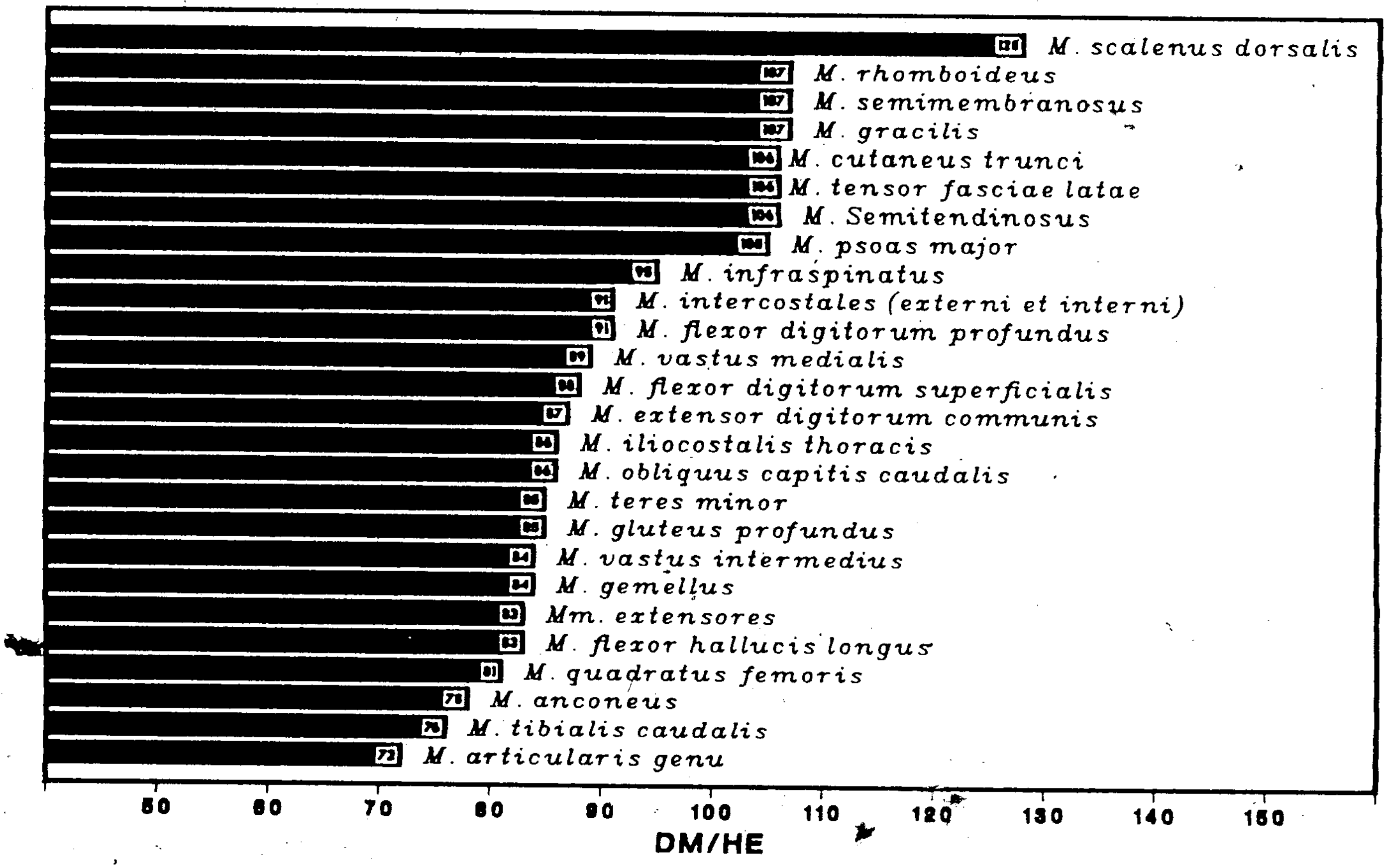


Figure III.2. Relative development of muscles in Double Muscled (DM) compared with Hereford (HE) at the same total muscle weight (- Muscles with ratios significantly different from 100 at $P < 0.05$).

early maturing pennate muscles, fibrous, non-fleshy muscles or those closely attached to the bones, deep muscles of the thicker parts of the carcass, rotators of the hip, and muscles of the ribs were most hypotrophied, while the relatively late maturing or large, heavy multisided muscles or those which had large contour areas were most hypertrophied. Somewhat similar findings have been reported by Vissac (1968), Lohman *et al.* (1971), Johnson (1981) and Dumont *et al.* (1982). Boccard and Dumont (1974) proposed that the hypertrophy of the peripheral muscles is considered to be a sequence of the general collagen deficit which allows certain muscles to expand. Berg and Butterfield (1976) suggested that the differential hypertrophy was due to variation in muscle fibers:connective tissue ratio in muscles.

From these observation, it should be restress that there was localized, differential and peripheral hypertrophy which tended to increase from inner to outer muscle layers which is illustrated in Figures III.3 and III.4. Similar findings have been reported by Pomeroy and Williams (1962) and Dumont *et al.* (1982).

In the present study, in the proximal hindlimb, the lateral and medial thigh muscles were better developed in DM, while the cranial thigh muscles were poorly developed in DM as compared with the more normal breed types (Figures 1 and 2). The relatively lesser development of the cranial thigh muscles could be related to a smaller femur in DM. It

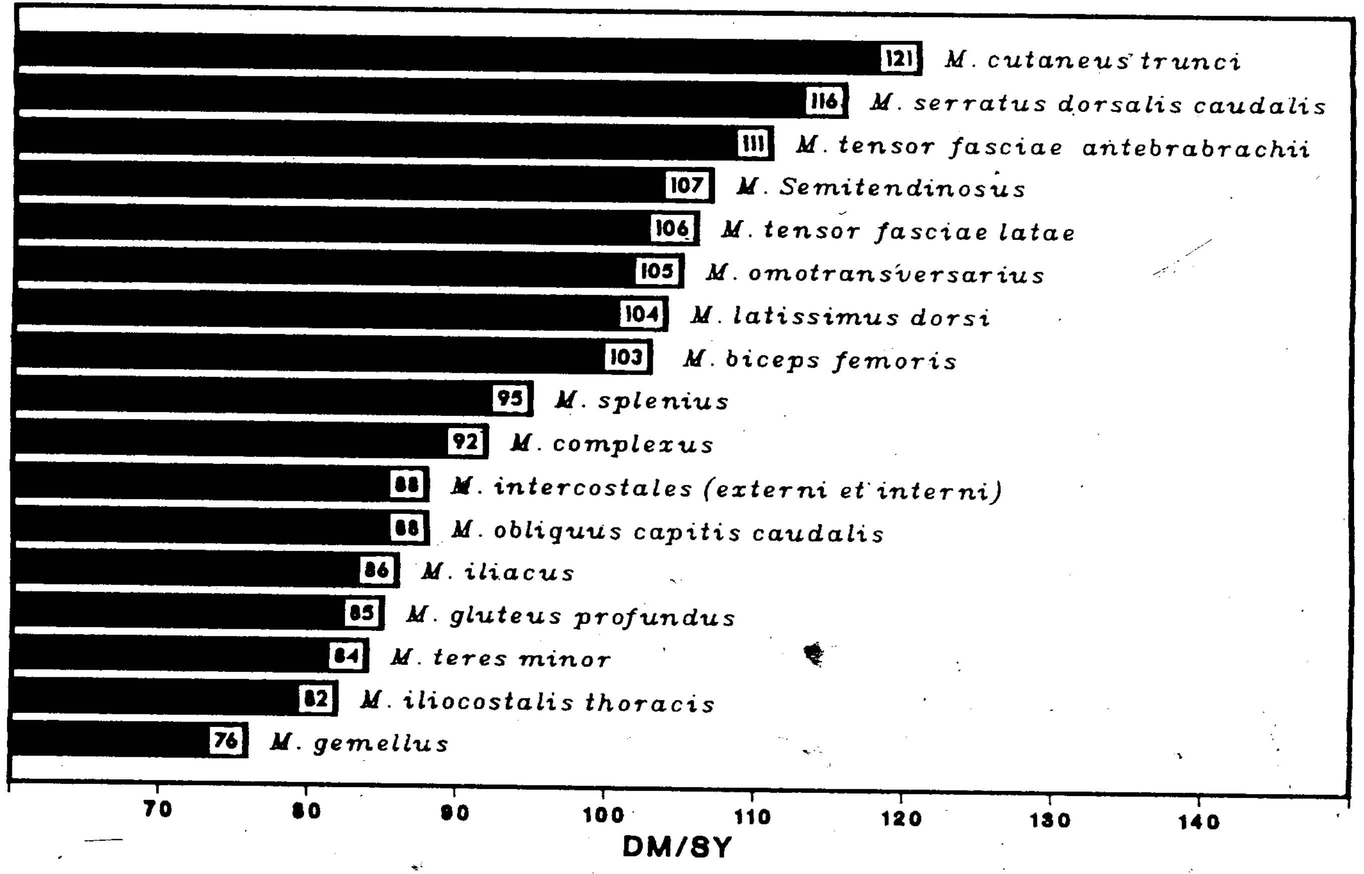


Figure III. 3. Inner–outer gradient of muscles in Double Muscled (DM) vs Beef Synthetic (SY) adjusted to same total muscle weight.

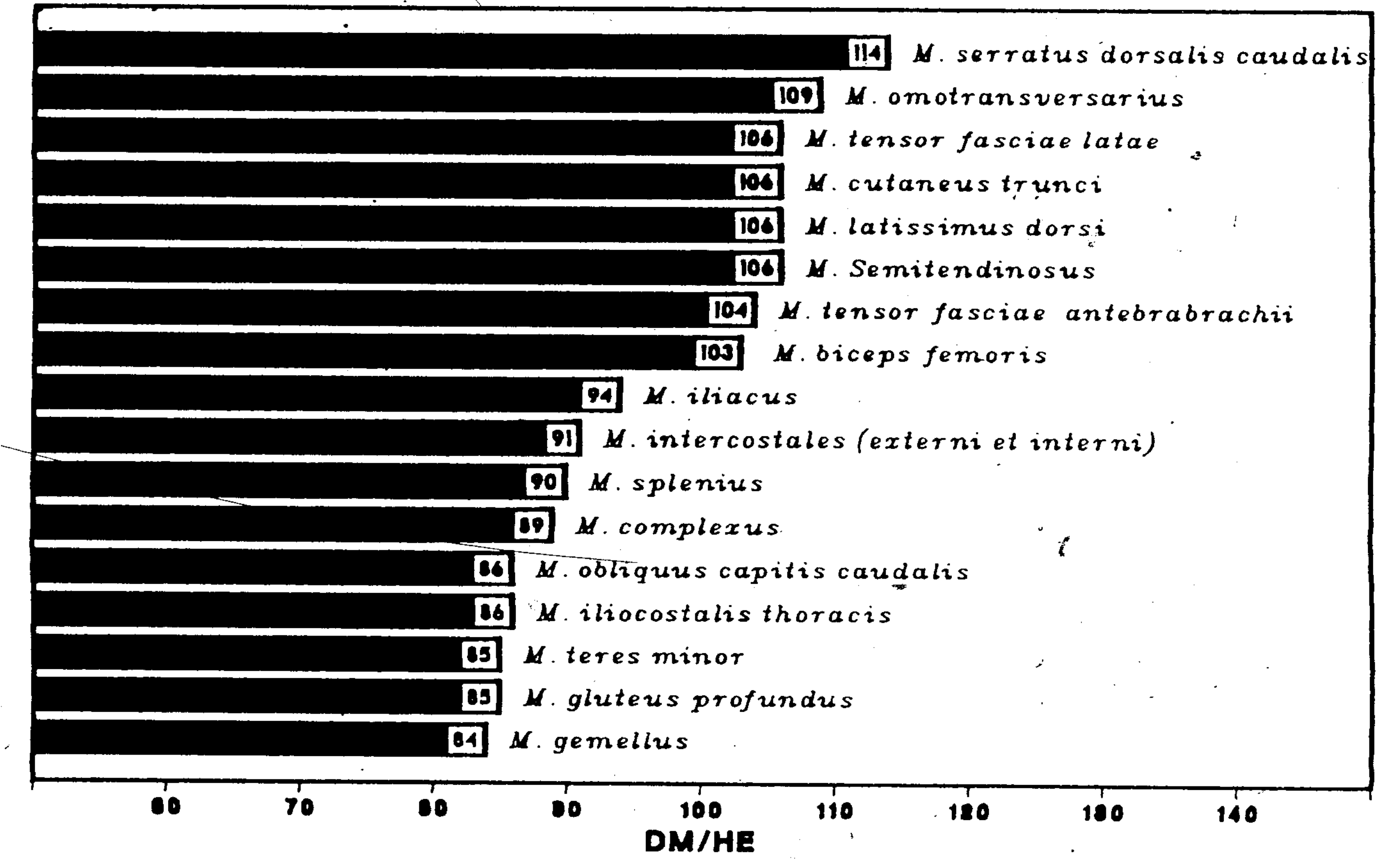


Figure III. 4. Inner-outer gradient of muscles in Double Muscled (DM) vs Hereford (HE) adjusted to same total muscle weight.

should be mentioned that of the cranial thigh muscles *m. quadriceps femoris* is the most powerful extensor of the stifle joint; if this muscle is non-functional the limb collapses. However, the interdependence of the serial development of muscles and bones will be dealt with in a subsequent chapter. Holmes *et al.* (1972) reported that one DM heifer collapsed after covering two miles, her *m. quadriceps femoris* felt very hard, and she become moribund and was destroyed nine hours later.

As was mentioned earlier *m. tensor fasciae latae* and *m. tensor fasciae antebrachii* in DM were proportionately heavier than in normal cattle. The main function of the former is to tense the fasciae lata, and to extend the stifle joint, similarly the main function of the latter is to extend the elbow joint, thus, the higher proportions of these muscles in DM could be related to specific functions.

Also compared with the more normal genotypes, DM had a higher proportion of *m. psoas major*. The chief function of this muscle is to flex the hip joint, rotate the thigh and to flex and stabilise the curvature of the bow (vertebral column and the spinal muscles) thus, the higher weight distribution for this muscle in DM could be related to construction of the body axis (Badoux, 1975). Boçcard and Dumont (1974) reported that DM had a higher proportion of *m. psoas major* than normal, but Johnson (1981) reported no significant differences between DM and normal animals.

Swiezynski *et al.* (1981) found the angle of the humeral joint in males in muscular hypertrophied animals were greater than in normal cattle. In the present study compared with SY, DM had proportionately higher *m. triceps brachii (Caput longum)*. The relatively higher proportion of this muscle in DM could be related to a greater angle of the scapulo-humeral joint, since it occupies the angle formed by the scapula and humerus.

Compared with the more normal breed types, DM had proportionately less weight in the muscles associated with respiration (i.e. *m. intercostales interni* and *m. intercostales externi*) (Figures 1 and 2), but at the same time, they had proportionately more bone weight in the ribs (chapter V). Dumont (1982) suggested that DM animals do not have the same potential to breathe as do normal (i.e. they breathe less) because they have less muscle equipment to do so.

In the present study compared with HE and SY, DM had proportionately less weight for *m. flexor digitorum superficialis*. Lawrie *et al.* (1964) found this muscle in DM had a lower potassium/sodium ratio as compared with normal.

The hypertrophy in DM of *m. rhomboideus* agrees with Johnson (1981) and Dumont *et al.* (1982) but Boccard and Dumont (1974) reported it among those which showed hypotrophy. It is a late developing muscle and comparisons could be influenced by relative maturity.

In the present study DM had nonsignificantly lower proportion of *m. splenius* than normal cattle which agrees with Boccard and Dumont (1974) who reported this muscle among the most hypotrophied, but Johnson (1981) reported it among those which showed hypertrophy. The differences between reports could be related to differences in the gender (bulls and steers) or differences in maturity.

The results of the present study and an earlier study of carcass composition (Chapter I) indicated that compared with more normal breed types, DM had quite different carcass composition and muscle weight distribution. In DM carcasses there were shifts in muscle weight distribution towards the more fleshy, luxury, multidimensional thick muscles. DM had proportionately less muscle weight in the distal muscles of both limbs, deep muscles, and neck muscles.

GENERAL CONSIDERATIONS

Many hypotheses have been proposed by different workers concerning the origin of muscular hypertrophy. Dumont and Schmitt (1973) showed that the perimysium was less abundant in the hypertrophied animal. Boccard and Dumont (1974) proposed that hypertrophy of the peripheral muscles is considered to be a consequence of the general collagen deficit which allows certain muscles to expand. Pomeroy and Williams (1962) suggested that an endocrine-enzyme imbalance, ultimately under genetic control, may have resulted in specific acceleration of muscle growth. Other workers reported that the enlargement of muscles was due to a relative increase in production of anabolic hormones (i.e GH) and a relative reduction in catabolic hormones such as adrenocorticotrophic hormone (ACTH). Strath *et al.* (1982) concluded that the Double Muscled animal is characterized by hyperthyroidism. Lawrie *et al.* (1964) reported that compared to normal, Double Muscled animals had higher nitrogen content, a higher potassium:sodium ratio (K/Na) but a lower hydroxyproline per cent. The size of any given muscle is a function of its cell size and number, the enlargement of some muscles in the muscular hypertrophied animals was due to more muscle fibers. Ouhayoun and Beaumont (1968) showed that the muscular hypertrophy was due to cell hyperplasia. Holmes and Ashmore (1972) reported that gross muscular hypertrophy was due to hyperplasia and hypertrophy of muscle fibers. Also, Swatland and Kieffer (1974) working on Double Muscled fetuses concluded that 'Double Muscling' was due to real myofiber hyperplasia during the early development of muscles. King *et al.* (1976) and King and Basrur (1979) proposed the hypothesis of defective cell membranes and Basarab *et al.* (1980) showed that the extreme Double Muscled cattle had an increased erythrocyte osmotic fragility as compared to carriers and normal cattle.

IV. FAT GROWTH AND PARTITIONING AMONG THE DEPOTS IN DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen Double Muscled (DM), 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls were serially slaughtered from approximately 250 to 800 kg live weight to determine the influence of maturity type and 'Double Muscling' on fat growth, partitioning and distribution. The fatty tissue was dissected into subcutaneous fat (SCF), intermuscular fat (IMF) and carcass cavity fat (CCF), the sum of these depots was used as total side fat (TSF).

Relative to TSF, DM did not differ significantly from the other maturity types in growth rates of SCF, IMF and CCF, but relative to fat percent in the side DM tended to have much lower growth rates for SCF and CCF. The common growth coefficients indicated that as TSF increased the proportion of SCF increased ($b > 1$; $P < 0.05$), the proportion of IMF decreased ($b < 1$; $P < 0.05$), and the proportion of CCF remained relatively constant ($b = 1$; $P > 0.05$). At equal TSF, as expected, HE tended to partition more of their fat to the subcutaneous depot, whereas DM and SY tended to partition more of their fat to the intermuscular and carcass cavity fat depots. Relative to HE, DM followed late developing fat partitioning patterns.

The hypodevelopment of fat depots in the carcasses of the muscular hypertrophied animals followed an inner-outer

gradient which was most pronounced in the subcutaneous fat depot.

INTRODUCTION

The fattening patterns of the American, British and European beef and dairy breeds and the manner in which fat is partitioned among the various depots and distributed throughout the carcass is well documented. The ideal carcass should contain a maximum amount of muscle, a minimum amount of bone to give its form and an optimum amount of fat (Berg and Butterfield, 1976). In North America, consumers no longer want excessive amounts of fat. The total amount of fat, partitioning among the major depots and distribution within each depot also influence carcass value.

The 'Double Muscling' condition in cattle is characterized by hyperdevelopment of muscle and hypodevelopment of fat. The hypodevelopment of fatty tissues especially subcutaneous fat are diagnostic discriminators of the 'Double Muscling' condition (Dumont, 1982 and the present study).

There are many factors which might influence fat growth, partitioning and distribution. These include species, breed, domestication, sex, endocrine system, activity, rate of growth, plane of nutrition, metabolic status, environment, slaughter weight, mature size, chronological and physiological age and 'Double Muscling'. Some of these factors are well known, whereas others need more investigation to clarify their influences.

Although considerable research has been done on carcass composition of Double Muscled cattle, there has been no research reported on growth and development of this type of cattle. This study was undertaken to determine the influence of maturity type and 'Double Muscling' in cattle, on the fattening patterns, fat partitioning among the depots and distribution of fat throughout the carcass as growth and development proceeds.

MATERIALS AND METHODS

The study was designed to permit comparison among early (HE), intermediate (SY) and late (DM) maturing breed types. Details of the experiment and description of the animals were given in Chapter I. The fatty tisssues in forequarter and hindquarter were dissected into subcutaneous fat, intermuscular fat and carcass cavity fat.

The following abbreviations and definition of terms were used to designate each of the fat depots.

Subcutaneous fat (SCF): Fat on the surface of the superficial muscles and and also included fat under the *cutaneus muscle* (*m. cutaneus et omobrachii*).

Intermuscular fat (IMF): Fat between the muscles and in the indentations of the origin and insertion of the muscles.

Carcass cavity fat (CCF): Fat lying directly below the endothoracic and transverse fascia of the thoracic, abdominal and pelvic cavity but excluding kidney knob and channel fat which were removed during slaughter.

Total side fat (TSF): The summation of SCF, IMF and CCF in the side.

The weights of forequarter subcutaneous fat, forequarter intermuscular fat, forequarter carcass cavity fat were recorded and the sum of these three depots was used as forequarter total fat. In a similar manner, the weights of hindquarter subcutaneous fat, hindquarter intermuscular fat, hindquarter carcass cavity fat were recorded and the sum of these three depots was used as hindquarter total fat. The weights of the three fat depots ranged from 1.82-47.29 kg for SCF, 4.51-83.05 kg for IMF and 1.37-17.17 kg for CCF. Figures IV.1 and IV.2 show the range of total side fat and the ranges of fat depots for each breed type.

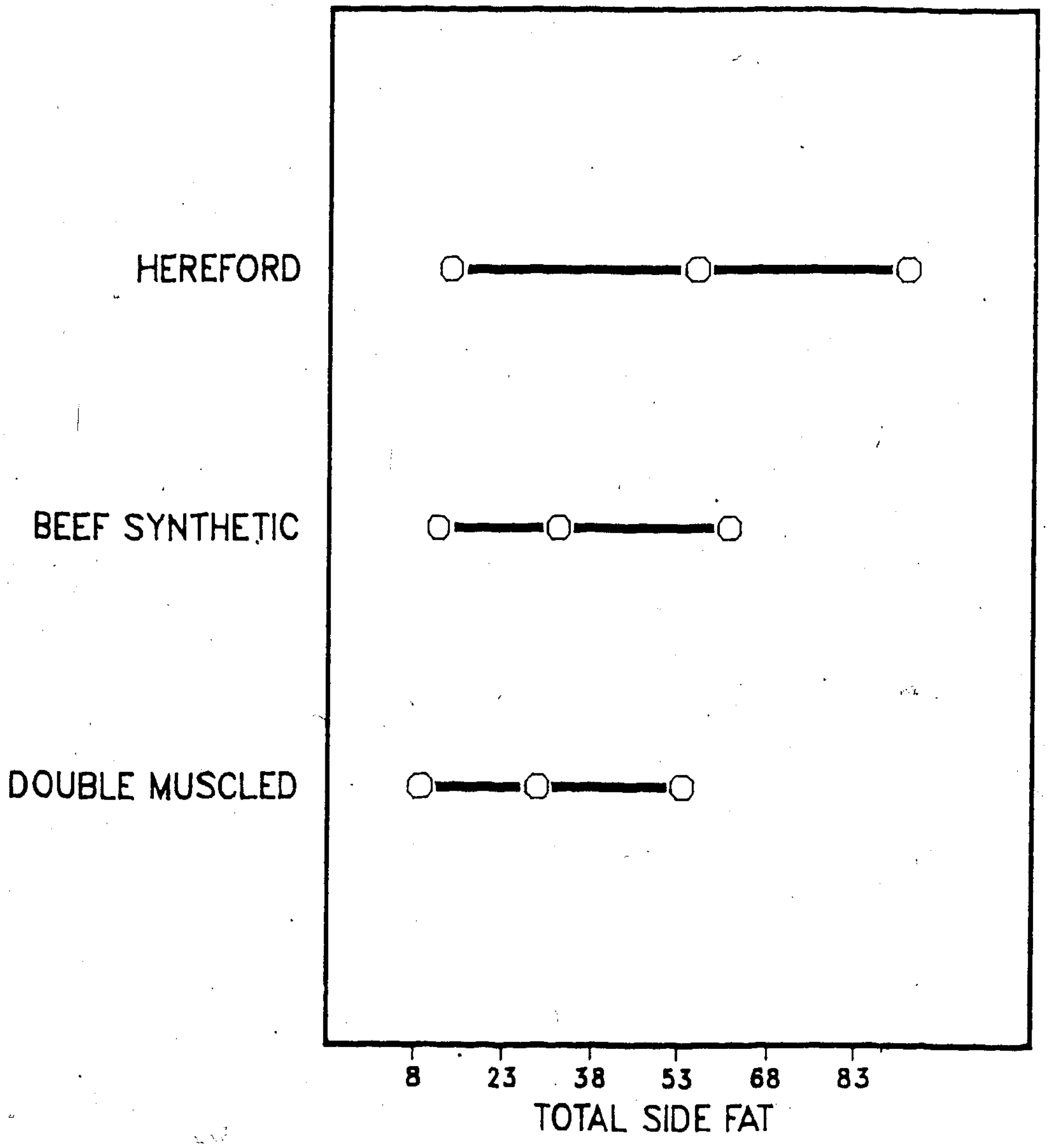


Figure IV.1. Range and mean of weight of total fat for each breed type.

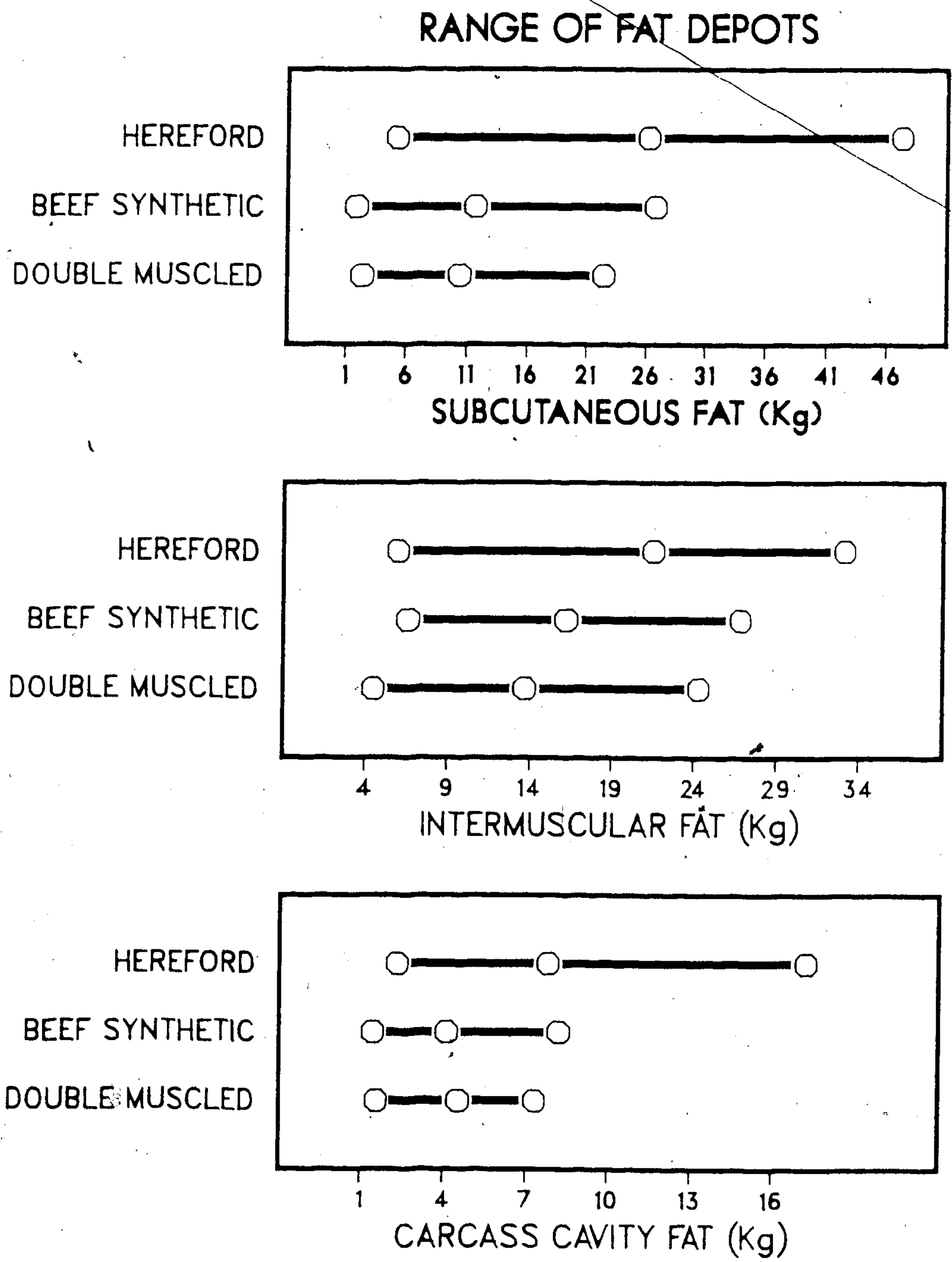


Figure IV.2. Ranges and means of fat depots for each breed type.

STATISTICAL ANALYSIS

The data were analyzed by one way analysis of covariance (Snedecor and Cochran, 1967). The statistical model was as follows:

$$\log Y_{ij} = A_0 + G_i + b \log X_{ij} + (Gb)_i \log X_{ij} + e_{ij},$$

where:

Y_{ij} = weight (kg) of a fat depot of the $_{ij}th$ animal;
A_0 = the intercept;
G_i = fixed effect of the $_{i}th$ breed group;
X_{ij} = total weight (kg) of the total side fat or fat percent in the side of the $_{ij}th$ animal;
b = regression coefficient of Y on X;
$(Gb)_i$ = interaction effect (breed x regression coefficient)
e_{ij} = error, assumed to be $NID\ (0, \sigma^2 e)$.

Individual breed group regression coefficients were computed and compared and in cases where the regressions were homogeneous ($P > 0.05$) the common regression coefficient was used for adjustment. However if between slopes were significant, adjusted means were computed using the appropriate breed group regression but not statistically tested for significance. Duncan's multiple range test (Steel and Torrie, 1980) was used to test the significant differences among adjusted means.

RESULTS

Unadjusted means and standard deviations for DSW, weights and percentages of TSF, SCF, IMF and CCF are presented in Table IV.1. Means of the major depots are presented graphically in Figure IV.3 for each breed type.

There were no significant differences among breed types in the slopes (rate of fat deposition) of each fat depot when regressed on TSF (Table IV.2). From the common allometric coefficients we see that as TSF increased the proportion of SCF increased ($b > 1$; $P < 0.05$), the proportion of IMF decreased ($b < 1$; $P < 0.05$) and the proportion of CCF remained relatively constant ($b = 1$; $P > 0.05$). Fattening patterns of the three breed types are illustrated in Figure IV.4.

Among the major fat depots, CCF was the most variable depot (CV = 20.1%) followed by SCF (CV = 13.4%) and then IMF (CV = 9.0%) (Table IV.2).

At the same TSF, the rate of forequarter total fat and forequarter SCF deposition were similar to those of hindquarter, but the rate of forequarter IMF deposition was somewhat higher than that of hindquarter IMF, whereas the hindquarter CCF deposition was somewhat higher than that of forequarter CCF (Table IV.2).

Among the forequarter and hindquarter depots, only for hindquarter SCF did breed type have an influence on relative growth (Table 2). As TSF increased the proportion of SCF in forequarter and hindquarter increased ($b > 1$; $P < 0.05$),

Table IV.1. Unadjusted means (kg) and standard deviations (S.D.) for live weight, carcass weight, dissected side, total fat and fat depots in the side

	Hereford		Beef Synthetic		Double Muscled		Overall	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Age	569.5	116.1	497.2	117.9	530.6	206.5	532.4	152.8
Live weight	612.5	119.9	544.3	128.0	523.2	137.7	556.0	132.0
HCW+	364.8	72.0	332.1	84.8	324.1	101.6	340.3	87.0
DSW	176.4	34.9	158.6	41.6	154.2	49.8	163.1	42.8
TSF	55.5	16.5	32.0	14.4	28.6	12.5	38.7	18.7
SCF	26.2	9.2	11.7	7.0	10.4	5.7	16.1	7.4
IMF	21.5	5.5	16.2	5.8	13.7	5.5	17.1	6.4
CCF	7.8	3.2	4.1	2.1	4.5	1.8	5.5	2.9
Percentages								
TSF %	30.9	5.1	19.5	4.8	18.8	6.2	23.1	4.2
SCF %	14.4	3.4	7.0	2.7	6.8	3.0	9.4	4.7
IMF %	12.1	1.8	10.1	2.0	9.1	2.7	10.4	2.5
Ratios								
SCF:IMF	1.20	0.25	0.68	0.23	0.72	0.19	0.87	0.32
SCF:(IMF+CCF)	0.88	0.17	0.54	0.17	0.55	0.15	0.65	0.22

+ The symbols are defined in the text.

Table IV.2. Growth Coefficients *(b)* and Adjusted Means for Weights of Fat Depots Relative to Total Side Fat (X)

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means** antilog (kg)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Half carcass														
Subcutaneous fat	**1.163**	0.05	**1.393**	0.08	**1.239**	0.06	**1.274**	0.04	13.37	13.81a	11.78b	12.49b	2.87	4.96*
Intermuscular fat	0.839	0.06	**0.788**	0.05	**0.883**	0.03	**0.839**	0.03	9.04	14.22a	17.26b	15.77c	1.20	16.56**
Carcass cavity fat	0.926	0.13	0.959	0.12	0.869	0.07	0.914	0.06	20.06	4.87a	4.19b	5.28a	0.22	6.22**
Subcutaneous fat														
Forequarter SCF	1.153	0.11	**1.409**	0.14	**1.275**	0.11	**1.293**	0.07	26.24	5.164	4.298	4.818	0.99	2.43
Hindquarter SCF	**1.165**	0.04	**1.375**	0.07	**1.214**	0.05	**1.258**	0.03	12.48	8.604	7.400	7.596	3.43*	—
Intermuscular fat														
Forequarter IMF	0.927	0.08	**0.854**	0.05	0.926	0.04	**0.901**	0.03	11.57	9.537a	10.998b	10.694b	0.54	6.14**
Hindquarter IMF	**0.593**	0.17	**0.670**	0.17	**0.791**	0.04	**0.702**	0.06	21.77	4.535a	6.148b	5.025a	0.94	9.65**
Carcass cavity fat														
Forequarter CCF	**0.737**	0.10	0.903	0.18	0.828	0.10	**0.833**	0.07	28.77	1.937a	1.396b	2.159a	0.34	14.46**
Hindquarter CCF	0.835	0.16	0.988	0.17	0.910	0.10	0.919	0.08	31.70	2.728	2.676	3.027	0.25	0.96
Totals														
Forequarter TF	0.983	0.02	0.986	0.02	0.999	0.01	0.990	0.01	3.55	17.066a	17.035a	17.899b	0.20	10.29**
Hindquarter TF	1.018	0.02	1.016	0.02	1.003	0.02	1.011	0.01	3.71	16.697a	16.717a	15.866b	0.19	10.35**

* Growth coefficients in bold type are significantly different from 1 at $P < 0.05$.
** Adjusted to geometric mean of total side fat = 33.8 kg along the slope of common regression line.
Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.
— Missing values mean covariance analysis was not legitimate.
• $P < 0.05$; •• $P < 0.01$.

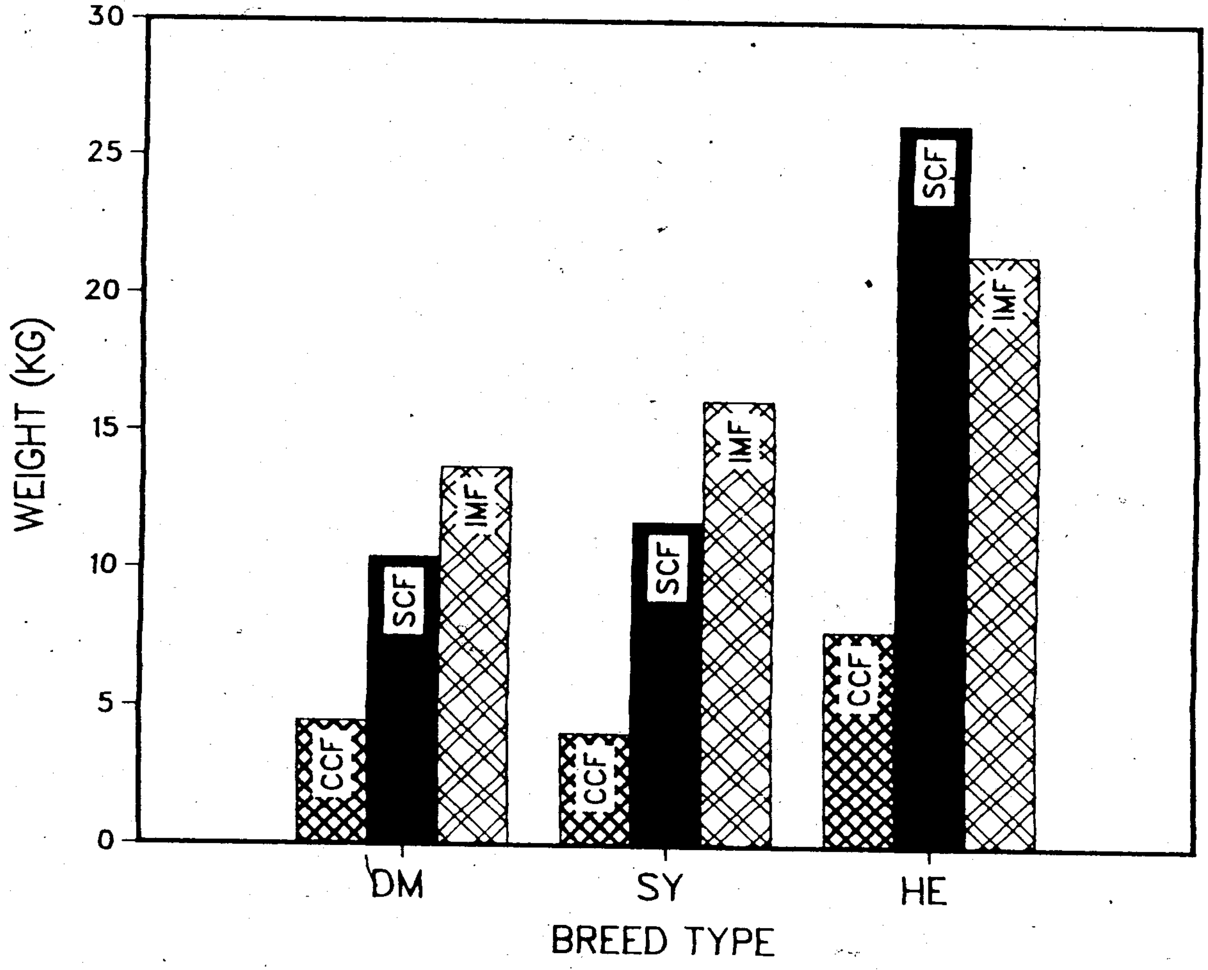


Figure IV.3. Mean fat weight by depot and breed type. CCF, carcass cavity fat; SCF, subcutaneous fat and IMF, intermuscular fat.

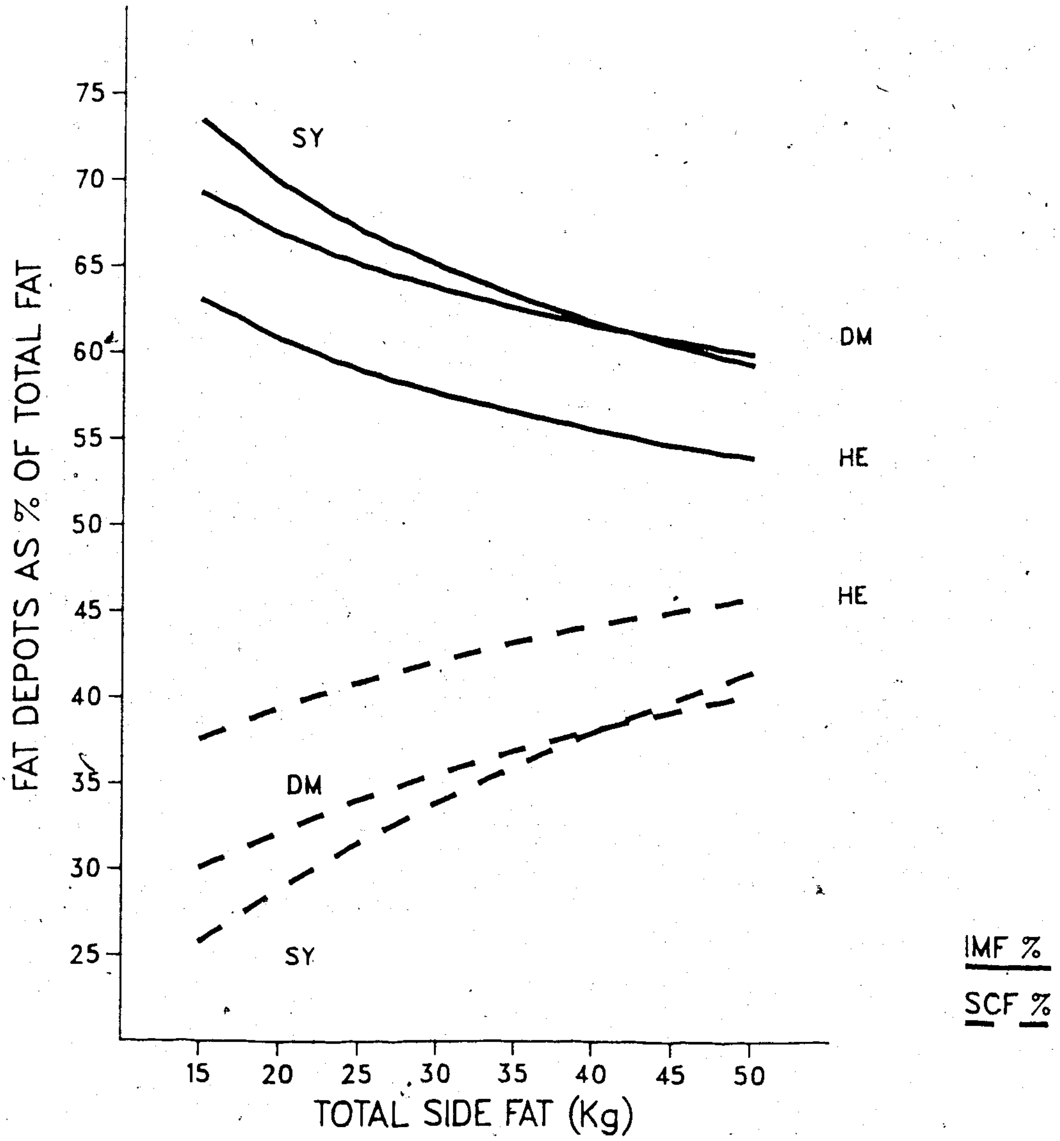


Figure IV. 4. Fattening patterns of Hereford (HE), Beef Synthetic (SY) and Double Muscled (DM) bulls.

the proportion of forequarter IMF, forequarter CCF and hindquarter IMF decreased ($b < 1$; $P < 0.05$) and the proportion of hindquarter CCF remained relatively constant ($b = 1$; $P > 0.05$).

There were differences ($P < 0.05$ and $P < 0.01$) among breed types in the adjusted means of SCF, IMF and CCF at equal TSF (Table IV.2). HE had more SCF than SY and DM, which did not differ from each other ($P > 0.05$). All breed groups differed in their adjusted weights of IMF; SY had more IMF than either DM or HE and DM had more IMF than HE. For adjusted CCF, SY had less than either HE or DM, which did not differ from each other. At the same TSF, DM had approximately 10% less SCF and 10% more IMF and CCF than HE. Compared to SY, DM had 6% more SCF, 26% more CCF and 9% less IMF. Since breed types had common slopes for fat deposition in each depot these percentage differences would be consistent over the range of weights studied.

In Table IV.2 are presented mean weights of SCF, IMF, CCF and total fat in the forequarter and hindquarter adjusted to the geometric mean of TSF. DM had more forequarter total fat but less hindquarter total fat than either HE or SY, which did not differ from each other. They had more forequarter IMF than HE, but did not differ from SY in this respect. SY had significantly more hindquarter IMF, but less forequarter CCF than both HE and DM, which did not differ from each other for these fat depots. Breed types did not differ in the weights of forequarter SCF and hindquarter

CCF.

The breed type differences in growth coefficients for hindquarter SCF on TSF did not permit the comparison of their means. Estimates of weights of hindquarter SCF at 15 and 50 kg of TSF, were calculated using individual breed regressions. At 15 kg TSF, DM had 19.5% less hindquarter SCF and at 50 kg TSF, DM had 14.5% less hindquarter SCF than HE. Irrespective of breed the proportion of IMF found in the forequarter was greater than that in the hindquarter, while the reverse was true for SCF (Figures IV.5 and IV.6).

As was found for the total carcass, within the forequarter and hindquarter, HE tended to partition more of their fat subcutaneously, while DM and SY tended to partition more of their fat intermuscularly.

Growth patterns and adjusted means of SCF, IMF and CCF relative to fat percent in the side are presented in Table IV.3. For IMF the DM bulls had a non significantly lower growth coefficient than the SY and HE bulls. Breed types differed in growth rate of SCF, CCF, forequarter total fat, hindquarter total fat, forequarter SCF and hindquarter SCF. The relatively low growth coefficients for these depots in DM bulls indicated a tendency to lay down SCF and CCF at a relatively slower rate than normal bulls. DM had the same forequarter IMF as HE and SY, and they had less hindquarter IMF and more forequarter CCF than SY, but did not differ from HE in this respect.

Table IV.3. Growth Coefficients *(b)* and Adjusted Means for Weights of Fat Depots Relative to Fat% in the Side (X)

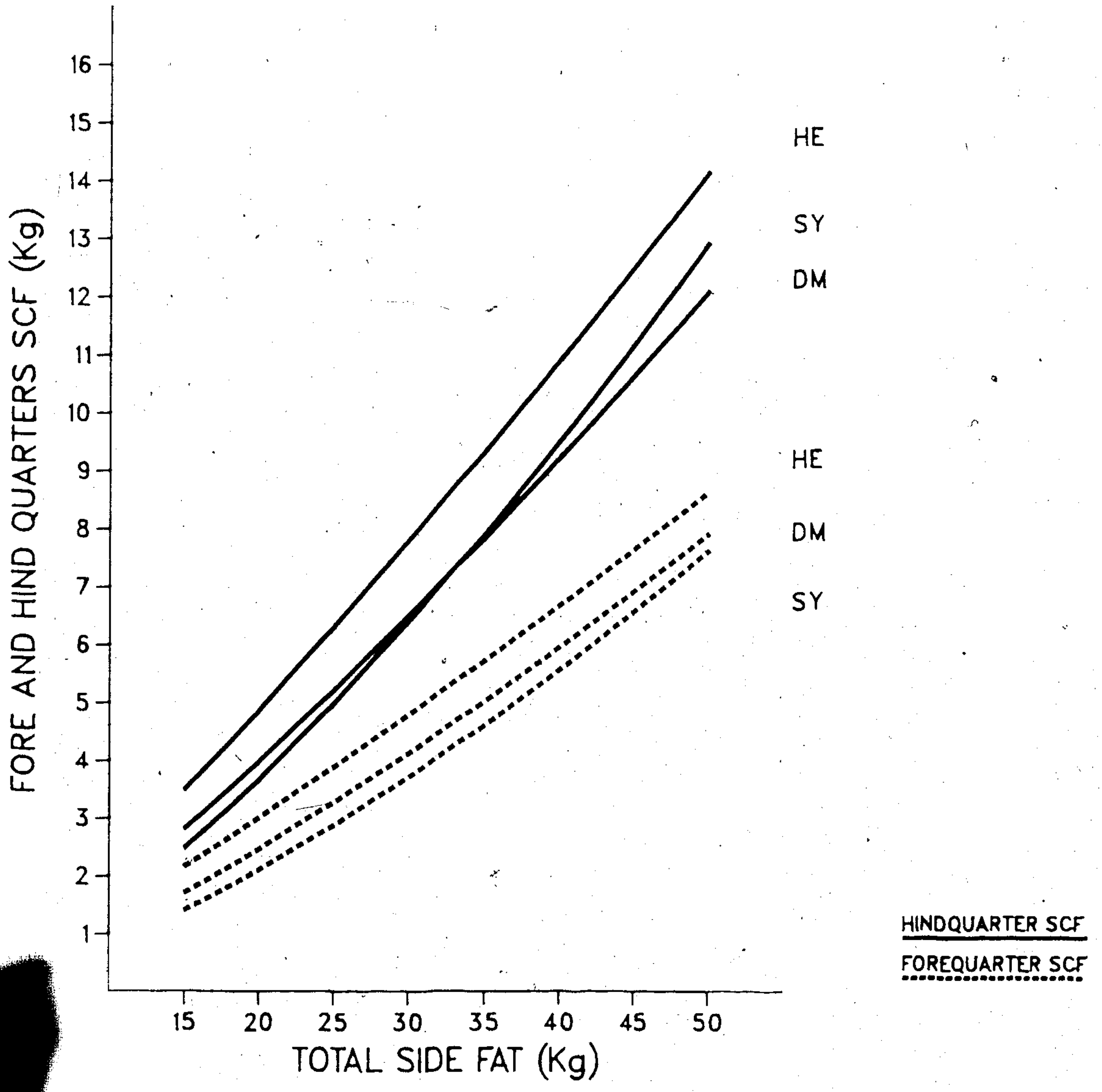
Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means'' antilog (kg)			F-Values	
	b'	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Half carcass														
Subcutaneous fat	**2.331**	0.31	**2.105**	0.23	1.277	0.26	**1.654**	0.16	38.8	13.670	12.093	12.287	4.42*	—
Intermuscular fat	**1.646**	0.26	1.038	0.20	0.793	0.21	0.965	0.13	31.4	14.750	17.260	15.208	2.29	1.40
Carcass cavity fat	1.807	0.38	1.304	0.28	0.610	0.26	0.962	0.17	42.9	5.226	4.138	4.988	3.55*	—
Subcutaneous fat														
Forequarter SCF	**2.325**	0.37	**2.218**	0.25	1.384	0.27	**1.751**	0.17	42.4	4.985	4.457	4.813	3.54*	—
Hindquarter SCF	**2.336**	0.31	**2.024**	0.25	1.213	0.26	**1.593**	0.16	40.0	8.639	7.549	7.415	4.34*	—
Intermuscular fat														
Forequarter IMF	**1.808**	0.31	1.086	0.23	0.840	0.22	1.025	0.35	35.1	9.952	10.981	10.263	2.40	0.40
Hindquarter IMF	1.174	0.41	0.938	0.19	0.694	0.20	0.824	0.13	34.0	4.646a	6.162b	4.893a	0.77	4.21*
Carcass cavity fat														
Forequarter CCF	1.431	0.30	1.144	0.37	0.548	0.27	0.834	0.18	47.1	2.095a	1.372b	2.031a	1.90	5.95**
Hindquarter CCF	1.580	0.44	1.379	0.34	0.661	0.28	0.989	0.19	50.2	2.905	2.651	2.869	2.17	0.23
Totals														
Forequarter TF	**1.947**	0.26	1.338	0.22	0.925	0.23	1.169	0.14	33.8	17.624	17.106	17.260	3.18*	—
Hindquarter TF	**2.031**	0.26	**1.438**	0.19	0.915	0.23	1.203	0.14	33.4	17.195	16.807	15.320	4.11*	—

' Growth coefficients in bold type are significantly different from 1 at $P < 0.05$.

'' Adjusted to geometric mean fat% in the side = 21.6 % along the slope of common regression line.
Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.

— Missing values mean covariance analysis was not legitimate.

* $P < 0.05$; ** $P < 0.01$.



[illegible]re IV. 5. *Subcutaneous fat distribution in Hereford (HE), Beef Synthetic (SY) and Double Muscled (DM) bulls.*

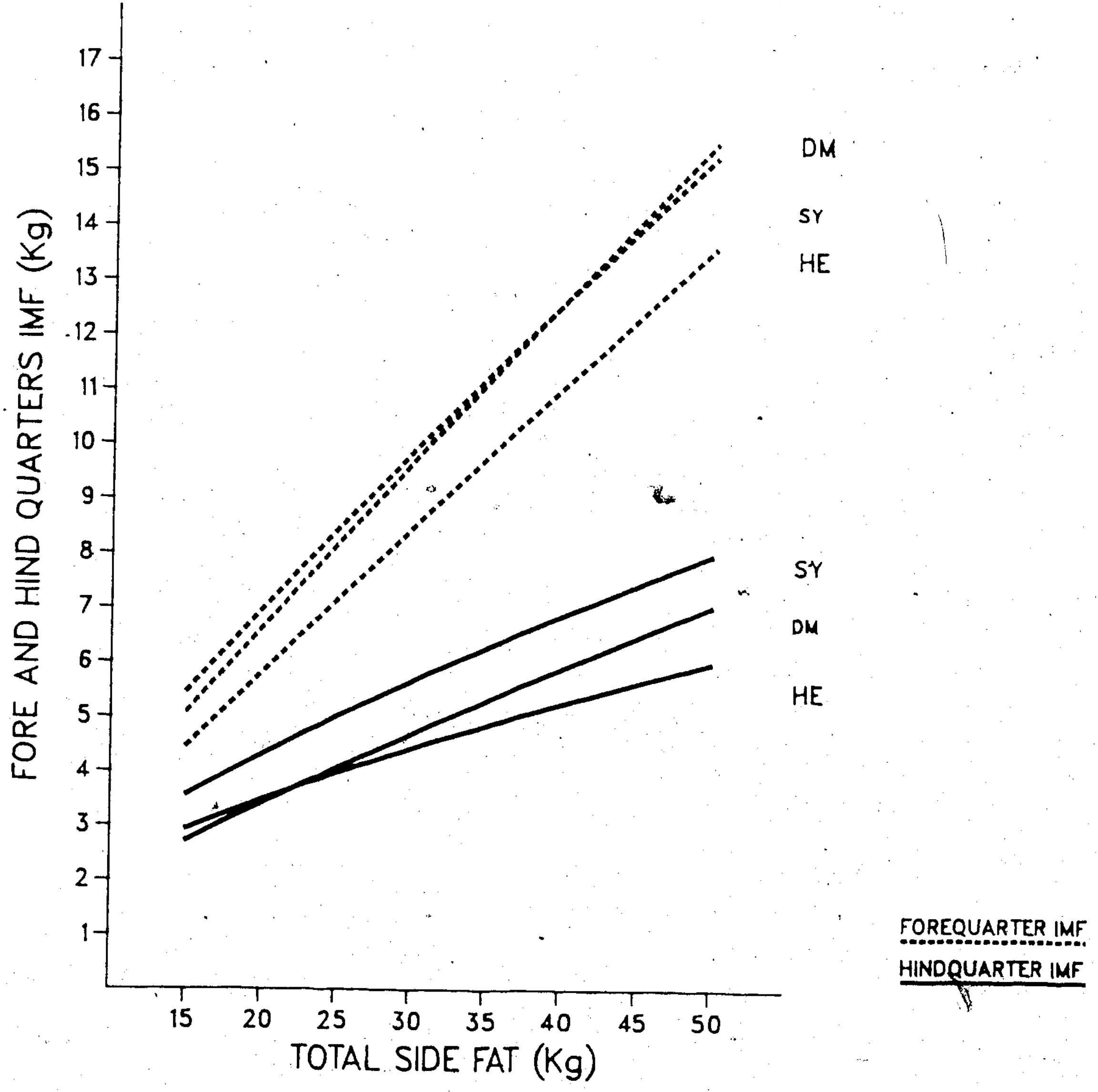


Figure IV. 6. Intermuscular fat distribution in Hereford (HE), Beef Synthetic and Double Muscled (DM) bulls.

Table IV.4 gives the ratios of fat depot weights in the side, forequarter and hindquarter of DM to normal (HE and SY) derived from means adjusted to same DSW, total side muscle (TSM) or TSF. Compared to HE all fat depots in DM showed hypotrophy when comparison was made at the same DSW or TSM, whereas when comparison was made at the same TSF, some fat depots showed hypertrophy, others showed hypotrophy. At the same DSW, the DM had 60% as much total fat as the HE, approximately 70% as much IMF and CCF but only 46% as much SCF. Compared to SY at the same DSW, DM had only slightly less total fat (94%), nearly the same SCF (98%), somewhat less IMF (87%) and higher proportion of CCF (120%). Comparisons at the same TSM reduced the DM fat ratios when compared to HE but were similar to those at standard DSW for DM/SY ratios.

Correlation coefficients among the major fat depots, were calculated within each genotype as well as for overall ignoring genotype (Table IV.5). The lower off-diagonal elements were computed from fat depots as a percentage of TSF, while the upper off-diagonal elements were computed from weight of the major fat depots. Irrespective of breed SCF% was positively correlated with TSF and negatively correlated with IMF%, CCF% and (IMF+CCF)%. IMF% and (IMF+CCF)% were negatively correlated with TSF. Within the DM group, IMF% and CCF% were positively correlated whereas in normal (HE, SY) cattle they were negatively correlated.

Table IV.4. Ratios of Fat Weights from DM *vs* HE or SY Based on Means Adjusted to the Same DSW, TSM and TSF

	Ratios at Same DSW⁺		Ratios at Same TSM⁺⁺		Ratios at Same TSF	
	DM/HE	DM/SY	DM/HE	DM/SY	DM/HE	DM/SY
Totals						
SCF	0.456	0.976	0.335	0.936	0.904	1.060
IMF	0.722	0.871	0.598	0.846	1.109	0.914
CCF	0.690	1.202	0.552	1.163	1.084	1.260
TSF	0.596	0.943	0.479	0.911		
Subcutaneous Fat						
Forequarter SCF	0.461	1.027	0.362	0.986	0.933	1.121
Hindquarter SCF	0.453	0.948	0.351	0.910	0.883	1.026
Intermuscular Fat						
Forequarter IMF	0.709	0.924	0.577	0.895	1.121	0.972
Hindquarter IMF	0.772	0.784	0.661	0.766	1.108	0.817
Carcass Cavity Fat						
Forequarter CCF	0.744	1.485	0.602	1.440	1.115	1.547
Hindquarter CCF	0.702	1.078	0.563	1.043	1.110	1.131
Totals						
Forequarter TF	0.629	0.990	0.506	0.958	1.049	1.051
Hindquarter TF	0.563	0.894	0.452	0.864	0.950	0.949

⁺ DSW, dissected side weight.
⁺⁺ TSM, total side muscle.

Table IV.5. Phenotypic Correlation Matrix for Major Fat Depots[+]

	Breed group	SCF	IMF	CCF	IMF+CCF	TSF
	HE		0.843	0.678	0.866	0.971
	SY		0.915	0.879	0.933	0.982
	DM		0.899	0.834	0.894	0.966
SCF*	O		0.878	0.842	0.909	0.980
	HE	-0.777		0.603	0.946	0.921
	SY	-0.933		0.852	0.990	0.970
	DM	-0.929		0.930	0.996	0.979
IMF	O	-0.927		0.787	0.979	0.946
	HE	-0.375	-0.292		0.829	0.773
	SY	-0.116	-0.250		0.917	0.915
	DM	-0.795	0.514		0.960	0.929
CCF	O	-0.288	0.094		0.896	0.887
	HE	-1.000	0.777	0.375		0.960
	SY	-1.000	0.933	0.117		0.984
	DM	-1.000	0.929	0.795		0.979
IMF+CCF	O	-1.000	0.927	0.288		0.974
	HE	0.615	-0.615	-0.027	-0.615	
	SY	0.772	-0.736	-0.046	-0.772	
	DM	0.679	-0.693	-0.439	-0.679	
TSF	O	0.813	-0.779	-0.167	-0.813	

[+] Above diagonal based on weights, below diagonal based on percentages of TSF.

* The symbols are defined in the text.

DISCUSSION

Generally any tissue within the body attains its mature size by hyperplasia and hypertrophy. In prenatal phases of growth all tissues grow by increasing in number and size of cells whereas in postnatal phases of growth some tissues increase by hypertrophy, others by hyperplasia. As far as the fatty tissue is concerned, Enser and Wood (1978) showed that the growth of fat depots up to slaughter is accompanied by an increase in size and number of fat cells. As early as 1909 Waters suggested that fattening was due to both hyperplasia and hypertrophy of adipocytes.

The major fat depots (*i.e.* SCF, IMF, CCF) grow and develop at relatively different rates. The common growth coefficients for the major fat depots indicate that IMF and CCF increased in weight at a slower rate and SCF at a faster rate relative to TSF. These results are in general agreement with Kempster *et al.* (1976), Thompson and Barlow (1981*b*) and Abdallah *et al.* (1982) who reported that the contribution of subcutaneous fat to total fat increased while that of intermuscular fat decreased as fattening progressed. On the other hand, Cianzio *et al.* (1982) reported that intermuscular fat is not an early developing depot and its contribution to total fat does not decrease as fattening progresses.

Undoubtedly there are many significant differences among breeds in their capacities to synthesize and to store fat. Some breeds have the capacity to synthesize and store fat at lighter and younger ages (*i.e.* Hereford, Angus), whereas others have this capacity at heavier weight and older ages (*i.e.* Charolais). As far as DM is concerned, Novakofsk and Kauffman (1981) claimed that the DM cattle have the capacity to store fat, but that fattening is delayed because of later maturing characteristics. This was confirmed in Chapter I using the same animals.

In the present study using TSF as a covariate for evaluating fattening patterns no breed type differences were detected in growth patterns of fat depots. But, when fat percent in the side was used as a covariate breed types differed in the growth rate of SCF and CCF in the side with DM bulls showing the lowest rate, while HE had the highest with SY intermediate. Kempster (1981) recommended fat percent as a covariate for examining breed differences in fat partitioning, especially if the breeds differed greatly in maturity. This is because fat percent takes into account differences in maturity allowing comparison at somewhat similar maturity. The relatively low growth coefficients for SCF and CCF depots in the DM bulls indicated a tendency to lay down these depots at a relatively slower rate than normal bulls.

The total amount and partitioning of fat in the carcass may be manipulated by controlling caloric input during the finishing phase. Leat (1974) suggested that fat synthesis could be depressed at critical phases of development, partitioning dietary energy in favour of tissues other than fat. Johnson *et al.* (1969) suggested possibilities to suppress waste fat but allow intermuscular fat to be deposited by dietary regimes. The present study examined genetic influences in fat partitioning.

Breed differences in the partitioning of fat among depots have been observed. Late maturing cattle or those selected for muscling or for draft usage generally tended to have more of their fat in the intermuscular fat depot (Robelin *et al.*, 1977), those selected for dairy characteristics tended to have more of their fat in the intermuscular and kidney knob and channel fat (Butler-Hogg and Wood, 1982), while those selected for the blocky conformation and early maturity of traditional British breeds of cattle tended to have more fat in the subcutaneous depot (Charles and Johnson, 1976; Truscott *et al.*, 1983). In the present study HE tended to partition more of their fat to the SCF depot, whereas DM and SY tended to partition more of their fat to the IMF and CCF depots. If the ratio of SCF:IMF reflects intensity of selection for 'traditional beef characteristics' as Callow (1961) suggested or reflects intensity of selection against SCF as Kempster and Evans (1979) and Kempster (1981) suggested, then, we might say HE have been more intensely selected for 'traditional beef characteristics', while DM have been intensely selected for muscling. Breed differences in fat partitioning may have impact on saleable meat yield and may affect predictability of carcass composition.

Berg and Butterfield (1976) suggested that the muscles and body shape may have an influence on fat distribution by creating variable pressures with fat being deposited in the least resistant regions. The results of the present study provided additional confirmatory evidence to the Berg and Butterfield hypothesis. The tendency to accumulate fat differentially in forequarter and hindquarter could be related to changes in function with maturity of the animal (*i.e.* changes in muscle metabolism or metabolic status of the animal), or as total muscle increased, the proportion of muscle in the cranial end of the animal increased and since the natural location of IMF is between the muscles, the increasing muscle weights and dimensions in forequarter is accompanied by greater accumulation of IMF. Hammond (1932) pointed out fat is deposited in large quantity in those parts of the body which interfere least with the movements of the muscles.

The negative correlation between SCF% and IMF% suggest that selection against subcutaneous fat% (*i.e.* reduction of SCF) may result in a relative increase of fat deposition in intermuscular and carcass cavity fat depots. Cuthbertson and Kempster (1976) reported that kidney knob and channel fat and IMF were closely positively related. Olsen *et al.* (1976) found negative genetic correlation between fat thickness at 12 *th* rib (adjusted for skinning variation) and percentage of kidney fat in the carcass which supports a negative relationship between proportions of SCF and CCF.

The present study and that of chapter I showed that maturity types did not differ in the rate of fattening, but did differ in the onset of fattening. However, relative to TSF, all maturity types tended to have somewhat similar growth rates for fat depots, but tended to be quite different in fat partitioning. As one would expect, when comparisons were made at somewhat similar maturity i.e. at same fat percent in the side, maturity types differed in regressions coefficient of SCF and CCF, which indicated substantial genetic differences in the proportional increase in these depots relative to fat percent. The effect of 'Double Muscling' on the hypodevelopment of fat especially SCF was more conspicuous when comparisons were made at the same DSW or TSM than when comparisons were made at the same TSF which reflects the general late fattening tendency of this maturity type.

V. A MULTIVARIATE ANALYSIS OF FATNESS AND FAT PARTITIONING IN DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen each of Double Muscled (DM), Beef Synthetic (SY) and Hereford (HE) bulls, serially slaughtered from approximately 250 to 800 kg live weight were used to compare fatness and fat partitioning in DM and more normal breed types. As fattening proceeded, fat partitioning index { subcutaneous fat/(intermuscular fat + carcass cavity fat) } increased, with HE having a higher fat partionining index than either SY or DM. Principal component analyses were applied to derive an index of fat partitioning independent of fatness. The first principal component (PC_1, a size or fatness index) in DM bulls accounted for a larger proportion of variation than it did in either HE or SY bulls. The percent of variance explained by PC_1 ranged from 89 to 95%. Contrary to PC_1, the second and third principal components (PC_2, PC_3) in normal cattle explained much more of the variation than in DM. PC_2 in DM and PC_3 in normal cattle contrasted subcutaneous fat (SCF) with other fat depots. PC_2 in HE and SY and PC_3 in DM contrasted carcass cavity fat with SCF and intermuscular fat. PC_2 in DM and PC_3 in normal cattle can be termed multivariate fat partitioning indices (MVFPI) and were fatness-independent. After the effect of fatness had been removed HE still had a higher MVFPI than either SY or DM, which would suggest that fat partitioning

among the depots is breed specific even after the effects of fatness or mature size have been removed.

INTRODUCTION

Traditional British beef breeds show relatively higher subcutaneous:intermuscular fat ratios as well as different patterns of fattening compared with dairy or Continental beef breeds. Callow (1948, 1961) suggested that the subcutaneous:intermusclar fat ratio reflects the degree of intensity of selection for meat qualities of species or breeds within species, and Ledger (1959) suggested that this ratio varied by adaptation in hot climates.

Studies have shown that, differences among breeds in fat partitioning among the depots were greater than differences in fat weight distribution within the depots which was largely controlled by the total amount of fatness achieved (Kempster, 1981 and Berg and Walters, 1983). A fat partitioning index { FPI, subcutaneous fat/(intermuscular fat + perinephric + inguinal fat) } has been proposed by Lister (1976) as an objective criterion of estimation of earliness or lateness of fattening, for distinguishing between different physiological types of cattle and as a means of identifying superior animals for efficient meat production. However, Truscott *et al.* (1983) have shown that FPI increases as fattening proceeds, thus if FPI is to be used, corrections will have to be made for differences in fatness and age.

Since FPI does not remain constant, but changes with maturity and fatness, the objective of this study was to attempt by use of principal component analyses to derive an index of fat partitioning which is independent of fatness.

MATERIALS AND METHODS

Details of the animals, and of their feeding regimen, management and dissection procedure were described in Chapters I and IV. The ratio of { SCF/(IMF+CCF) } was used as a fat partitioning index (**FPI**)

STATISTICAL ANALYSIS

The data were analyzed by principal component techniques after transformation to common logarithms ($\log_{10}$). Separate analyses were done for each breed type and for the total ignoring breed type. The analysis was carried out on the correlation matrix of the fat depots.

Principal component analysis is a transformation of a set of N correlated variables into another set, which are independent linear functions of the original. These new functions are uncorrelated with each other (i.e. orthogonal). Thus, principal components are composites of the original variables. The first principal component (PC_1) is that weighted combination of all the original variables which accounts for the largest possible proportion of the total variation, the second, and further components are similarly, the weighted combinations of the original variables which are uncorrelated with all of the previous components, and representing the next largest portion of the remaining variance (Anderson, 1958 and Morrison, 1967).

The general model in the analysis was:

$$PC_j = a_{1j}Z_1 + a_{2j}Z_2 + \ldots + a_{nj}Z_n \qquad (j = 1,2,\ldots,n)$$

Where PC_j is the $_j$th principal component of the observed variables Z_1, $Z_2, \ldots, Z_n$, and $a_{1j}, a_{2j}, \ldots, a_{nj}$ are the elements of characteristic vector (weighting coefficients).

Each component may be given a descriptive name to summarise the major variation and signs of the coefficients in it. The amount of variance for each component is designated as an Eigenvalue (λ_j) and the sum of Eigenvalues ($\Sigma\lambda_j$) represents an estimate of the total variance. The ratio of $\lambda_j/\Sigma\lambda_j$ gives an estimate of the variance explained by each principal component.

Step-wise multiple regression was used to predict FPI from principal component scores derived from principal component analysis. Principal component scores were analyzed by least squares analysis of variance (Harvey, 1975). Duncan's multiple range test (Steel and Torrie, 1980) was used to test for significant differences between means.

RESULTS

In Figure V.1 fat partitioning indices are illustrated for each breed type. Regardless of breed type, as TSF increased FPI increased. Moreover, the rate of increase in this index was more rapid in HE than in SY and DM, and at all levels of fatness studied SY and DM had lower FPI's than HE.

Principal components analysis (no rotation) of fat depots by breed type is presented in Table V.1. Irrespective of breed type the first principal component (PC_1) was characterized by the high positive loadings on the three fat depots. [illegible] component accounted for 89, 91, and 95% of the variation [illegible] the original variables in HE, SY and DM, respectively. Since this component had high loadings on all three fat depots, it can be interpreted as a size or 'fatness index'. The second principal component (PC_2) in DM accounted for a further 4% of the variation which was different from HE (8%) and SY (6%). In HE and SY this component contrasted (SCF and IMF) and CCF, while in DM it contrasted SCF and (IMF and CCF). These components were not correlated with PC_1. The third principal component PC_3 in HE and SY contrasted SCF with the other fat depots, while in DM it contrasted IMF with (SCF and CCF). PC_3 accounted for the remaining variation in the fat depots. PC_2 in DM and PC_3 in normal cattle can be termed 'multivariate fat partitioning indices (MVFPI)'. HE varied more in PC_2 and PC_3 and less in PC_1 (fatness) than the other breed types. When the analysis

Table V.1. Principal Component[+] Loadings and Percentage of Variance Accounted for by Each Component

	Hereford			Beef Synthetic			Double Muscled			Overall		
Variable[++]	PC_1	PC_2	PC_3	PC_1	PC_2	PC_3	PC_1	PC_2	PC_3	PC_1	PC_2	PC_3
SCF	0.968	-0.122	-0.218	0.972	-0.068	-0.227	0.967	0.248	0.064	0.975	-0.044	-0.218
IMF	0.950	-0.256	0.176	0.953	-0.260	0.157	0.991	-0.010	-0.133	0.959	-0.249	0.138
CCF	0.918	0.394	0.047	0.940	0.333	0.076	0.969	-0.238	0.072	0.952	0.295	0.084
Eigenvalues	2.683	0.236	0.081	2.735	0.183	0.082	2.855	0.118	0.027	2.780	0.151	0.074
% Variance	89.4	7.9	2.7	91.2	6.1	2.7	95.2	3.9	0.9	92.5	5.0	2.5
Description	Fatness		MVFPI	Fatness		MVFPI	Fatness	MVFPI		Fatness		MVFPI

[+] No rotation

[++] The symbols are defined in the text.

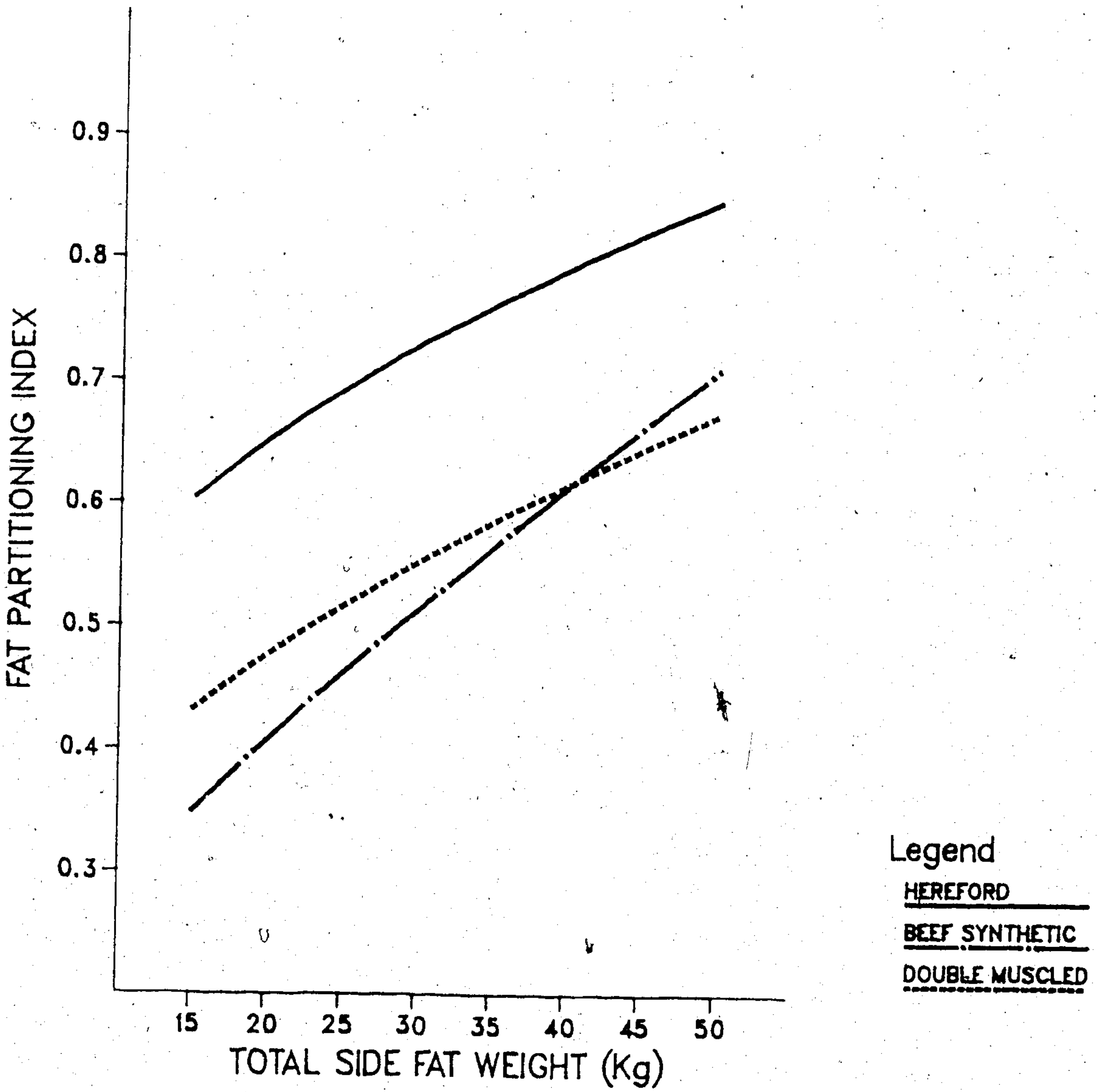


Figure V.1. Fat partitioning index (see text) relative to total fat weight for three breed types of young bulls.

was done for each breed ignoring breed type the same trend was found.

The correlation coefficients between the $_i$th original variable and the $_j$th component scores are presented in Table V.2. These correlations were computed after varimax rotation. PC_1 was highly correlated with CCF ($r=0.824$, $N=54$; $P < 0.01$); PC_2 was highly correlated with IMF ($r=0.808$, $N=54$; $P < 0.01$), and PC_3 was highly correlated with SCF ($r=0.686$, $N=54$; $P < 0.01$).

Fat partitioning index (FPI) was highly correlated with PC_3 (MVFPI) (overall, $r=.920$, $N=54$; pooled within group, $r=.849$, $N=51$; DM, $r=.993$, $N=18$; $P < 0.01$, Table 2).

In Table V.3 regression of FPI on principal component scores are presented. PC_3 alone accounted for 84.6% of the variation in FPI. The R^2 progressed from .846, to .969, to .999 as the orthogonal PC_3, PC_2 and PC_1 were added. The standard error of the estimate decreased from .063 to .006. In Table V.3 also, are presented a corresponding analysis predicting FPI from the original fat depots. Subcutaneous fat was predominant on FPI, in that it accounted for 81% of the variation.

Least squares analyses of variance of principal component scores of pooled data indicated that there were highly significant differences among breed types for all the components (untabulated). The mean of each component score vector was zero and the standard deviation was 1.0 (pooled data). Least squares means for principal component scores

Table V.2. Correlation Coefficients between Principal Components and Fat Depots and Fat Partitioning Index (FPI).

		PC_1	PC_2	PC_3
SCF	O	0.505**	0.524**	0.686**
	P	0.426*	0.648**	0.520**
IMF	O	0.436*	0.808**	0.396*
	P	0.428*	0.880**	0.205*
CCF	O	0.824**	0.423**	0.378**
	P	0.813**	0.559**	0.100
FPI	O	0.350*	0.172	0.920**
	P	0.114	0.193	0.849**

O = Overall; P = Pooled within group.
[+] The symbols are defined in the text.
* $P < 0.05$. ** $P < 0.01$.

Table V.3. Regression Analysis for Predicting Fat Partitioning Index

Independent Variable[+]	R^2	Standard Error	b
	Overall		
PC_3	0.846	0.063	0.146
PC_3, PC_2	0.969	0.028	0.056
PC_3, PC_2, PC_1	0.999	0.006	0.027
Constant			-0.212
	Hereford		
PC_3	0.992	0.008	0.083
PC_3, PC_2	0.995	0.006	0.005
PC_3, PC_2, PC_1	0.998	0.005	0.004
Constant			-0.065
	Beef Synthetic		
PC_3	0.839	0.063	0.139
PC_3, PC_1	0.968	0.029	0.055
PC_3, PC_1, PC_2	0.999	0.003	0.027
Constant			-0.292
	Double Muscled		
PC_2	0.985	0.015	0.119
PC_2, PC_3	0.999	0.001	-0.015
PC_2, PC_3, PC_1	0.999	0.001	-0.0002
Constant			-0.278
	Overall		
SCF	0.806	0.071	1.003
SCF, IMF	0.976	0.025	-0.782
SCF, IMF, CCF	0.999	0.006	-0.226
Constant			-0.230

[+] The symbols are defined in the text.

for each breed type are presented in Table V.4. HE tended to have higher PC_1 and PC_3 scores than either SY or DM. DM tended to have a lower PC_2 score than HE and SY which did not differ significantly from each other. In Figure V.2 are illustrated plots of the first and second component scores for each breed type.

Table V.4. Least Square Means for Component Scores by Breed Type

	Hereford	Beef Synthetic	Double Muscled
PC_1	0.521a	-0.637b	0.116a
PC_2	0.065a	0.427a	-0.491b
PC_3	0.802a	-0.381b	-0.421b

[+] The symbols are defined in the Text.

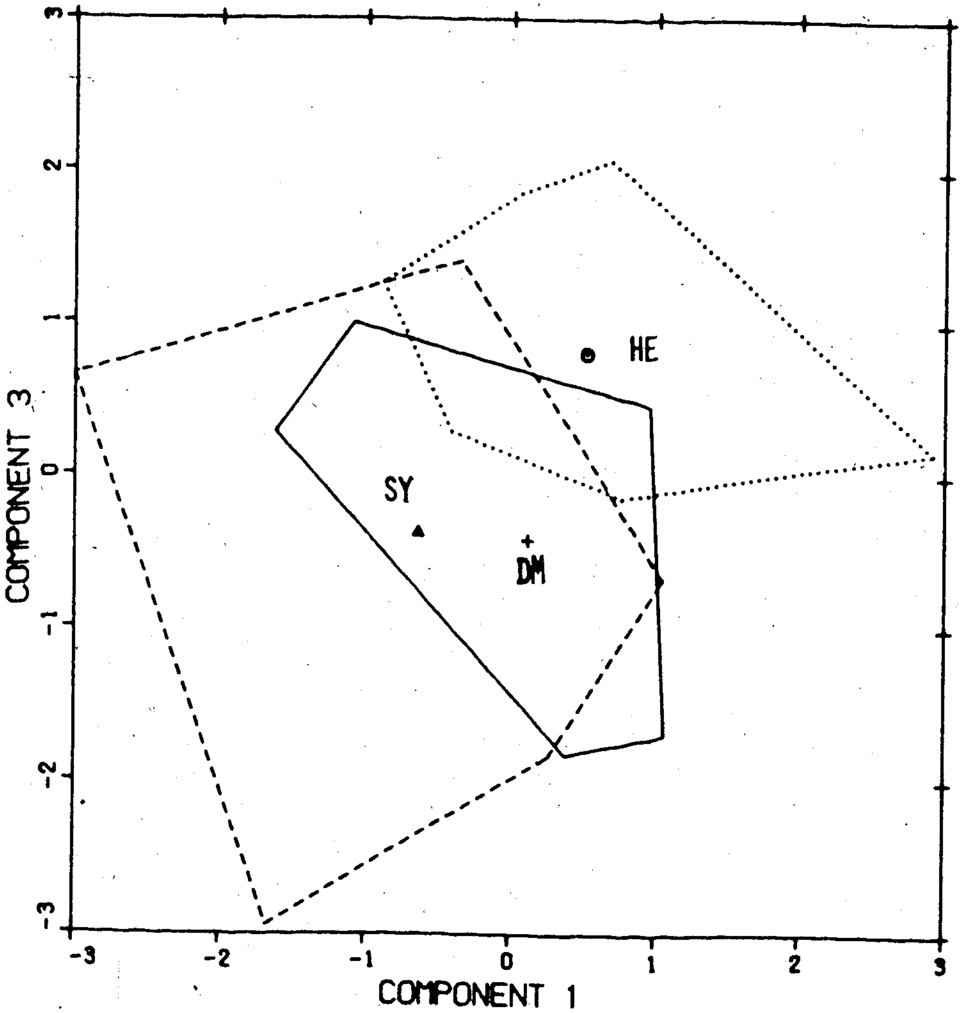


Figure V.2. Groupings of breed types by principal components.

DISCUSSION

Lister (1980) concluded that fat partitioning indices were associated with total fat in the carcass and with genotype of the animal. Wood (1982) pointed out that fat partitioning between carcass fat and abdominal fat is not influenced by mature size but rather by breed itself. In Chapter I it was found that HE had more total fat and more fat in each depots than either SY or DM. In the present Chapter, breed types differed in fat partitioning, with HE having a higher FPI than either SY or DM. Also, it was found as fattening progressed FPI increased. These results are in general agreement with Callow (1948) and Truscott *et al.* (1983). Thus, if FPI is to be used to characterize breed differences, corrections have to be employed for differences in fatness. Principal components analysis offer the experimenter a means to derive indices which are independent of fatness as noted by Truscott *et al.* (1983).

In the present study the first component in all breed types had high positive loadings on the three fat depots. The similar signs of the coefficients implies that all fat depot were increasing together. The first component in DM accounted for a larger proportion of variance than in HE and SY. It should be mentioned that, the proportion of variance explained by any component is influenced by the degree of correlation among the original variables. The higher the correlation, the greater the amount of variance which can be explained by that component. If there are perfect correlations among the original variables, the first principal component will explain all the variance. Thus, the relatively high proportion of variance accounted for by PC_1 in DM was due to the relatively high correlations among fat depots. Unlike PC_1, PC_2 and PC_3 in DM explained much less of the variance than in the other breed types (HE and SY). DM showed more variance in fatness and less in fat partitioning.

In DM, the second principal component was designated a multivariate fat partitioning index, while in HE and SY, the third principal component was the multivariate fat partitioning index. The multivariate fat partitioning index in the present study differed from that of Truscott *et al.* (1983) in that it contrasted SCF with IMF and CCF, as opposed to carcass (SCF and IMF) with intra-abdominal depots for those authers.

Since principal component scores were uncorrelated it was of interest to use them in multiple regression analysis to predict FPI. When this was done it was found that the third component (MVFPI) accounted for approximately 85% of the variance. These data indicated that FPI can be predicted with a high degree of accuracy from MVFPI and supports the use of MVFPI as a measure of fat partitioning. MVFPI has the advantage over FPI of being independent of fatness which agrees with Truscott *et al.* (1983) who reported that at 20 months of age the FPI was strongly correlated with the MVFPI ($r=-.95$; $N=28$).

In the present study HE had higher MVFPI than SY and DM which supports the assumption that the fatter breed type tended to have a higher fat partitioning index than the leaner ones. Even after the effect of fatness had been removed, there were still differences among breed types in fat partitioning which would suggest that fat partitioning among the depots is a breed specific trait and not only related to total fat or mature size which agrees with Truscott *et al*. (1983). Similarly, Garn (1955) studied humans and reported that relative fat patterning is a stable or individual characteristic (may be genetically determined) in contrast to fatness.

In summary, as fattening proceeded, fat partitioning index { SCF/(IMF+CCF) } increased, with HE having a higher fat partionining index than either SY or DM. Principal component analyses were applied to derive an index of fat partitioning independent of fatness. After the effect of fatness had been removed HE still had a higher multivariate fat partitioning index than either SY or DM, which would suggest that fat partitioning among the depots is a breed specific trait even after the effects of fatness or mature size are removed.

VI. GROWTH AND DISTRIBUTION OF BONE WEIGHT IN DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen Double Muscled (DM), 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls, serially slaughtered from approximately 250 to 800 kg live weight, were used to determine the influence of 'Double Muscling' and maturity type on bone growth patterns and distribution.

Relative to total side bone (TSB), breed types tended to have similar growth coefficients for all bones or bone groups except the vertebral column where HE tended to have a higher growth coefficient than either SY or DM. As TSB increased the proportion of bone in scapula, costae, vertebrae lumbales and os coxae increased ($b > 1$; $P < 0.05$), the proportion of bone in humerus, radius *et* ulna, tibia, carpus and atlas decreased ($b < 1$; $P < 0.05$) and the proportion of bones in vertebrae cervicales with atlas, vertebrae thoracicae, sternum and femur remained relatively constant ($b = 1$; $P > 0.05$). The appendicular skeleton, followed an increasing disto-proximal growth gradient, whereas the vertebrae followed an increasing cranio-caudal gradient.

Compared with the more normal breed types, adjusted to the same TSB, DM had proportionately less bone weight in the proximal hindlimb and total long bones, but they had proportionately more bone weight in costae and sternum. The

hypodevelopment of bones in the muscular hypertrophied animals followed a disto-proximal gradient which was most pronounced in the proximal pelvic limb.

INTRODUCTION

Quantitative growth and development of bone is known for various species. The effect of breed, sex, slaughter weight and rate of growth, on bone growth has been described. Increased muscling in cattle and the most extreme example Double Muscling, results in a relative decrease in the skeleton (Vissac, 1973 and Chapter I). However, the reduction in bone is not the same for all parts of the skeleton as shown by Dumont (1982).

Although the influence of 'Double Muscling' on bone distribution has been described at fixed live weights and ages, because of paucity of animals and absence of serial slaughter, little information is available on relative or differential growth patterns of the parts of the skeleton of these unique genotypes. Therefore this study was designed to investigate the consequences of 'Double Muscling' on bone growth patterns and distribution as well as on interrelationships among skeletal constituents.

MATERIALS AND METHODS

Details of the animals, and of their feeding regimen, management and dissection procedure were described in Chapter I. The weight of bones in the axial skeleton, forelimb and hindlimb were recorded. The axial skeleton included the following bones: vertebrae lumbales, vertebrae thoracicae, vertebrae cervicales, costae (ribs) and sternum. The forelimb (pectoral or thoracic limb) included: scapula, humerus, radius *et* ulna and carpus. The hindlimb (pelvic limb) included: Os coxae, femur, patella, tibia *et* fibula, and ossa tarsi (tarsus). The sum of the weight of the humerus, radius *et* ulna, femur and tibia was used as 'total long bone weight' and the sum of all vertebrae was used as 'total vertebra weight'. The sum of the weight of individual ~~bones~~ was used as the weight of 'total side bone' (TSB). Figure VI.1 shows range and mean for TSB for each breed type.

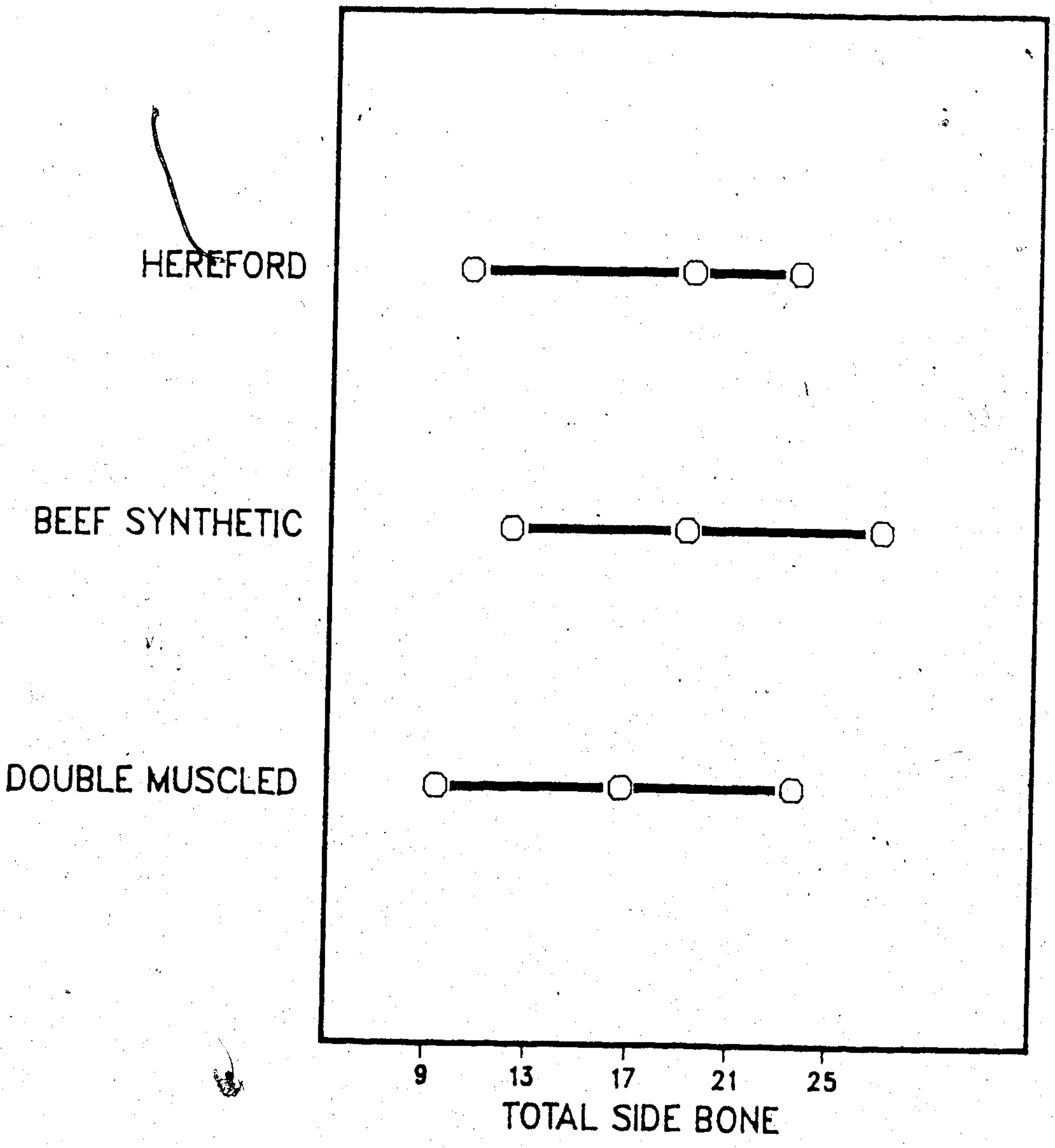


Figure VI.1. Range and mean of total side bone weight for each breed type.

STATISTICAL ANALYSIS

The data were analyzed by one way analysis of covariance (Snedecor and Cochran, 1967), according to the following model:

$$\log Y_{ij} = A_0 + G_i + b \log X_{ij} + (Gb)_i \log X_{ij} + e_{ij},$$

where:

Y_{ij} = weight (g) of individual bone of the $_{ij}th$ animal;

A_0 = the intercept;

G_i = fixed effect of the $_{i}th$ breed type;

X_{ij} = total weight (g) of the total side bone of the $_{ij}th$ animal;

b = regression coefficient of Y on X;

$(Gb)_i$ = interaction effect (breed x regression coefficient), and

e_{ij} = error assumed to be $NID (0, \sigma^2 e)$.

Individual breed type regression coefficients were computed and compared and in cases where the differences among slopes were not significant ($P > 0.05$) the common regression coefficient was used for adjustment. However if the differences among slopes were significant, adjusted means were computed using the appropriate breed group regression but not statistically tested for significance. Duncan's multiple range test (Steel and Torrie, 1980) was used to test for significant differences among adjusted means.

RESULTS

In Table VI.1 are presented unadjusted means and standard deviations for weights of individual bones, bone groups and total side bone (TSB).

There were no significant differences among breed types in regression of individual bones and bone groups, except for total vertebrae, on TSB (Table VI.2). As TSB increased the proportion of bone in scapula, costae, vertebrae lumbales, and Os coxae increased ($b > 1$; $P < 0.05$), the proportion of bone in humerus, radius *et* ulna, tibia, carpus, and atlas decreased ($b < 1$; $P < 0.05$), and the proportion of bones in vertebrae cervicales with atlas, vertebrae thoracicae, sternum, and femur remained relatively constant ($b = 1$; $P > 0.05$). The DM bulls had higher relative growth rate coefficients for scapula and femur than either HE or SY bulls ($P > 0.05$). Relative to TSB, the HE bulls had a higher growth rate for total vertebrae than did the SY and DM bulls ($P < 0.05$). The SY bulls had a non significantly higher relative growth rate for Os coxae than did the bulls in the other breed types. The apparently higher growth rate for femur in DM or Os-coxae in SY was not associated with larger proportions of these bones in those breed types.

At a common TSB there were significant differences among breed types in bone weight of scapula, sternum, Os coxae, femur, costae and total long bones. Double Muscled bulls had significantly less bone in femur than either HE or

Table VI.1. Unadjusted Means (g) and Standard Deviations (S.D.) of the Weights of Bones by Breed Type

	Hereford		Beef Synthetic		Double Muscled		Overall	
	Mean	S.D.	**Mean**	S.D.	**Mean**	S.D.	**Mean**	S.D.
Axial Skeleton								
Vertebrae lumbales	1030	318.7	964	252.7	890	405.4	961	330.3
Vertebrae thoracicae	1699	367.1	1632	442.2	1436	425.2	1589	420.2
Vertebrae cervicales	1351	363.3	1408	344.6	1145	296.0	1302	348.6
Costae	3307	645.0	3158	819.6	2846	871.6	3103	794.8
Sternum	1086	266.8	1177	324.0	1082	275.0	1115	287.6
Forelimb								
Scapula	1166	200.1	1084	263.0	992	313.1	1081	268.6
Humerus	1609	235.3	1650	355.3	1421	343.1	1560	325.8
Radius et ulna	1166	165.2	1178	257.3	1025	246.2	1123	238.1
Carpus	258	42.2	258	63.7	228	56.7	248	55.8
Hindlimb								
Os coxae	2422	480.4	2299	632.9	1895	582.6	2205	602.6
Femur	2045	277.2	2122	456.3	1698	530.0	1955	464.8
Patella	134	19.8	135	27.7	116	30.4	128	27.3
Tibia et fibula	1261	164.4	1321	252.7	1198	285.0	1260	240.5
Ossa tarsi	706	132.1	676	196.8	614	157.7	665	165.9
Total side bone								
Total vertebrae	2935	678	2799	684	2493	783	2742	728
Total long bone	6080	83[illegible]	6271	1309	5342	1262	5898	1203
Total side bone (kg)	19.2	3.3	19.1	4.3	16.6	4.4	18.2	4.1

Table VI.2. Estimates of Parameters of Allometric Regression and Adjusted Means for Weights of Individual Bones and Bone Groups

Dependent variate	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted Means** antilog (g)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Axial Skeleton														
Vertebrae lumbales	**1.654**	0.18	0.859	0.19	**1.235**	0.11	**1.215**	0.09	21.45	907	885	924	2.73	0.15
Vertebrae thoracicae	1.142	0.12	1.132	0.17	**1.058**	0.08	1.100	0.07	12.12	1548	1494	1545	0.14	0.38
Vertebrae Cervicales	1.286	0.19	0.823	0.14	**0.823**	0.12	0.929	0.08	14.19	1230	1318	1224	2.84	1.53
Atlas	0.975	0.13	0.902	0.11	**0.774**	0.10	**0.859**	0.06	12.38	192	190	176	0.63	0.25
Costae	1.128	0.07	1.153	0.10	**1.187**	0.04	**1.163**	0.04	6.67	3013ab	2399b	3064a	0.17	3.44*
Sternum	0.959	0.21	1.098	0.14	0.932	0.08	0.989	0.08	13.89	992a	1086ab	1162b	0.39	5.35**
Forelimb														
Scapula	1.039	0.09	1.069	0.04	**1.215**	0.06	**1.129**	0.04	6.26	1068a	1003b	1061a	2.44	5.53**
Humerus	**0.806**	0.05	**0.912**	0.04	**0.907**	0.04	**0.886**	0.03	4.49	1506	1554	1515	1.37	2.87
Radius et ulna	**0.800**	0.04	**0.925**	0.03	**0.963**	0.04	**0.868**	0.03	4.25	1093	1109	1092	1.64	0.32
Carpus	**0.754**	0.11	0.967	0.11	**0.798**	0.09	**0.840**	0.06	10.68	242	241	242	0.92	0.01
Hindlimb														
Os coxae	1.056	0.09	**1.177**	0.06	1.103	0.06	**1.115**	0.04	6.59	2216a	2113b	2037b	0.66	6.94**
Femur	**0.729**	0.05	**0.888**	0.05	1.009	0.17	0.908	0.07	11.99	1915a	1996a	1777b	1.21	4.0*
Patella	**0.764**	0.09	**0.768**	0.11	0.880	0.08	**0.819**	0.05	9.04	126	127	123	0.55	0.83
Tibia et fibula	**0.696**	0.05	**0.798**	0.05	**0.655**	0.15	**0.708**	0.06	10.73	1196	1259	1255	0.46	1.28
Ossa tarsi	0.774	0.16	0.985	0.16	**0.784**	0.12	0.844	0.08	13.76	659	629	650	0.66	0.50
Totals														
Total vertebrae	**1.316**	0.07	0.952	0.07	1.032	0.05	1.072	0.05	7.4	3706	3731	3741	6.27**	–
Total long bones	**0.754**	0.05	**0.881**	0.04	**0.861**	0.04	**0.842**	0.02	4.12	5715a	5924b	5683a	2.12	4.27*

* Growth coefficients in bold type are significantly different from 1 at $P < 0.05$.

** **Adjusted to geometric mean total side bone (TSB) = 17.80 kg along the slope of common regression line. Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.**

*** $P < 0.05$; ** $P < 0.01$.**

SY (Figure VI.2), they were significantly less than HE for Os coxae (Figure VI.3) and significantly greater than HE for sternum but did not differ from SY for this bone. The DM bulls had significantly less bone in the total long bones but more bone in costae than SY, but did not differ from HE in this respect. There were no differences ($P > 0.05$) among breed types in the weight of humerus, radius *et* ulna, atlas, vertebrae cervicales and thoracicae, patella, tibia, tarsus or vertebrae lumbales.

Since growth coefficients for total vertebrae differed significantly among breed types, estimates of weights of total vertebrae at 12 and 22 kg of TSB, were calculated using individual breed regressions. At 12 kg TSB, DM bulls had 14% more and 3% less bone in total vertebrae, while at 22 kg TSB, DM had 4% less and 2% more than HE and SY bulls, respectively.

Table VI.3 gives the ratios of bone weights of DM bulls to HE and SY bulls derived from unadjusted means and means adjusted to same TSB and TSM (total side muscle). At the same TSB, DM bulls showed 7 and 11% hypotrophy for the femur, 4 and 8% for the Os coxae, and 2 and 3% for the patella, whereas they showed 2 and 4% hypertrophy for vertebrae lumbales, 0 and 3% for vertebrae thoracicae, 2 and 6% for costae and 7 and 17% for the sternum. The effect of 'Double Muscling' on the rest of the skeleton was not consistent, since the DM was similar in percentage to one or the other breeds in all cases. All individual bones, or bone

Table VI.3. Ratios of Bone Weights from DM *vs.* HE or SY Based on Unadjusted Means, Means Adjusted to the Same TSB and Means Adjusted to the Same TSM

	Ratios (unadjusted means)		Ratios (same TSB)⁺		Ratios (same TSM)⁺⁺	
	DM/HE	DM/SY	DM/HE	DM/SY	DM/HE	DM/SY
Axial Skeleton						
Vertebrae lumbales	0.864	0.923	1.019	1.044	0.818	0.894
Vertebrae thoracicae	0.845	0.880	0.998	1.034	0.819	0.898
Vertebrae cervicales	0.848	0.813	0.995	0.929	0.842	0.822
Costae	0.681	0.901	1.017	1.057	0.824	0.912
Sterum	0.996	0.919	1.171	1.070	0.979	0.942
Forelimb						
Scapula	0.851	0.915	0.993	1.058	0.809	0.916
Humerus	0.883	0.861	1.006	0.975	0.856	0.870
Radius *et* ulna	0.879	0.870	0.999	0.985	0.855	0.881
Carpus	0.884	0.884	0.996	1.000	0.860	0.899
Hindlimb						
Os coxae	0.782	0.824	0.919	0.964	0.752	0.835
Femur	0.830	0.800	0.928	0.890	0.787	0.792
Patella	0.866	0.859	0.976	0.969		
Tibia et fibula	0.950	0.907	1.049	0.997	0.923	0.910
Ossa tarsi	0.870	0.908	0.986	1.033	0.848	0.925
Totals						
Total Vertebrae	0.844	0.854	1.009	1.003	0.832	0.873
Total long bones	0.879	0.852	0.994	0.959	0.854	0.861

⁺TSB, Total side bone.
⁺⁺TSM, Total side muscle.

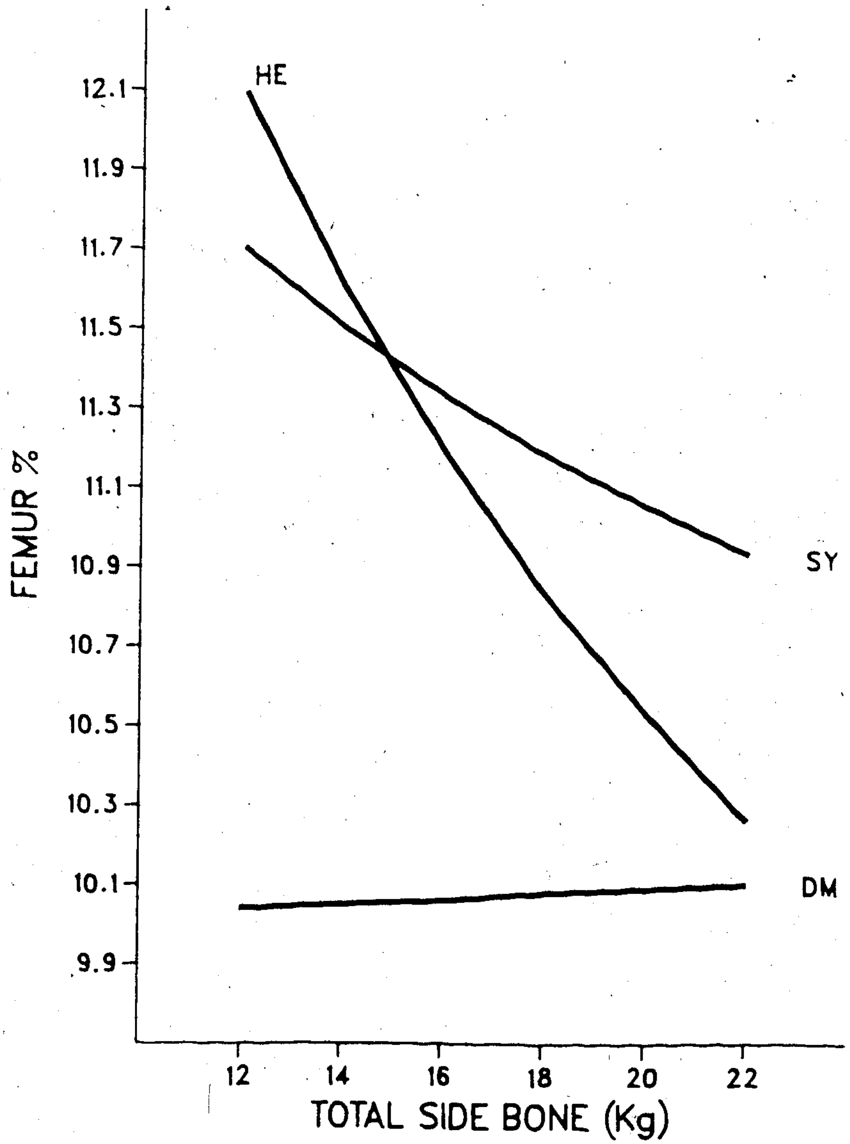


Figure VI. 2. Femur weight as % of total side bone weight relative to total side bone weight weight in three groups of young bulls.

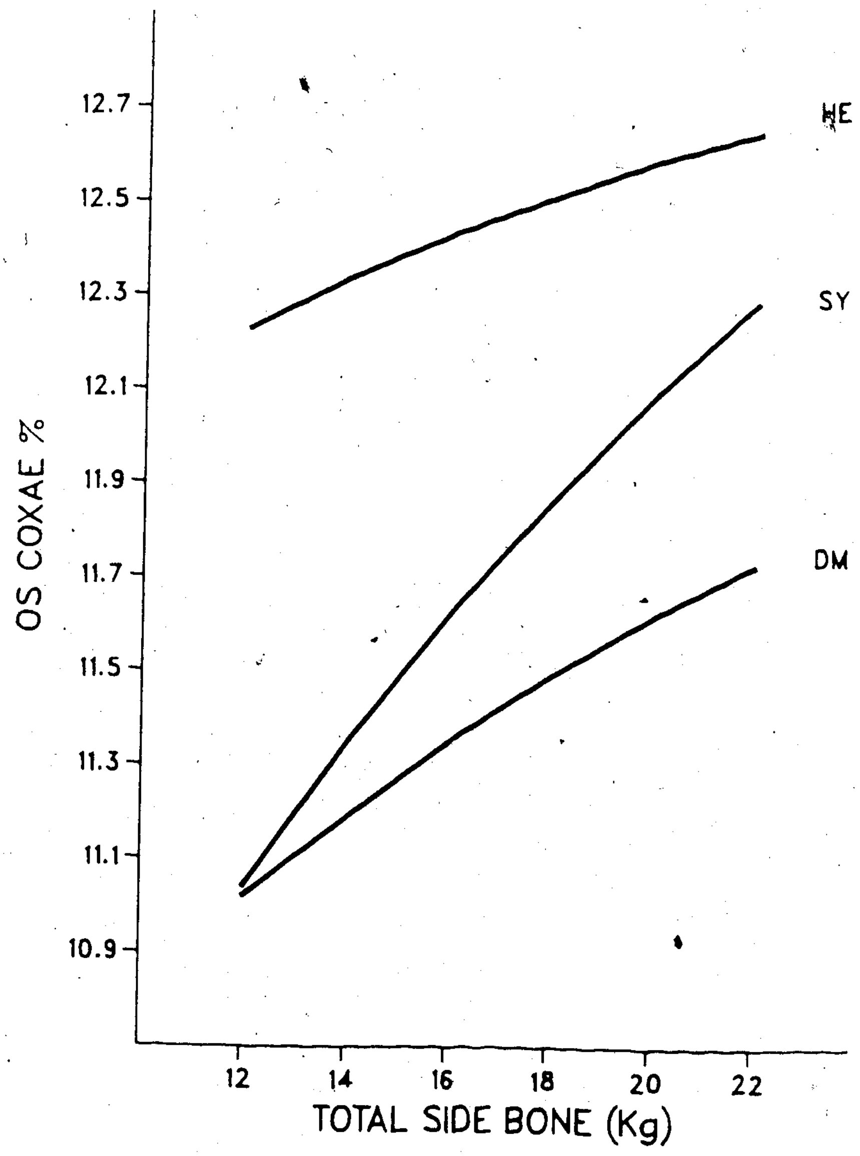


Figure VI.3. Os coxae weight as % of total side bone weight relative to total side bone weight in three groups of groups in DM bulls showed hypotrophy when comparison was made at the same total muscle or when unadjusted means were used, whereas when comparison was made at the same TSB, some bones showed hypertrophy (Figure VI.4), others showed either hypotrophy, or were not significantly different from normal.

The pooled within group phenotypic correlation matrix as well as the individual within breed phenotypic correlation matrix for individual bones of fore and hind limb are presented in Table VI.4. The upper off-diagonal elements were computed from the weight of individual bones, while the lower off-diagonal elements were computed from individual bones as a percentage of TSB. In HE the highest correlation coefficient (r=0.925) was found between femur% and tibia%, and the lowest (r=-0.289) was between humerus% and Os coxae%. In SY the highest correlation (r=0.724) was found between femur% and radius *et* ulna%, while the lowest (r=-0.659) was between Os coxae% and humerus%. In DM the highest correlation (r=0.823) was found between humerus% and radius *et* ulna%, while the lowest (r=-0.727) was between femur% and tibia%. It is interesting to note that within DM, the femur% was positively correlated with Os coxae% and scapula%, while in the normal (HE,SY) cattle femur% and Os coxae% and scapula% were negatively correlated.

In Table VI.5 growth relationships of selected individual bones are examined by analysis of covariance.

Table VI.4. Phenotypic Correlation Matrix for Fore- and Hind-Limb Bones[1]

	Breed[+]	Os Coxae	Femur	Tibia	Scapula	Humerus	Ru
Os Coxae	**HE**		0.866	0.887	0.822	0.864	0.886
	SY		0.942	0.956	0.943	0.923	0.945
	DM		0.875	0.561	0.952	0.942	0.937
	0		0.887	0.771	0.914	0.915	0.927
Femur	HE	-0.202		0.974	0.868	0.985	0.963
	SY	-0.377		0.980	0.966	0.966	0.983
	DM	**0.211**		**0.333**	0.854	0.894	0.908
	0	-0.281		0.666	0.892	0.932	0.941
Tibia	**HE**	-0.085	0.925		0.963	0.957	0.941
	SY	-0.400	0.635		0.973	0.957	0.978
	DM	-0.531	**-0.727**		0.678	0.663	0.667
	0	-0.233	0.792		0.813	0.827	0.835
Scapula	**HE**	-0.274	-0.209	-0.126		0.906	0.947
	SY	-0.071	-0.195	-0.087		0.978	0.977
	DM	**0.254**	-0.366	-0.108		0.963	0.964
	0	-0.198	-0.200	-0.109		0.953	0.961
Humerus	HE	-0.289	0.916	0.812	-0.041		0.980
	Y	-0.659	0.514	0.342	-0.031		0.988
	DM	-0.225	**0.163**	0.227	-0.316		0.978
	0	-0.452	0.746	0.604	-0.037		0.983
Radius *et* ulna	**HE**	-0.216	0.799	0.753	0.250	0.854	
	SY	-0.462	0.724	0.542	-0.178	0.779	
	DM	-0.328	**0.304**	0.294	-0.452	0.570	
	0	-0.323	0.768	0.660	0.114	0.823	

[1] Above diagonal based on weights, below diagonal based on percentages.

[+] HE, Hereford; SY, Beef Synthetic; DM, Double Muscled; 0, Pooled within group.

Table VI.5. Allometric Relationships Among Selected Bones by Breed Group

Dependent Variate (Y)	Independent Variate (X)	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV %	Adjusted Means** Antilog (g)			F-Values	
		b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
Humerus	Femur	1.085	0.04	0.980	0.06	**0.629**	0.11	**0.769**	0.06	1.1	1511	1504	1559	6.38**	—
Radius *et* ulna	Femur	1.042	0.07	1.007	0.05	**0.612**	0.10	**0.759**	0.06	8.8	1096	1074	1125	8.14**	—
Os coxae	Femur	**1.314**	0.14	**1.229**	0.10	**0.782**	0.09	0.954	0.08	13.7	2226	2032	2108	4.88*	—
Tibia	Femur	0.942	0.05	**0.871**	0.05	**0.208**	0.18	**0.457**	0.09	17.9	1212	1246	1252	7.82**	—
Radius *et* ulna	Tibia	1.069	0.08	1.109	0.07	0.707	0.17	0.889	0.08	12.0	1142	1103	1051	3.16*	—
Scapula	Os coxae	0.855	0.12	0.859	0.07	1.047	0.08	0.943	0.05	10.4	1030	1010	1093	1.75	2.59
Radius *et* ulna	Humerus	0.904	0.05	1.002	0.04	0.933	0.05	0.961	0.03	4.0	1107	1090	1097	0.67	0.92

* Growth coefficients in bold type are significantly different from 1.0 at $P < 0.05$.

— Missing values mean covariance analysis was not legitimate.

** Adjusted to geometric mean of femur = 1894 g, Os coxae = 2120 g, and humerus = 1525 g.

• $P < 0.05$; •• $P < 0.01$.

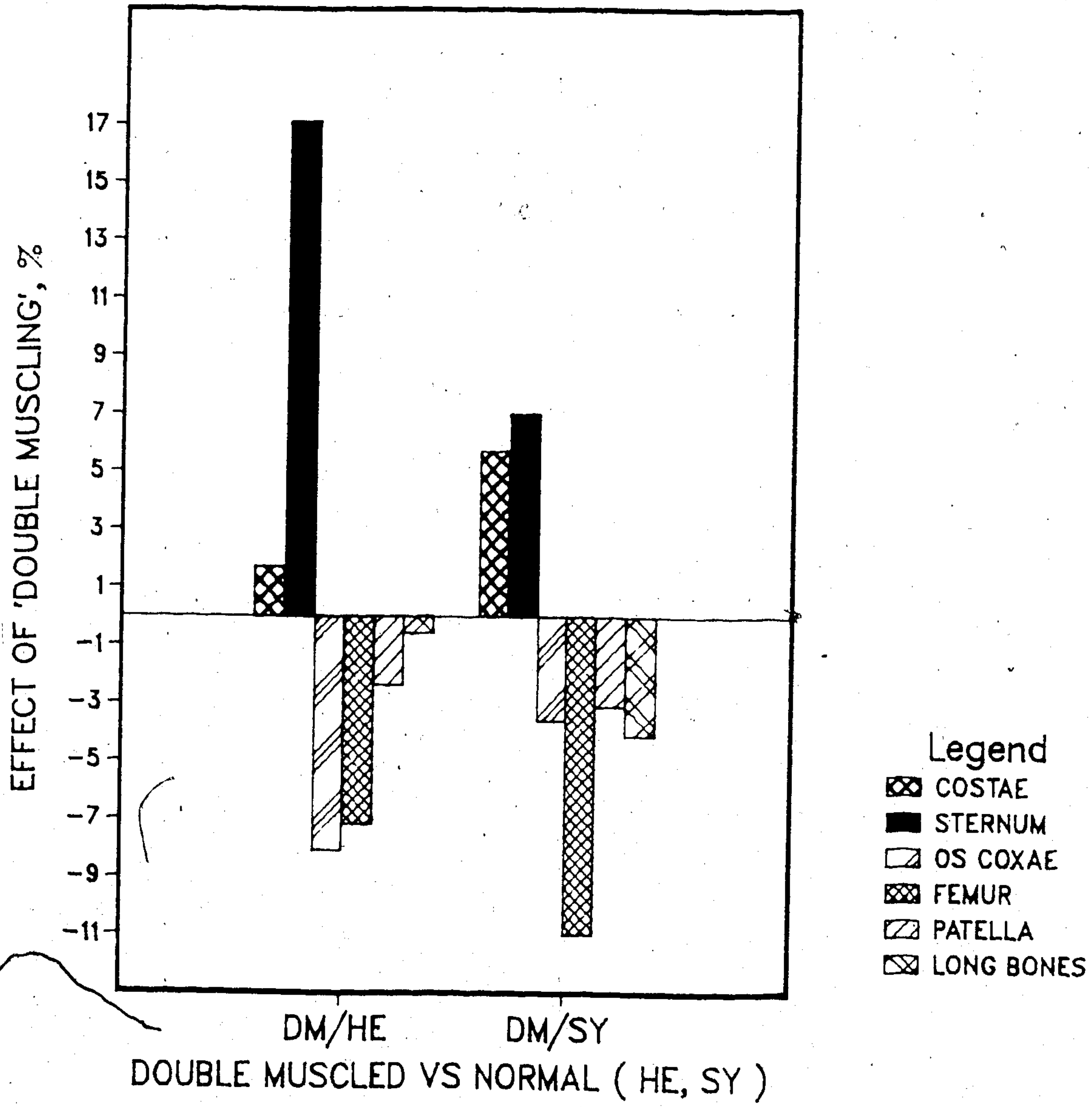


Figure VI.4. Comparative bone development in Double Muscled and normal cattle.

[illegible] a differential effect on the relative growth rate of the humerus, the radius *et* ulna, the Os coxae and the tibia when regressed on the femur (among slopes differences were significant). Relative to the femur the DM bulls had lower growth rates for the humerus, the radius *et* ulna, Os coxae and the tibia than did the bulls in the other breed types. There were differences among breed types in the regressions of the radius *et* ulna relative to tibia ($P < 0.05$). No significant differences were found among breed groups in the regressions of radius *et* ulna on humerus and of scapula on Os coxae. As the humerus increased the proportion of bone in the radius *et* ulna decreased ($b < 1$; $P < 0.05$) while as Os coxae increased the proportion of bone in the scapula remained relatively constant ($b = 1$; $P > 0.05$).

DISCUSSION

Bone Growth Patterns

Each tissue in the body performs certain specialized functions. Bones serve as anchorages for the attachment of skeletal muscles, provide a framework for the softer tissues and give protection to certain delicate or important structures in the body and with muscles and tendon provide a means of locomotion (Wasserman, 1977). Bones are sites for manufacture of the red blood cells (or erythrocytes) of the body. Bone growth rate reflects the structural requirements of the maturing animal and in the adult, its internal conformation can change in response to new mechanical stresses and strains (Wasserman, 1977).

Breed types did not differ significantly in the relative growth rate of each bone or bone groups except the vertebral column. Somewhat similar findings have been reported by Berg *et al.* (1978) and Jones *et al.* (1978). The homogeneity of the growth coefficients for each individual bone and bone group in the present study, implies there is no differential effect of the genotype on the relative growth of these bones. Thus any differences among adjusted means reflect breed type differences established earlier in development than the start of the present experiment or the lack of sensitivity of the statistical test used.

Hammond (1932) suggested the theory of growth gradients. According to his theory, the growth of the axial skeleton follows anterio-posterior, while the growth of limbs follow disto-proximal gradients. He showed that the cranium is the earliest maturing part in the axial skeleton, while the metacarpus and metatarsals are the earliest maturing parts in the fore and hind limb and the costae are the latest maturing bones of the skeleton as a whole. In the present study, the common growth coefficients of the appendicular skeleton of fore and and hind limb, relative to total side bone revealed an increasing disto-proximal and those of the vertebrae revealed an increasing cranio-caudal gradient in ageement with Hammond's theory. Davies (1975) working with pigs, had similar findings, but Jones *et al*. (1978) and Richmond *et al*. (1979) had results at variance with Hammond's theory, since the anterio-posterior or disto-proximal gradients were not evident. The late maturity of bones in the proximal pelvic and proximal thoracic limbs reflect changes in function with maturity of the animal, while the late maturity of costae reflect increased weight support requirment of the thoracic and abdominal regions.

Results are often not consistent among species and among reports. The inconsistancy might be due to differences in the way the weight is distributed, the maturity of animals studied, the range of slaughter weights of the experiment, the starting weights, or in differences in dissection techniques. Variation might be contributed by inaccuracies in splitting vertebrae during halving the carcass especially in the cervical region. It should be mentioned that the values of growth coefficients depend upon the range of slaughter weights and the stage of maturity, and the number of observations; the smaller number of observations, the larger the variation expected in the results and the larger will be the standard error of the estimate. In order to make precise or meaningful interpretations for growth coefficients, it is desirable to have very low standard errors.

In Table VI.6 growth coefficients from the literature for various species are summarized as greater than (>), less than (<) or equal to unity. In the present study vertebrae lumbales (VL) had high or average growth coefficients, while vertebrae thoracicae (VT) and vertebrae cervicales (VC) grew proportional to total bone. Other reports and other species show generally similar results for vertebrae lumbales and vertebrae thoracicae, but results for vertebrae cervicales were a little more inconsistant with most reports for species other than cattle showing higher growth coefficients. Shahin (unpublished) found all vertebrae groups of buffalo to have growth coefficients greater than 1 (b=1.27 ± 0.02 for vertebrae lumbales, b=1.24 ± 0.04 for vertebrae thoracicae, b=1.09 ± 0.03 for vertebrae cervicales). With vertebrae lumbales generally having higher growth coefficients than other vertebrae groups in cattle, the antero-posterior gradient of the axial skeleton is in agreement with Hammond's theory.

The growth coefficient of costae seems to be high in most species with a few reports indicating an average

Table VI.6. Growth Coefficients Classified as Less than (<), Greater than (>) or Equal to 1 for Various Species from the Present Study and the Literature

Species	Breed	Axial Skeleton*					Forelimb				Hindlimb					References
		VL	VT	VC	Costae	Sternum	Scapula	Humerus	RU	Carpus	OC	Femur	Patella	TF	OT	
Cattle	Hereford	>	1	1	1	1	1	<	<	<	1	<	<	<	1	Present study
	Beef Synthetic	1	1	1	1	1	1	<	<	1	>	<	<	<	1	Present study
	Double Muscled	>	1	1	>	1	>	<	<	<	1	1	<	<	1	Present study
	Common	>	1	1	>	1	>	<	<	<	>	1	<	<	1	Present study
	Angus	1	1	1	1	1	1	<	1	1	1	<	1	<	<	Seebeck & Tulloh (1968)
	Mixed	>	1	>		1	1		<	<	1	1		<	<	Kempster *et al.* (1977)
	Mixed	>		1			1		<	<	1			<	<	Berg *et al.* (1978)
	Mixed	1	1	<	>	1	>	<	<	<	>	<	<	<	<	Jones *et al.* (1978)
Buffalo		>	>	>	>	1	>	1	<	<	>	<	1	<	<	Shahin (unpublished)
Pigs	Pietrain						>	1	<	<		1	1	1	<	Davies (1975)
	Mixed	>	1	>	>	1	1	1	<	1	1	<	>	1	<	Richmond *et al.* (1979)
	Large White x Landrace						>	1	1		1	1	>	1		Davies *et al.* (1980)
Sheep	Merinos d-Arus	>	1	>	>		>	<	<	<	[illegible]	<		<	<	Prud'han *et al.* (1978)
Rabbit		>	<	1	>	1										Dulor *et al.* (1976)

* VL = Vertebrae Lumbales, VT = Vertebrae Thoracicae, VC = Vertebrae Cervicales, RU = Radius *et* ulna, OC = Os coxae, TF = Tibia *et* fibula, OT = Ossa tarsi.

coefficient. The sternum grew proportional to total bone (b=1) for all species from all reports. Although there are differences in the magnitude of growth coefficients reported for the limb bones, most reports for all species indicate disto-proximal gradients. Exceptions are the patella in some studies and the ossa tarsi in the present study.

Since the effect of 'Double Muscling' is mainly on the limb bones, an examination was undertaken to see what morphological changes had occurred and the interrelationship among limb bones as a consequence of selection for muscling. In the DM, the correlation between femur and tibia was negative in spite of the fact that they are in the same limb. When growth rates of selected bones relative to the femur were examined, a differential effect was found with DM bulls having a lower relative growth rate for the radius *et* ulna, the humerus, Os coxae and the tibia than did the bulls in the other breed types. Thus the covariance analysis of bones relative to the femur provided additional evidence of the influence of 'Double Muscling' on relative bone growth. The differences in the size and shape of some bones in the proximal pelvic limb in the muscular hypertrophied animal could be a correlated response to the increasing load they have to bear.

Bone Weight Distribution

When comparing breed types one must consider differences in their size and maturity, because as Hammond (1932) pointed out, early maturing breeds are characterized by greater development of the Os coxae, vertebrae lumbales, costae, and upper parts of the limbs, whereas the large, late maturing breeds are characterized by the greater development of their limbs as compared to the later maturing bones (vertebrae lumbales, costae, scapula, os coxae). Also he showed that the early maturing breeds have a thicker femur than the late maturing. In the present study compared with HE, DM tended to have more of their bone in the sternum, but less in Os coxae and femur, but compared with SY, DM tended to have more of their bone in costae and the scapula, but less in the femur and total long bones. On the other hand, compared with HE, SY tended to have more of their bone in total long bones, but less in the scapula and Os coxae. From these observations, HE was earlier maturing than either SY or DM. Assuming that costae are late developing bones, the differences between DM and SY reflect differences in the stage of maturity, DM being skeletally more mature when compared at the same total bone weight. Chapters I, II and IV provided evidence of the late maturity of Double Muscled as compared with either HE or SY in terms of carcass composition, fat and muscle development.

In chapter II it was found with the same animals as in the present study that compared with DM, SY had proportionately less muscle in the abdominal wall and in pectoral girdle and shoulder and elbow. These findings and those of the present study on costae and scapula, provide an anatomical explanation of similarities in muscle and bone distribution. Also, it may be argued that the relatively heavier costae in DM could be due to compensatory hypertrophy. This is because in DM there is a reduction in muscles associated with respiration, and the increasing physiological demands for respiration led to hypertrophy of costae. Seebeck (1973) found that Africander cross steers had heavier costae than Brahman crosses. Truscott *et al.* (1976) found that Friesians had less bone in the thoracic region than Angus crosses. Berg *et al.* (1978) found that at same total bone weight Hereford-sired bulls (early maturing) tended to have more of their bone weight in vertebrae thoracicae and vertebrae lumbales whereas the Chianina, Charolais or Romagnola sired bulls (late maturing breeds) were heavier in the hind shank.

As was mentioned earlier breed types differed significantly in the relative growth rate of total vertebrae which implies that the adjusted means of this group of bones are conditional on the weight of total bone. At lighter weights of total bone, DM had more weight of the vertebral column than HE, but at heavier weights of total bone, HE was heavier. In chapter II using the same animals as in the present study found that muscles surrounding the spinal column behave in the same way. These similarities in muscle and bone distribution in back and loin might imply functional peculiarities between breed types.

DM had proportionately larger sternum than HE, but did not differ from SY in this respect. It is not known whether this difference is related to excessive subcutaneous fat in this area (i.e. subcutaneous fat accumulating at the expense of sternum in HE), or to special breed characteristics peculiar to DM or to other factors. Jones *et al.* (1978) found that at the same total bone, Charolais crossbreds had 8% heavier sternum than British beef types ($P > 0.05$). Hammond (1932) reported that the late maturing breeds of sheep have a longer sternum than the earlier maturing breeds.

Studies have shown that compared with normal, at the same live weight or carcass weight, DM had lighter limb bones. However, there is little available information in the literature regarding the effect of 'Double Muscling' on axial skeleton development. In the present study at the same total muscle, compared with the more normal breed types, there was general but not uniform bone hypotrophy, being greater in proximal limb bones and lower in distal limb bones. However, when comparisons were made at the same total bone, there was differential hypotrophy in different parts of the skeleton. 'Double Muscling' had a greater hypotrophic effect on bones of the hindlimb than the forelimb. Along the limbs hypotrophy followed a disto-proximal gradient in agreement with observations of Vissac (1968), Hanset and Ansay (1972) and Ansay and Hanset (1979). It may be argued that the relatively lower proportion of bone in the proximal hindlimb in DM, might be related to rapid growth rate of muscle in this area rather than to the malfunctioning of endocrine glands. On the axial skeleton Boyajean *et al.* (1971) showed that hypodevelopment of bones seemed to follow an antero-posterior gradient, similar to the present study when comparisons were made at the same total muscle.

In summary, relative to total side bone, DM did not differ from the more normal breed types in the growth rate in all bones or bone groups except those of the vertebral column. At the same total side bone, compared with the more normal breed type, in DM carcasses there were shifts in bone weight distribution towards the thoracic region. DM had proportionately less bone in the proximal hindlimb. There was general but not uniform bone hypotrophy when comparisons were made at the same total muscle, but when comparisons were made at the same total side bone, there was differential and localized bone hypotrophy and the hypodevelopment of bones in the muscular hypertrophied animals followed a disto-proximal gradient which was most pronounced in the proximal pelvic limb.

VII. INFLUENCE OF BONE GROWTH ON MUSCLE GROWTH AND BONE-MUSCLE RELATIONSHIPS IN DOUBLE MUSCLED AND NORMAL CATTLE

ABSTRACT

Eighteen each of Double Muscled (DM), Beef Synthetic (SY) and Hereford (HE) bulls, serially slaughtered from approximately 250 to 800 kg live weight, were used to determine the influence of bone growth on muscle growth and muscle bone relationships in Double Muscled and normal breed types.

Relative to total side bone (TSB), DM had significantly higher growth rate for muscles in the all areas which exhibited gross muscular hypertrophy, i.e. proximal hindlimb and proximal forelimb. The superior muscling in DM animals is manifested primarly by generalized increase in regional muscle growth relative to bone. The pooled within-group coefficient of variation (a component of variance which is not being explained by the regression of muscle groups on bone) ranged from 10 to 19%. These relatively high coefficents suggest that there are other factors which influence muscle growth relative to bone growth or that muscle growth is somewhat independent of bone growth and makes suspect the belief that animals must possess large bone in order to produce large muscles.

At equal bone weight in the same anatomical region DM had significantly higher proportions of muscle in the

proximal parts of both limbs, back and loin and expensive regions of the carcass when compared with the more normal breed types.

The superiority of the DM bulls over normal in muscle:bone ratios was most pronounced in the proximal hindlimb, and least pronounced in the distal forelimb and distal hindlimb. The hyperdevelopment of muscle and the hypodevelopment of bone or the increase of muscle:bone ratios in the muscular hypertrophied animals followed a disto-proximal gradient along the limbs.

INTRODUCTION

Cattle manifesting heavy or 'Double Muscling' show, relative to normal cattle, an increase in muscular tissue, a decrease in the skeleton and a higher muscle:bone ratio. In Chapters I, II and VI, I have shown that the relative hypertrophy of muscles and the relative hypotrophy of bones are not the same for all parts of the muscular tissue or of the skeleton.

Many breeders believe that animals must possess large bones in order to produce large muscles. Nathusius as cited by Hammond (1932) suggested that the tissues derived from the same embryonic layer are correlated in their development and since muscular tissue and bone are derived from the same embryonic layer (i.e. mesoderm), the growth of muscle and bone would be correlated. According to Hammond (1932) bone size and shape (dimensions) are the true determinators of the size and shape of muscle rather than *vice versa*. He also, showed that the degree of development of an individual bone affects the size of the attached muscles, a more highly developed bone having larger muscles attached to it.

Tulloh and Romberg (1963) suggested that the dimensions of the long bones in the leg are affected by the weight they support. Stewart (1972) suggested that the development of bone and muscle weight might not be independent and that muscle development follows bone development rather than the reverse.

Butterfield (1966*b*) did not agree with the proposition that animals must possess large bones in order to produce large muscles. Arguing this hypothesis from a functional point of view, he claimed the functional necessity for such a relationship does not appear to have been established and it seems doutful if it does exist. Butterfield (1976) claimed there is little evidence of any constant relation between bone weight and muscle weight. He based his opinion on his observation of the Double Muscled animal where very heavy muscle can be grown on light bone.

Although the superiority of DM for muscle:bone ratio and differential proportioning of muscle over the body has been well established, there is little information on muscle:bone ratios and growth relationships of muscle and bone in different anatomical regions. The present study was designed to assess the influence of bone growth on muscle growth and bone-muscle relationships in Double Muscled and more normal cattle.

MATERIALS AND METHODS

Details of the animals, and of their feeding regimen, management and dissection procedure were described in Chapter I. A description of muscle groups was given in Chapter II.

The weights of bones in the axial and appendicular skeleton were grouped based on their anatomical location: P+F (pelvis and femur), proximal hindlimb; tibia, distal hindlimb; LUMTHV (lumbar + thoracic vertebrae), back and loin; S+H (scapula and humerus), proximal forelimb and radius *et* ulna, distal forelimb. The sum of pelvis, femur, lumbar and thoracic vertebrae (PFLUMTHV) were used as total bones in G_{10} and the sum of bone in G_{10} plus scapula and humerus were used as total bones in G_{11}. The sum of the individual bones was used as total-side bone (TSB). The ratios of muscle groups to bones in the same region were calculated and used as indices of muscle:bone relationships.

STATISTICAL ANALYSIS

The data were analyzed by one way analysis of covariance (Snedecor and Cochran, 1967), according to the following model.

$$\log Y_{ij} = A_0 + G_i + b \log X_{ij} + (Gb)_i \log X_{ij} + e_{ij},$$

where:

Y_{ij} = weight (g) of a specific muscle group of the $_{ij}th$ animal;

A_0 = the intercept;

G_i = fixed effect of the $_ith$ breed group;

X_{ij} = total weight (g) of the total side bone or weight of associated bones of the $_{ij}th$ animal;

b = regression coefficient of Y on X;

$(Gb)_i$ = interactions effect (breed x regression coefficient)

e_{ij} = error, assumed to be NID ($0, \sigma^2e$).

Individual breed group regression coefficients were computed and compared and in cases where the difference among slopes was not signifi~~ic~~ant ($P > 0.05$) the common regression coefficient was used for adjustment. However if the difference among slopes was significant, adjusted means were computed using the appropriate breed group regression but not statistically tested for signficance. Duncan's multiple range test (Steel and Torrie, 1980) was used to test the significant differences between adjusted means.

RESULTS

In Table VII.1 are presented the analyses of covariance for muscle groups regressed on TSB. No significant breed type differences were found in the regressions of muscle groups G_2, G_3, G_6, G_7 and G_9. At the same TSB there were significant differences among breed types ($P < 0.01$) in adjusted muscle weight in G_2, G_3, G_6, G_7 and G_9. DM had more muscle in G_3, G_6 and G_7 than both HE and SY which did not differ from each other in this respect. However, for muscle in G_9 all breed types differed significantly.

Breed type had a differential effect on the relative growth rate of muscle relative to TSB in G_1, G_4, G_5, G_8, G_{10} and G_{11} (between slopes were significant). Relative to TSB, the DM bulls had a higher growth rate in all above mentioned muscle groups than did the HE and SY bulls.

Coefficients of variation (CV%) of muscle groups when adjusted to TSB ranged from 9.6-18.7% (Table 1); the lowest coefficients were found in the early maturing muscle groups of the distal limbs, while the highest coefficients were found in the late maturing muscle groups (i.e. G_4, G_9, G_7 and G_8).

Analysis of covariance (Table VII.2) showed no significant differences between breed types in the regressions of all muscle groups on the associated bones in the same anatomical region. As P+F increased the relative amount of muscle in G_1 remained relatively constant ($b = 1$; $P > 0.05$); as tibia increased the relative amount of

Table VII.1. Growth Coefficients (*b*) and Adjusted Means for Weights of Muscle Groups Relative to Total Bone in the Side (X)[1]

Muscle group[2]	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV%	Adjusted antilog Means (kg)			F-Values	
	b*	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
G_1	0.960	0.09	0.958	0.11	**1.333**	0.12	1.132	0.07	11.2	25.80	27.86	32.48	4.35*	—
G_2	0.892	0.11	0.826	0.08	1.113	0.09	0.974	0.06	9.6	3.61a	3.89b	4.07b	2.92	6.85**
G_3	1.157	0.09	0.971	0.11	**1.273**	0.11	**1.153**	0.06	11.1	11.25a	11.94a	13.93b	2.16	17.24**
G_4	1.109	0.17	0.884	0.18	**1.469**	0.18	1.206	0.11	18.7	9.22	9.23	11.46	3.17*	—
G_5	1.056	0.10	1.040	0.12	**1.435**	0.11	**1.227**	0.07	11.5	11.34	11.88	14.15	4.47*	—
G_6	0.917	0.09	0.860	0.08	1.104	0.11	0.986	0.06	9.9	2.04a	2.17a	2.34b	2.03	9.05**
G_7	1.125	0.11	1.125	0.18	**1.506**	0.15	**1.301**	0.09	16.4	9.44a	10.15a	12.13b	2.33	11.81**
G_8	**1.296**	0.10	1.210	0.18	**1.724**	0.14	**1.468**	0.09	15.1	5.37	5.75	7.15	4.08*	—
G_9	1.236	0.16	1.217	0.20	**1.582**	0.14	**1.390**	0.10	17.5	10.87a	11.71b	13.08c	1.72	5.34**
G_{10}	1.018	0.09	0.962	0.11	**1.316**	0.11	**1.139**	0.06	10.6	37.06	39.81	46.46	3.79*	—
G_{11}	1.026	0.09	0.980	0.11	**1.342**	0.11	**1.158**	0.06	10.5	48.41	51.70	60.63	4.13*	—

* Growth coefficients in bold type are significantly different from 1 at $P < 0.05$.
Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.

[1] Adjusted to geometric mean TSB = 17.80 kg along the slope of common regression line.

[2] Muscle groups as defined in the text.

— Missing values mean covariance analysis was not legitimate.

* $P < 0.05$. ** $P < 0.01$.

Table VII.2. **Growth Coefficients** ***(b)*** **and Adjusted Means of Muscle Groups on Appropriate Bones**[1]

Dependent Variate (Y)	Independent Variate • (X)	Hereford		Beef Synthetic		Double Muscled		Common		Residual CV %	Adjusted Means Antilog (g)''			F-Values	
		b[+]	S.E.	b	S.E.	b	S.E.	b	S.E.		HE	SY	DM	Among slopes	Among adjusted means
G_1	**P+F**	1.035	0.10	0.891	0.12	1.121	0.15	1.036	0.07	14.3	25191a	27329b	33915c	0.88	19.78**
G_2	**Tibia**	1.236	0.15	1.001	0.10	0.927	0.23	1.002	0.11	16.2	3792	3867	3899	0.54	**0.12**
G_3	**LUMTHV**	**0.790**	0.09	0.711	0.14	1.004	0.12	**0.862**	0.06	15.4	11303a	12275ab	13477b	1.77	**6.16****
G_5	**S+H**	1.171	0.10	1.069	0.12	**1.378**	0.11	**1.245**	0.06	11.1	11306a	11957a	14096b	2.43	**18.35****
G_6	**RU**	1.107	0.12	0.903	0.09	1.246	0.13	1.100	0.07	10.3	2050a	2148a	2347b	2.69	7.63**
G_{10}	**PFLTHV**	1.034	0.09	0.881	0.12	1.151	0.12	1.022	0.07	12.6	36467a	39714b	47322c	1.89	18.91**
G_{11}	**PFLTHVSH**	1.002	0.09	0.939	0.11	1.225	0.11	1.093	0.06	11.8	47734a	51658b	61533c	2.26	21.40**

[+] Growth coefficients in bold type are significantly different from 1.0 at $P < 0.05$.

— Missing values mean covariance analysis was not legitimate.

[1] Adjusted to geometric mean of P+F = 4024 g, tibia = 1236 g, LUMTHV = 2449 g, S+H = 2571 g, RU = 1098 g, PFLUMTHV = 6490 and PFLUMTHVSH = 9067 g, along the slope of common regression line.

[2] Muscle and bone groups as defined in text

Adjusted means in a row bearing different superscripts differ significantly at $P < 0.05$.

• $P < 0.05$; ** $P < 0.01$.

muscle in G_2 remained relatively constant ($b = 1$; $P > 0.05$); as LUMTHV increased the relative amount of muscle in G_3 decreased ($b < 1$; $P < 0.05$); as S+H increased the relative amount of muscle in G_5 increased ($b > 1$; $P < 0.05$) and as radius *et* ulna increased the relative amount of muscle in G_6 remained relatively constant ($b = 1$; $p > 0.05$).

At standard bone weights in the respective regions, DM exceeded HE and SY in muscle weight in G_1, G_3, G_5, G_6, G_{10} and G_{11} (Table VII.2). At the same LUMTHV, DM bulls were significantly greater than HE for muscle in G_3 but did not differ from SY in this respect.

In Table VII.3 are presented muscle:bone ratios in different anatomical regions in HE, SY and DM. Within a breed type, muscle:bone ratio varied with anatomical region, generally it tended to be high in the thicker parts of the carcass i.e. G_1 and G_5 and it tended to be low in the distal parts of both limbs. DM had higher muscle:bone ratios in all anatomical regions. Superiority of DM in muscle:bone ratio over HE and SY, respectively was most pronounced in the proximal hindlimb (24 and 35%) followed by the proximal forelimb (17 and 25%), thorax to forelimb (22%) and back and loin (10 and 20%). Less hypertrophy was found for the distal forelimb (5 and 11%) and least for the distal hindlimb (3%).

Table VII.3. **Muscle:Bone Ratios and Hypertrophy Ratios by Breed Groups**

	Muscle:bone ratio[+]			**Hypertrophy ratios**[++]	
	HE	SY	DM	**DM/HE**	**DM/SY**
Proximal Hindlimb	6.3	6.8	**8.4**	**1.35**	**1.24**
Distal Hindlimb	3.1	3.1	**3.2**	**1.03**	**1.03**
Back and Loin	4.6	5.0	**5.5**	**1.20**	**1.10**
Proximal Forelimb	4.4	4.7	5.5	**1.25**	**1.17**
Distal Forelimb	1.9	2.0	2.1	**1.11**	**1.05**
Expensive Region[1]	5.6	6.1	7.3	**1.30**	**1.20**
Expensive Region[2]	5.3	5.7	6.8	**1.28**	**1.19**
Total Side[3]	5.3	6.0	7.3	**1.36**	**1.22**

[+] Muscle group weights adjusted to equal bone in the respective region.

[++] Muscle:bone ratio of **DM** divided by muscle:bone ratio of **HE** and **SY**, respectively.

[1] Proximal hindlimb and back and loin.

[2] Proximal hindlimb, back and loin and Proximal forelimb.

[3] At 220 kg DSW.

DISCUSSION

Since muscular growth is assumed by many workers to be dependent on bone growth it was of interest to see to what extent this supposition is true. Results of the present study showed that, relative to total bone, breed types differed significantly in the growth rate of muscles in areas which exhibited gross muscular hypertrophy (i.e. muscles of the proximal limbs) with DM having higher growth rate than the more normal breed types. Figure VII.1 illustrates the increase of muscles in the proximal hindlimb with increasing bone by breed type. In DM, growth coefficients for muscle groups other than those of the distal limbs indicated that muscle increased in weight at a proportionately faster rate than bone, while in HE and SY they increased in proportion to bone. It becomes fairly clear that superior muscling in DM animals is manifested primarly by the proportionately greater growth rate of muscle in those anatomical regions which contained large proportions of muscle to bone compared to those anatomical regions which contained relatively small proportions of muscle to bone.

Studies have shown that in DM the regions which exhibit gross muscular hypertrophy were the same as those which showed bone hypotrophy (Hanset and Ansay, 1972 and the present study). In Chapter VI it was found that the effect of the 'Double Muscling' on bone growth and distribution was mainly in the limb, and the hypodevelopment of bones in the

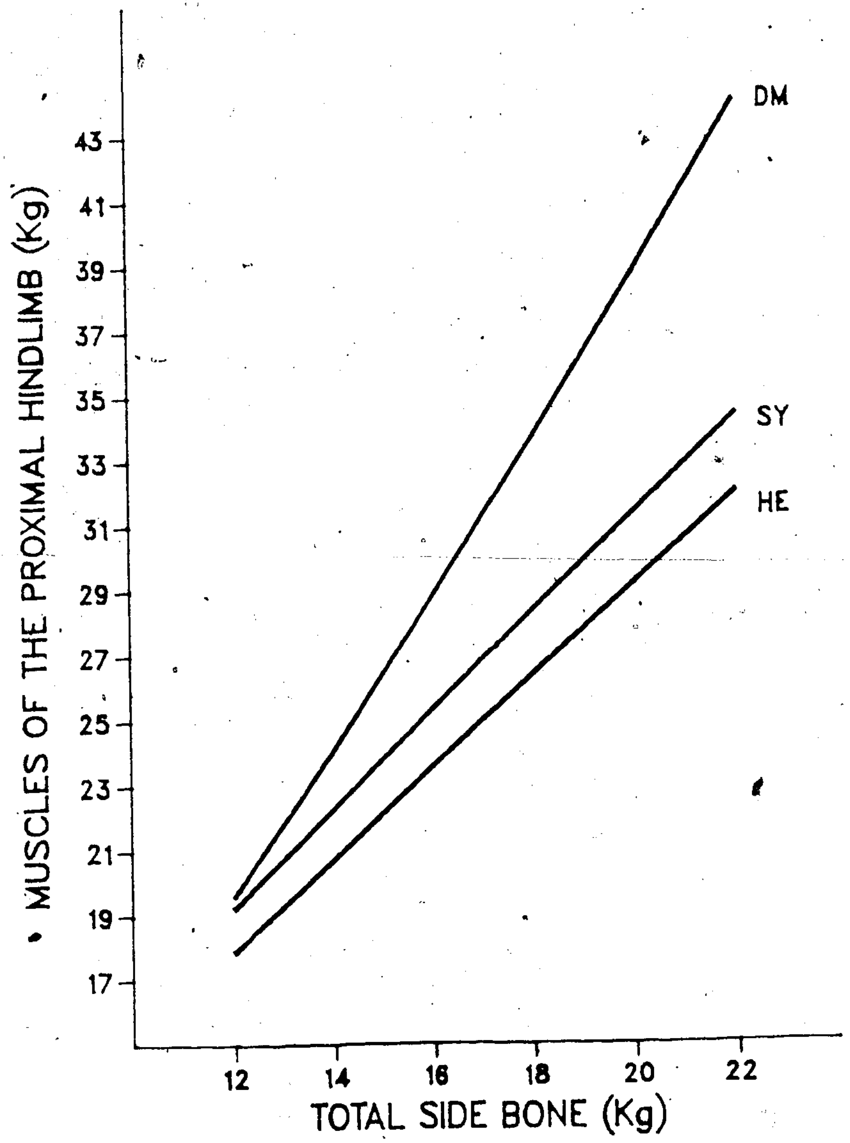


Figure VII.1. Increases of muscles in the proximal hindlimb with increasing total bone in three groups of young bulls.

muscular hypertrophied animals followed a disto-proximal gradient which was most pronounced in the proximal hindlimb (femur and Os coxae). The hyperdevelopment of muscle and the hypodevelopment of bone in the same region lead some workers (Berg and Butterfield, 1976) to believe that the growth of muscle is independent of that of bone. It may be argued that the relatively lower proportion of bone in the proximal hindlimb in DM might be related to rapid growth rate of muscle in this area (i.e. to some extent excessive muscle growth in this anatomical region may interefere with growth of bone rather than reflecting weight-bearing). However, the differences between DM and the more normal breed types could be related to differences in the centres of gravity and weight distribution. Wise (1970) with poultry reported that increased stress on bones might arise as a result of increasing skeletal loading or as a result of alterations in the normal pattern of body weight distribution.

In the present study the pooled within-group coefficient of variation (a component of variance which is not being explained by the regression of muscle groups on total side bone) ranged from 10 to 19%. These relatively high coefficents suggest that there are other factors which might have influence on muscle growth relative to bone growth or that muscle growth is somewhat independent of bone growth. This agrees with the concept of Butterfield (1976) and makes suspect the belief that animals must possess large bones in order to produce large muscles.

Hammond (1932) pointed out that the growth of muscles varied with age and he suggested that these variations in growth might be due to changes in the relative points of attachment as a consequence of differential rate of growth in the bone and to alteration in the relative proportions and angles of bones. Also, he has shown muscle length to be earlier maturing than muscle thickness or width, also studies have shown that bone weight or dimensions are earlier maturing than muscle weight and dimensions.

Stewart (1972) suggested that in early stages of development, increases in bones length produce increases in passive tension on muscles or in other words in early stages of developement passive tension is the principal factor in stimulating muscle growth while in post-natal phases of growth active tension is the more important factor. Berg and Butterfield (1976) concluded that in the ante-natal phase of growth, differential muscle growth is probably stimulated by passive tension from skeletal elongation, while in the immediate post-natal, pre-pubertal and adolescent phases functional demand imposed on muscle is the most important factor stimulating muscle growth.

In order to find to what extent the relation between increases in muscle and bone weight in specific regions are dependent or independent, bone weight was used as a covariate. Breed types did not differ significantly in growth rate of *m. semimembranosus* and *m. semitendinosus* relative to that of femur and *m. infraspinatus* and *m. supraspinatus* relative to scapula (not tabulated). At the same femur weight DM had significantly heavier weight for *m. semimembranosus* and at the same scapula weight DM had significantly heavier weight for *m. infraspinatus* than the more normal breed types (Figures VII.2 and VII.3). In the previous report it was found that DM had significantly lighter femur weight than either HE or SY, but yet they had heavier weight for *m. semimembranosus* and *m. semitendinosus*. It is clear that muscle development does not follow the development of the bone it surrounds. It would appear that muscles of the muscular hypertrophied animals had increased in weight without proportionate increase of bones. It seems that growth of muscle length follows that of bone which is attached to or around it. However, once bone has reached its mature size and dimensions (i.e. growth of bone nearly ceased), growth of muscle size and dimensions might be independent of that of bone and continue with factors other than bone growth having more stimulating effects on muscle growth.

In chapter 2 it was found that at the same total side muscle, there was differential muscular hypertrophy. In the present study at the same total bone, there was general but not uniform muscular hypertrophy, being greater in proximal limbs and lower in distal limbs.

Breeds selected for thickness or for draft usage generally have higher muscle:bone ratios than those selected

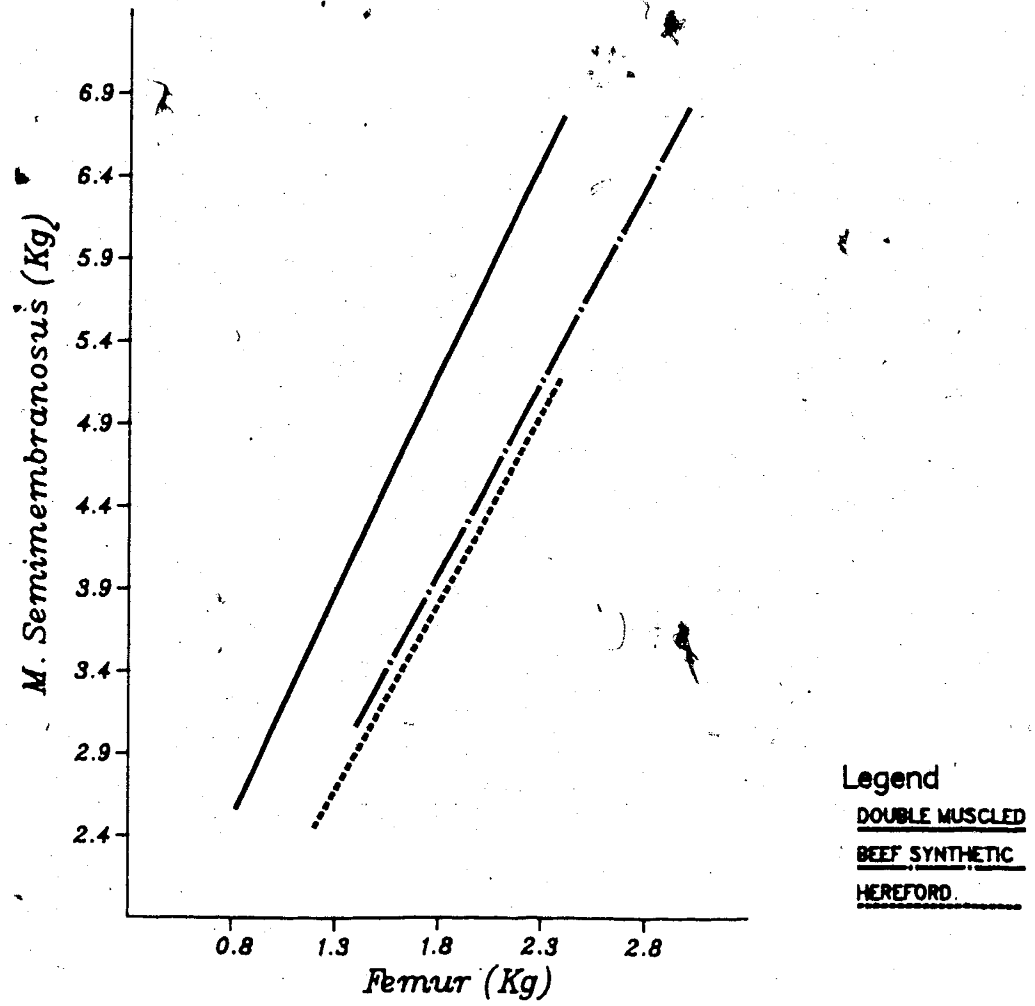


Figure VII.2. Relationship between weights of m. semimembranosus and femur in three groups of young bulls

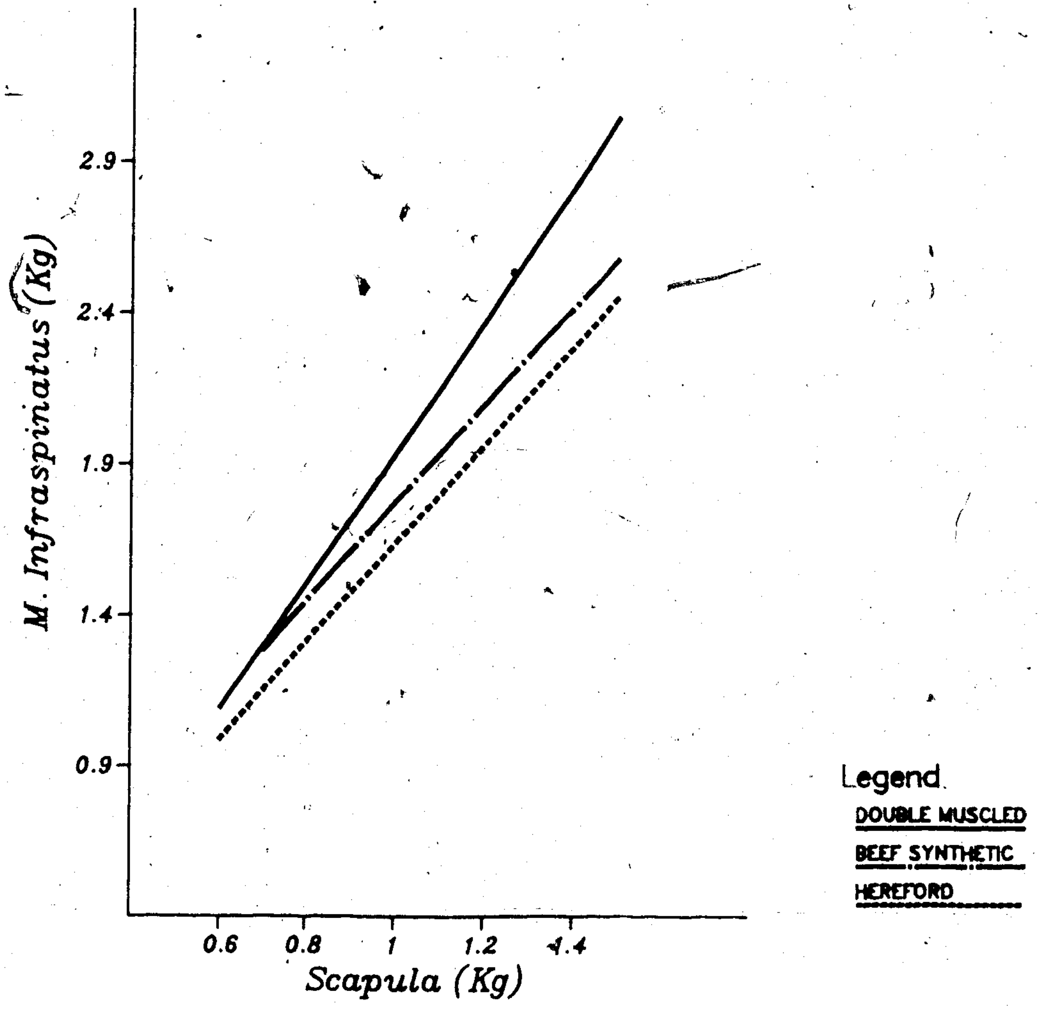


Figure VII. 3. Relationship between weights of m. infraspinatus and scapula in three groups of young bulls.

for dairy characteristics (Berg and Butterfield, 1976). Studies have shown that compared with normal cattle, DM have higher muscle:bone ratios. In normal cattle muscle:bone ratio seldom exceeds 5:1, but in DM it often exceeds 7:1 reaching as high as 9:1 in extreme cases. Similar to results of Hanset and Ansay (1972), in the present study, irrespective of breed type, muscle:bone ratios were highest in the proximal parts of the fore and hind limbs and were lowest in the distal parts of both limbs and the differences between breeds in muscle:bone ratios were most pronounced in the proximal parts of hind and fore limbs and were least pronounced in the distal hindlimbs (Figures VII.4 and VII.5). The 35% higher muscle:bone ratio in the proximal hindlimb shown by DM in the present study is similar to that reported by Boccard and Dumont (1974). DM in the present study were also similar to DM Charolais of Boccard and Dumont (1974) with hypertrophy of 11% and 25% for muscle:bone ratio in the distal forelimb and proximal forelimb, repectively. It is very clear that the higher muscle:bone ratios in DM carcasses is ascribed to a regional as well as a general difference in tissue development.

In summary, relative to total side bone, DM differed significantly from the more normal breed types in the growth rate of muscles in all regions which exhibited gross muscular hypertrophy. The superior muscling in DM animals is manifested primarly by generalized increase in regional muscle growth relative to bone. At equal bone weight in the

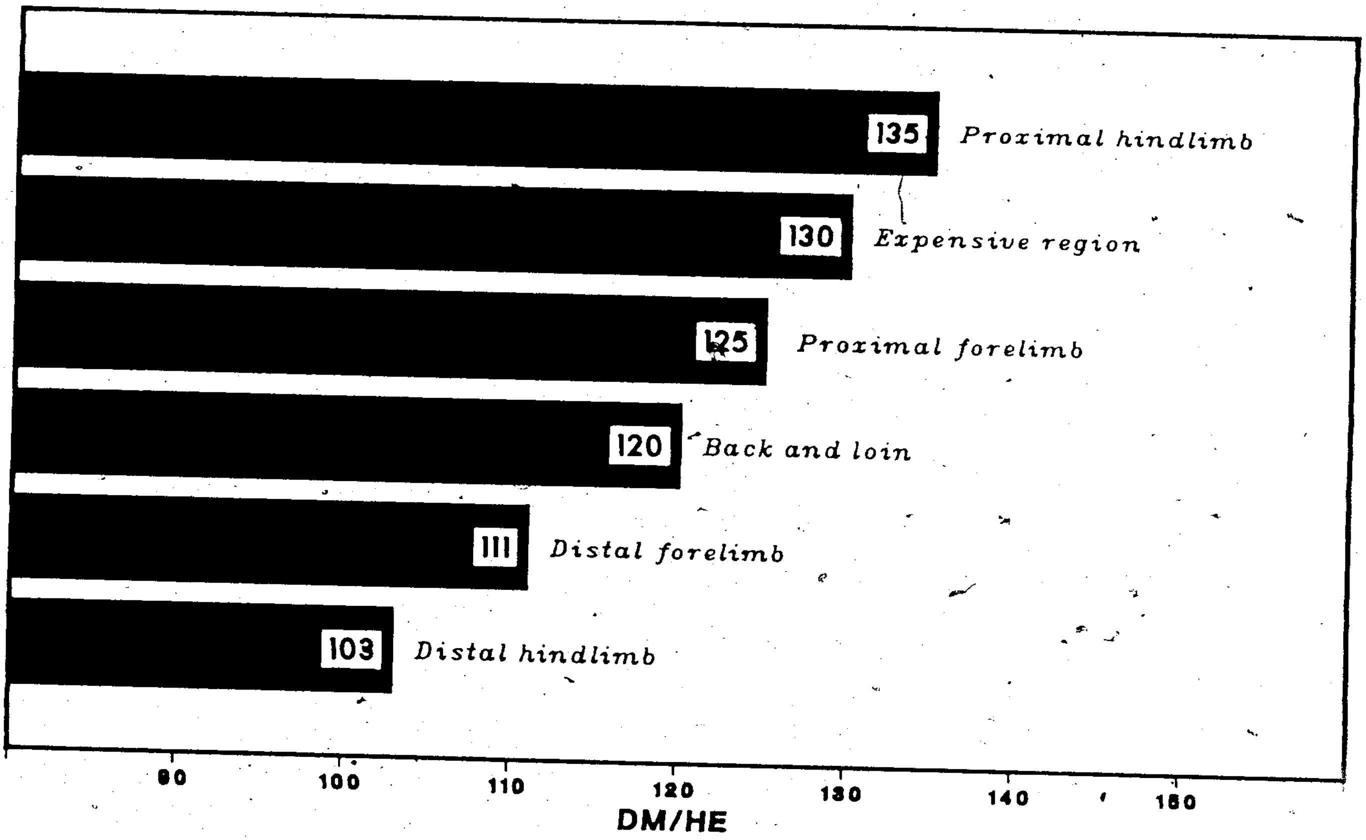


Figure VII. 4. Relative development of muscle:bone ratios by anatomical region in Double Muscled (DM) compared with Hereford (HE) young bulls.

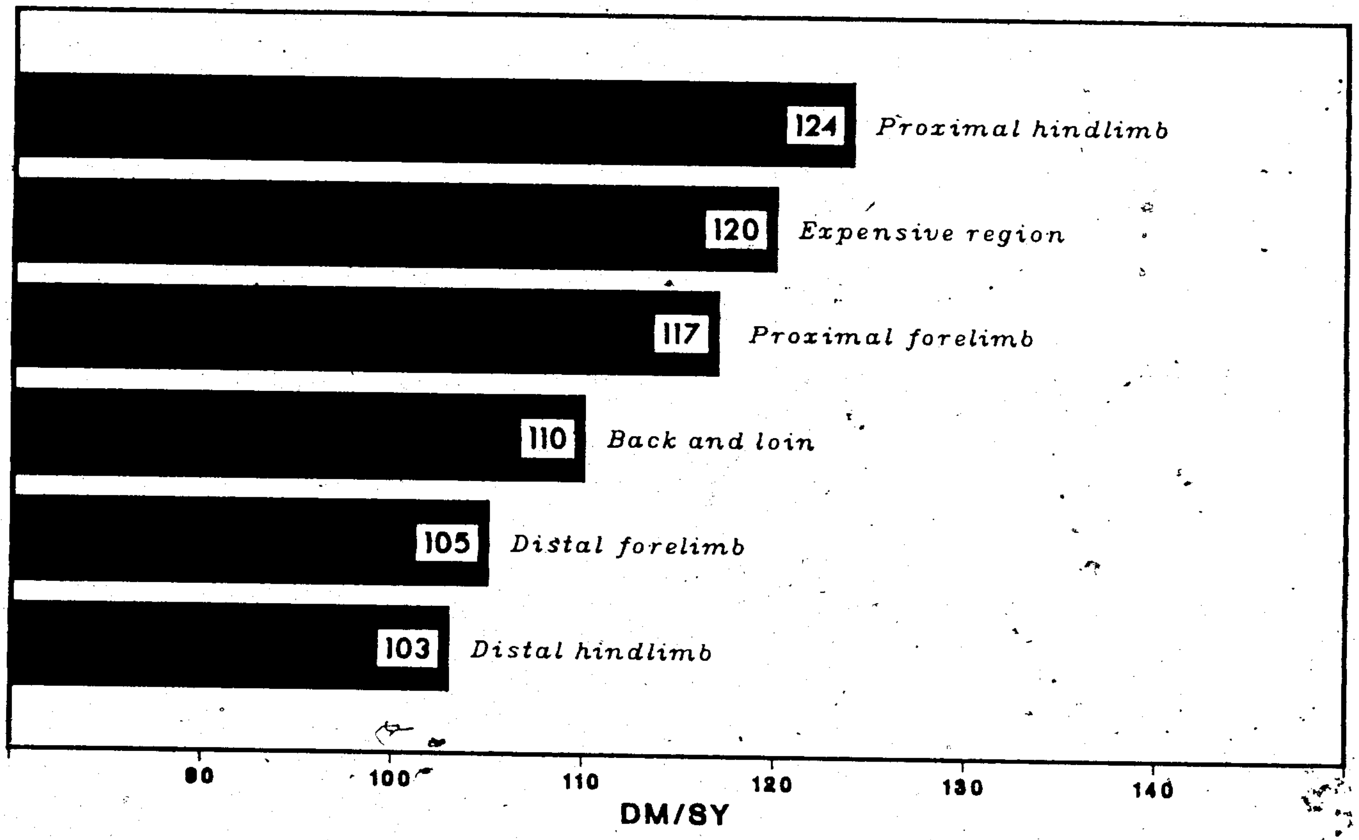


Figure VII.5. Relative development of muscle:bone ratios by anatomical region in Double Muscled (DM) compared with Beef Synthetic (SY) young bulls.

same anatomical region, DM had significantly higher proportions of muscle in the proximal parts of both limbs, back and loin and expensive regions of the carcass when compared to the more normal breed types. In the muscular hypertrophied animals, the regions which showed gross muscular hypertrophy were the same as those which showed bone hypotrophy. Consequently muscle:bone ratios were most visible in these regions, which would suggest that muscles in these animals had increased in weight without proportionate increase of bones, and makes suspect the belief that animals must possess large bones in order to produce large muscles.

SYNTHESIS

Cattle exhibiting extreme muscular appearance express what is known as 'Double Muscling' or muscular hypertrophy which is a genetically controlled character and is quite variable in phenotypic expression. This phenomenon is characterized by spectacular bulging conformation most visible in the caudal part of the proximal hindlimb and in the brachium where muscles appear extremely enlarged. It presents a very interesting model for growth and development of carcass tissues particularly of muscles.

Eighteen **Double Muscled (DM)**, 18 Beef Synthetic (SY) and 18 Hereford (HE) bulls serially slaughtered from approximately 250 to 800 kg live weight were used in this study.

The first study (Chapter I) was designed to investigate the influence of 'Double Muscling' compared to more normal breed types, on growth patterns of carcass tissues and on carcass composition and to develop methods to identify the 'Double Muscling' condition by application of the discriminant analysis technique. It was found that, relative to carcass weight and total bone, DM had much higher growth rates for total muscle than either HE or SY. DM was characterized by a high muscle:live weight ratio, a high proportion of muscle in the carcass, high muscle:bone and muscle:fat ratios and a low proportion of fat compared to more normal genotypes. 'Double Muscling' boosted muscle:bone ratio by 22 and 36 per cent compared to SY and

HE respectively.

Objective criteria to discriminate between HE and DM were **subcutaneous fat, muscle:bone and muscle:intermuscular fat** ratios, and between SY and DM were **TSB and muscle:bone** ratio.

The second study (Chapter II) was undertaken to examine the influence of'Double Muscling' and maturity type on the relative growth patterns and distribution of anatomically defined muscle groups during growth and development. Relative to total side muscle, DM did not differ from the more normal breed types in the rate of muscle deposition in all muscle groups except those surrounding the spinal column. At the same total side muscle, in DM carcasses there were shifts in muscle weight distribution towards the more fleshy, expensive muscles. DM had proportionately less muscle weight in the distal parts of both limbs, and in neck muscles. Differences were more pronounced when comparisons were made at the same dissected side weight than when comparisons were made at the same total side muscle. This is a reflection of the generally higher proportion of muscle in the carcasses of DM's compared to more normal breed types as shown in Chapter I.

Muscular hypertrophy revealed an increasing disto-proximal gradient along the limb. The hyperdevelopment of the large superficial muscles of the proximal part (thigh) and the hypodevelopment of the distal part in the hindlimb gives the DM animal the typical 'bottle thigh' appearance.

In Chapter III growth patterns and distribution of individual muscle weights of DM's are examined and compared with more normal breed types. Breed types differed significantly in the relative growth rate of 5 of the 95 muscles and in adjusted mean weights of 33 of the 95 muscles. Compared with more normal breed types, DM had quite different muscle weight distribution. In DM carcasses there were shifts in muscle weight distribution towards the more fleshy, luxury, multidimensional thick muscles. DM had proportionately less muscle weight in the distal muscles of both limbs, deep muscles, and neck muscles. Muscular hypertrophy tended to increase from inner to outer muscle layers. Also, fat depots hyoptrophy tended to increase from inner to outer depots (i.e. subcutaneous fat hypotrophied more than other depots, Chapter IV). The lack of subcutaneous fat especially over the hindquarter along with excessive muscular development in this area is responsible for the externally visible grooves on intermuscular septa.

In the present study 'Double Muscling' had a greater hypertrophic effect on those muscles that crossed more than one joint than on those that crossed only one joint. However, it should be mentioned that muscles with a high proportion of red fibers usually unite adjacent segments of the limb, while muscles with a high proportion of white fibers often pass over one or more joint.

In the proximal hindlimb, the lateral and medial thigh muscles were better developed in DM, while the cranial thigh muscles were poorly developed in DM as compared with the more normal breed types. The relatively lesser development of the cranial thigh muscles could be related to a smaller femur in DM. It should be mentioned that of the cranial thigh muscles *m. quadriceps femoris* is the most powerful extensor of the stifle joint; if this muscle is non-functional the limb collapses. This supports the contention of Oliver and Cartwright (1968) that Double Muscling was detrimental to range cattle, because it affected the animal's ability to walk long distances.

Compared with the more normal breed types, DM had proportionately less weight in the muscles associated with respiration (i.e. *mm. intercostales interni et externi*), but at the same time, they had proportionately more bone weight in the ribs. It may be argued that the relatively heavier ribs in DM could be due to compensatory hypertrophy, since in DM there is a reduction in muscles associated with respiration, and the increasing physiological demands for respiration led to hypertrophy of ribs.

Chapter IV was undertaken to determine the influence of maturity type and 'Double Muscling' in cattle, on the fattening patterns, fat partitioning among the depots and distribution of fat throughout the carcass as growth and development proceeds. Relative to total fat, DM did not differ significantly from the other maturity types in growth rates of subcutaneous fat, intermuscular fat and carcass cavity fat, but relative to fat percent in the side DM tended to have much lower growth rates for subcutaneous fat and carcass cavity fat. At equal total side fat, HE tended to partition more of their fat to the subcutaneous depot, whereas DM and SY tended to partition more of their fat to the intermuscular and carcass cavity fat depots. Relative to HE, DM followed late developing fat partitioning patterns.

In Chapter V as fattening proceeded, fat partitioning index { subcutaneous fat/(intermuscular fat + carcass cavity fat) } increased, with HE having a higher fat partionining index than either SY or DM. Principal component analyses were applied to derive an index of fat partitioning independent of fatness. After the effect of fatness had been removed HE still had the higher multivariate fat partitioning index than either SY or DM, which would suggest that fat partitioning among the depots is breed specific even after either fatness or mature size influences are removed.

Chapter VI was designed to investigate the consequences of 'Double Muscling' on bone growth patterns and distribution as well as on interrelationships among skeletal constituents. Relative to total side bone, breed types tended to have similar growth coefficients for all bone or bone groups except the vertebral column where HE tended to have a higher growth coefficient than either SY or DM. At the same total side bone, compared with the more normal breed types, in DM carcasses there were shifts in bone weight distribution towards the thoracic region. DM had proportionately less bone in the proximal hindlimb. There was general but not uniform bone hypotrophy when comparisons were made at the same total muscle weight, but when comparisons were made at the same total side bone weight, there was differential and localized bone hypotrophy and the hypodevelopment of bones in the muscular hypertrophied animals followed a disto-proximal gradient which was most pronounced in the pelvic limb.

Chapter VII was designed to assess the influence of bone growth on muscle growth and bone-muscle relationships in Double Muscled and more normal cattle. Relative to total side bone, DM differed significantly from the more normal breed types in the growth rate of muscles in all areas which exhibited gross muscular hypertrophy. The superior muscling in DM animals is manifested primarly by generalized increase in regional muscle growth relative to bone. At equal bone weight in the same anatomical region, DM had significantly higher proportions of muscle in the proximal parts of both limbs, back and loin and expensive regions of the carcass when compared to the more normal breed types. In the muscular hypertrophied animals, the areas which showed gross muscular hypertrophy were the same as those which showed bone hypotrophy. Consequently muscle:bone ratio differences were most marked in these regions, which would suggest that muscles in these animals had increased in weight without proportionate increase of bones, and makes suspect the belief that animals must possess large bone in order to produce large muscles.

General observations from Chapters II, and VI indicate that at lighter weights of total bone, DM had more weight of the vertebral column than HE, but at heavier weights of total bone, HE was heavier. Interestingly, muscles surrounding the spinal column behave in the same way. These similarities in muscle and bone distribution in back and loin might imply functional peculiarities among breed types.

RETROSPECT AND PROSPECT

Grading System

Under the current Canada grading system extremely lean carcasses are penalized (downgraded to B or C or E, Appendixes 2 and 3). It is apparent that grading tends to give a premium to the relatively fatter carcasses which is associated with relatively lower proportion of muscle but higher proportion of fat. Similarly Kieffer and Cartwright (1980) reported that the relatively lower fat proportion in the DM animals prevents the carcass from grading in the choice and prime USDA grades. If Double Muscled cattle are to be introduced into the beef industry, then, a special grade and cutting system is needed for heavy muscling carcasses.

Calving Difficulties

Each segment of the beef industry has its own particular requirements, the butcher wants the maximum of muscle and the minimum of bone in the carcass, while the breeder must avoid an animal with too much muscle and too fine bone because of the poor overall fitness and increasing calving difficulties associated with these traits (Lauvergne *et al.*, 1963; Vissac *et al.*, 1973; Mckellar and ouhayoun, 1973; Hanset and Jaudrain, 1979).

In some countries i.e. Italy, Belgium and France, Double Muscled cattle are sought after by sectors of the beef industry, but in the North America they are avoided. One of the limiting factors in the propagation of Double

Muscled cattle is calving difficulty. To utilize the advantages of 'Double Muscling', we will have to select specialized lines, some for terminal crossing (slaughter animals), while for breeding females we will have to select for calving ease or against calving difficulties. Double Muscled sires may be used on mature small cows which are known to calve easily. If we accomplish that, we will retain the advantages of 'Double Muscling' while at the same time avoiding its major drawback.

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APPENDIX I
COMPUTATION OF DISCRIMINANT FUNCTION

$$\begin{array}{cccc} \text{Within groups covariance matrix (dispersion)} & \text{Weighting coefficients} & & \text{Vector of mean differences} \\ \begin{bmatrix} W_{11} & W_{12} & \ldots & W_{1n} \\ W_{21} & W_{22} & \ldots & W_{2n} \\ \ldots & \ldots & \ldots & \ldots \\ W_{n1} & W_{n2} & \ldots & W_{nn} \end{bmatrix} & \begin{bmatrix} a_1 \\ a_2 \\ \cdot \\ a_n \end{bmatrix} & = & \begin{bmatrix} d_1 \\ d_2 \\ \cdot \\ d_n \end{bmatrix} \end{array}$$

or in matrix notation

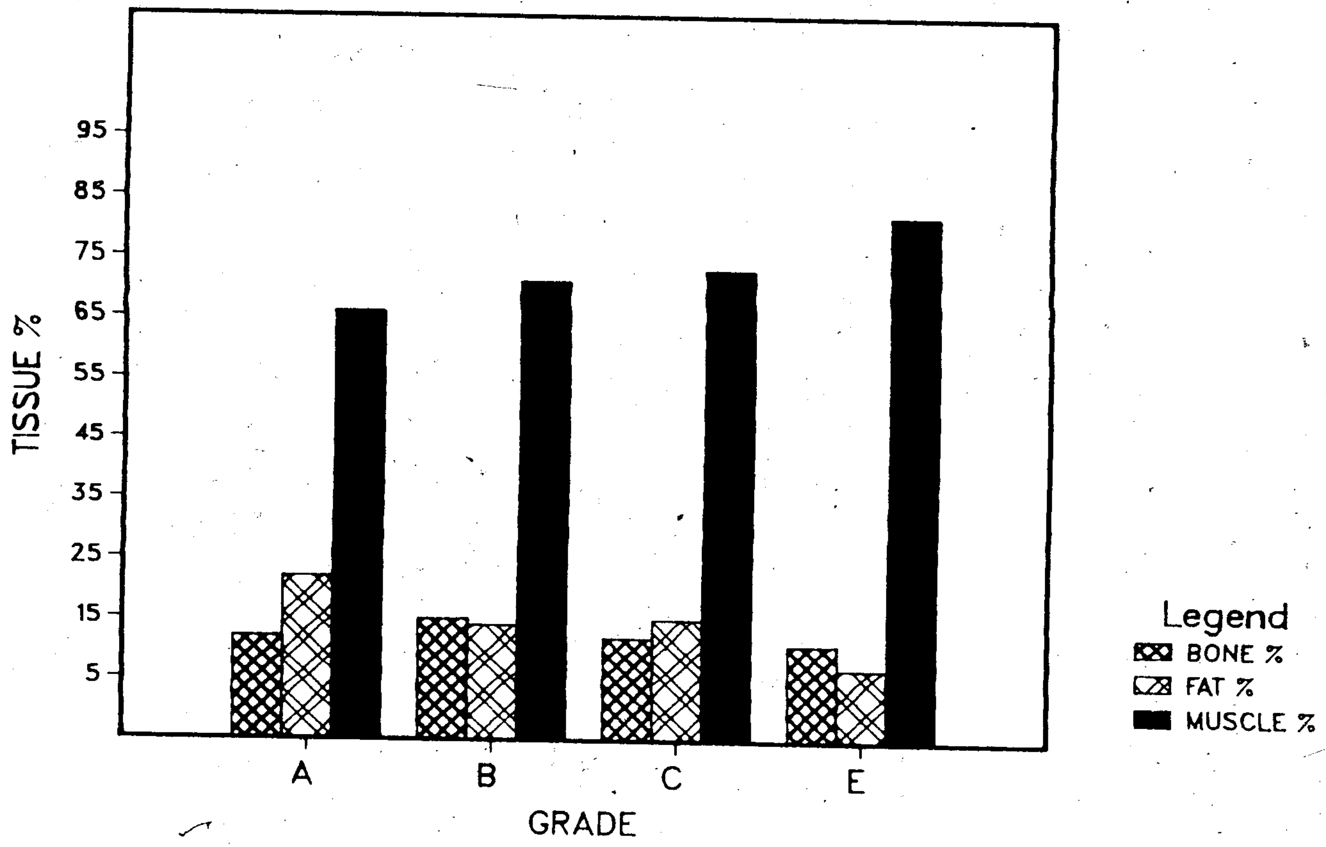
$Wa = d$ (1)

The vector a can be obtained by premultiplication of both sides by W^{-1}

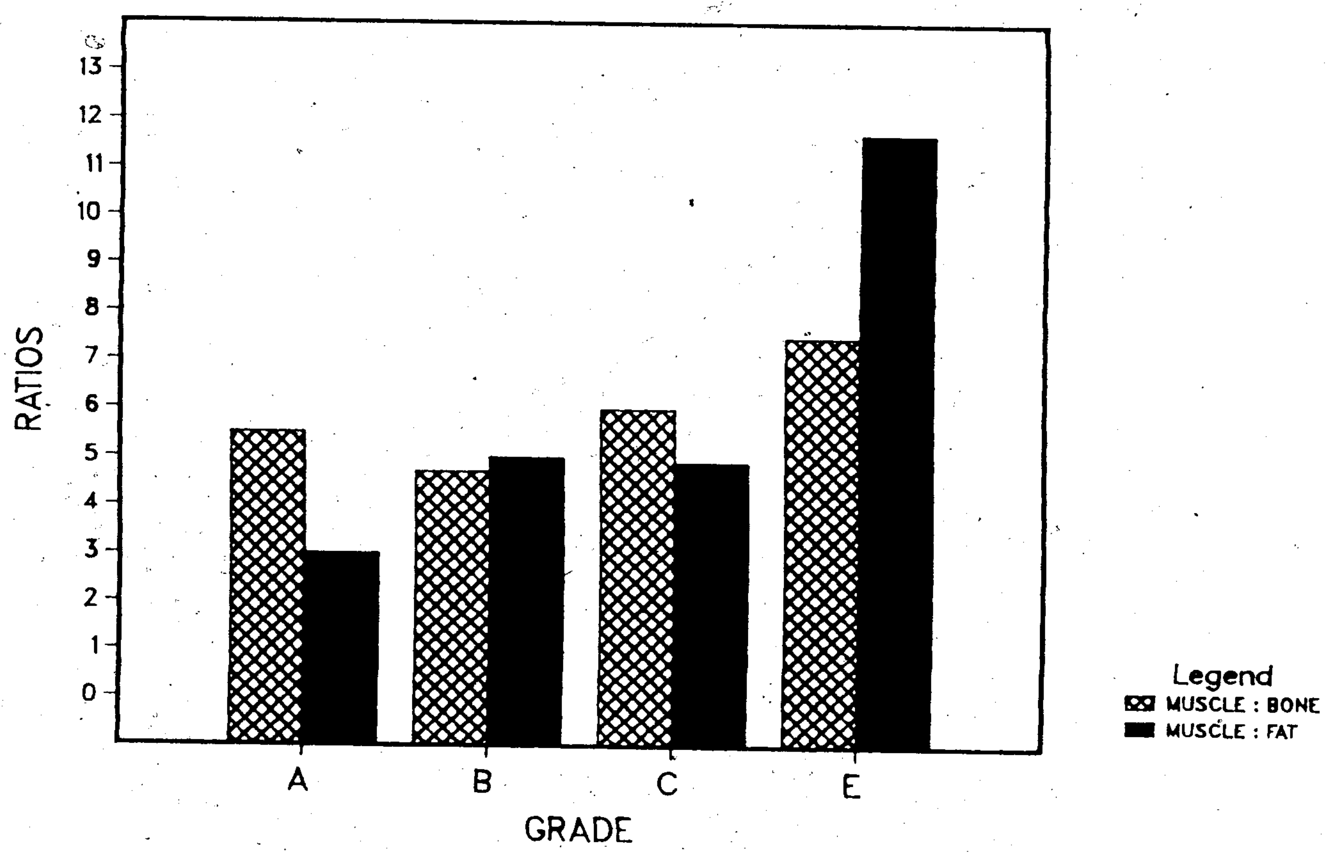
$a = W^{-1}d$ (2)

Where W^{-1} is the inverse of the within-group variance-covariance (dispersion) matrix and d is the vector of mean differences.

Standarized canonical discriminant function coefficients can be obtained by multipling each coefficient by the standard deviation of the particular variable to which the weight is applied.



Appendix 2. Grades and percentage of carcass composition.



Appendix 3. Grades and muscle:bone ratio and muscle:fat ratio.