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Foreword by St C. S. Taylor

SYDNEY UNIVERSITY PRESS



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Original Publisher SYDNEY UNIVERSITY PRESS University of Sydney 1976, ISBN 0 424 00002 4

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Ithaca, NY March 2005

SYDNEY UNIVERSITY PRESS Press Building, University of Sydney UNITED KINGDOM, EUROPE, MIDDLE EAST, AFRICA, CARIBBEAN Prentice/Hall International, International Book Distributors Ltd Hemel Hempstead, England

National Library of Australia Cataloguing-in-Publication data

Berg, Roy Torgny
New concepts of cattle growth/ [by] Roy T. Berg
[and] Rex M. Butterfield.—Sydney: Sydney University
Press, 1976.
Index.
Bibliography.
ISBN 0 424 00002 4.

1. Cattle-Physiology. I. Butterfield, Rex Milton, joint author. II. Title.

636.208

First published 1976 © Roy T. Berg and Rex M. Butterfield 1976

This book is funded by money from THE ELEANOR SOPHIA WOOD BEQUEST

Printed in Australia by Macarthur Press, Parramatta

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FOREWORD

Animal growth is a vast subject. In its present stage of rapid development, a severe limitation of subject matter is essential for clear presentation in one volume. Contained within this book is a very direct and well integrated account of the growth of fat, muscle and bone, in which patterns of growth, changes in chemical composition, muscle weight distributions, and the influence of nutrition, breed and sex are all clearly and vigorously described.

Throughout the 7,000 years that cattle have been part of man's social development, their growth has remained largely a mystery. Significant experimental studies concerned with beef production began possibly about fifty years ago. The results that have accumulated since then—many of them contributed by the authors themselves—have now been brought together in this book, making it an excellent source of factual information and reference. The book is predominantly about cattle. The section on muscle growth, however, includes new results on several other species, and many of the conclusions and ideas discussed are of considerable relevance to animal growth generally.

It is a privilege to write this brief foreword and I take the opportunity of expressing open appreciation of the authors' rare blend of enthusiasm and dedication which has produced a very useful, vivid, absorbing and 'meaty' description of growth that will greatly aid and stimulate the continuing development towards more knowledge and perhaps more production also.

ARC Animal Breeding Research Organization, ST C. S. TAYLOR Edinburgh

PREFACE

Growth is a fascinating process. Understanding its intricacies has been the quest of many scientists and laymen alike. An animal starting from a single fertilized egg, through division and differentiation, grows and develops into a complex unit, capable of carrying out all of life's functions—obtaining and utilizing food, surviving nature's stresses and reproducing to continue the species. Animals in their adaptation to particular conditions of life have developed a form and function uniquely suited to survival and reproduction under the natural conditions to which the species has been exposed during its evolution.

Man, first as a hunter then as a herdsman, has utilized animals as a source of food. As a herdsman—more specifically as a breeder—man has attempted to mould the form of domestic animals better to satisfy his wants for a more desirable food product. In so doing he may have impinged on the functional characteristics developed over centuries of natural selection. A study of growth in any domestic species must include consideration of the implications of altering form and composition on functional efficiency. It is our hope in this book, in elucidating a few of the intricacies of growth and of its possible control and direction toward utilitarian goals, also to present guidelines by which functional efficiency may be retained.

Beef is produced by the growth of body tissues of cattle. An understanding of how cattle grow may lead to methods for manipulation of the process toward improved efficiency or a more desirable product. Beef is a commodity which is sought by consumers, not because they are conscious of its protein content, or of any special food value, but because it has particular eating qualities. The demand for beef is rising in many countries of the World as the level of disposable income rises. There seems to be every indication that as long as consumers can afford beef they will continue to eat it.

In manipulation of the growth process in cattle toward goals of greater efficiency, we must be cognizant of the character of beef which makes it desirable to consumers and this basic character must be retained. There may be a fair degree of leeway in altering carcass composition without affecting the basic characteristics of beef, for

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there is currently a wide range of carcass types which are each regarded as optimum in various parts of the World. Cultural traditions, habits and personal tastes affect the kind of beef consumers seek. The amount and distribution of fat influence the desirability of beef but this varies for different countries and cultures. Where some fat is desired there is often a roughly defined optimum, levels in excess of which render the product less acceptable. Excess fat also affects the yields of saleable beef sought by the butchering trade as it often represents a trimming loss in processing. Amount of fat desired in a carcass may evolve to a fairly critical optimum dictated by a balance between trimming losses to the butcher and eating satisfaction to the consumer.

All adult cattle produce beef of some type at slaughter irrespective of their classifications as 'beef', 'dairy' or 'draft' animals; irrespective of age, sex or fatness. Hence the beef produced is a highly variable product, according to how these many factors affect the process of growth of the muscle, fat and bone, which are the three major tissues of beef, and how they affect the particular qualities of the two edible tissues, muscle and fat. It is entirely possible that the great demand for beef is in part related to the variety of the product as influenced by age, sex and fatness as well as by the variety which results from preparation of distinctive products from different parts of the carcass.

Many of the changes which people would like to see in beef cattle are unlikely to be achieved. As Vaughan (1939) said, 'the beef calf is "born wrong" from a beef standpoint and no known method of feeding and management can correct its deficiency'. What we must realize is that the animal body, be it cattle or horse or giraffe, has evolved to grow in such a manner that it is functionally efficient. As Goss (1964) put it: 'Since structures without function persist during evolution only at the risk of reducing an organism's general efficiency, there is little chance that mechanisms of growth regulation which are independent of functional considerations would have sufficient selective advantage to survive'.

Of course, we can thwart the normal evolutionary changes which are aimed at the maintenance of functional efficiency, and by artificial selection we can perpetuate some most inefficient monstrosities, such as is the peculiar delight of the dog fanciers in many breeds. However, this perpetuation of a functionally inefficient animal seems to have little place in the cattle industry, the survival of which as a producer of beef within the economic reach of sufficient consumers is surely linked with animals which are adapted to the conversion of inexpensive feeds into muscle.

There may be a place for specialized production from such immobile genetic deviants as the 'Culard' or double-muscled animal to supply a special high-priced market, just as there is a place for limited numbers of animals with a tendency to become grossly overfat. However, these should not distract us from the mainstream of beef production which will come from animals capable of harvesting the cheaper feeds. Such a role will not be possible if our animals do not retain a functionally efficient body capable of considerable mobility and also capable of calving unaided on open range.

Changes in body composition towards what has been accepted as 'meat-type' conformation of the last few decades have undoubtedly increased the problems of calving. The extreme again is the 'Culard' where hysterotomy (Caesarian Section) is necessary in all births, at least in some breeds. Such a procedure may be justified for the production of sires used for a terminal cross, but it will have little place in the normal scene of cattle production. It may well serve as a warning of the balance between function and production which must be maintained if one is to select for increased muscle development.

The publication of a monograph by a geneticist and an anatomist may be seen by some as an unusual undertaking as few have seen a relationship between the philosophies and activities of the two disciplines. However, John Hammond was well aware of the need for such a relationship when he stated in 1932:

The Animal Breeder requires of the comparative anatomist not only a descriptive statement of what has been done in evolution, but also an indication of how he can best produce the form he requires; it is clear that it is in experimental anatomy, or the physiology of anatomy that the solution of these problems will be found.

In 1964 Roy Berg, while on sabbatical leave in Australia, realized the value of the anatomical techniques which he saw being used by Rex Butterfield for the assessment of progress in genetic improvement in cattle.

It became obvious early in the association that each could benefit from the special training of the other to bring about effective utilization of anatomical techniques for assessment of genetic potential and progress in meat animal breeding, and particularly in cattle breeding. So an association began which has resulted in the accumulation of a large amount of information resulting from analysis of total dissection data obtained by a single dissection technique in both Australia and Canada.

In this present undertaking we have brought together the findings from our own studies, supplemented by the information supplied by colleagues around the world, either in published work or in personal communications in an attempt to give a new appreciation of the process of growth and the importance of its understanding to cattle production.

In the 1930s Hammond stimulated a great deal of enquiry into the growth phenomena of meat animals, and it is a tribute to the extent of his influence that since then, until recently, few have been keen to take the studies further. Over the last few years a great deal of interest has been rekindled and it seems to us that it is time to attempt to coordinate some of the old and the new into a composite whole, so that some useful synthesis may emerge—for new ideas can contribute to progress only if they are assembled into applicable concepts.

In this monograph we do not attempt to present a review of the literature but rather to extract from it the most relevant aspects of the knowledge of growth in cattle which assist in the formation of functionally sensible concepts. We know that there will be many gaps, some due to inadvertent omission, some due to lack of investigations having been reported. We hope that this monograph will highlight some of these gaps and stimulate other workers to fill them.

Those areas in which we possess no expertise have been avoided as far as possible. We have left the endocrinological basis of growth to the endocrinologists, and the histological basis to the histologists; and in so far as possible, we have avoided detailed aspects of chemical and mathematical knowledge of the subject. We hope our gross approach will form some framework, no matter how shaky, on which the sophisticated studies of other specialists may build.

Many people have helped us in the preparation of this book, by a wide spectrum of assistance. The typing of many drafts has been undertaken by several patient ladies including Mrs Irene Murray, of Trannent, Scotland, Mrs Sharon Crawford of Edmonton, Canada and Mrs Lynette Hicks of Sydney, Australia. The preparation of figures was by Mr Ray Strettles of Sydney. The technical assistants who loyally maintained the high standard of dissection which has been the basis of our confidence in our data played an important role. Among these we must particularly thank Mr Dallas Baker of the University of Queensland and Miss Inez Gordon of the University of Alberta. Much assistance in the compilation and analysis of data was provided by Mrs Marion Peebles and Mr Ray Weingardt. A number of students and colleagues have participated in much of the research on which this monograph is based. Although we do not list them individually, their names appear as co-authors in our list of references.

Several colleagues have read parts of the book and made useful suggestions. We thank them most heartily for this assistance but do not imply that they necessarily agree with what we have written. Among these people we particularly thank Dr St C. S. Taylor, Dr H. Lloyd Davies and Dr Ian Robertson. Professor Sir Alexander Robertson encouraged us to spend a period in Edinburgh and assistance in many ways was provided by the late Professor Alan Muir and Dr Ian Robertson during our stay.

The financial support for much of the work on which this monograph is based came from the cattle industry. However the sources of funds, since the first anatomical project on growth in cattle commenced in the Veterinary Anatomy Department of the University of Queensland in 1960 with a working budget of \$700, have been wide and varied. It says a great deal for the foresight of those administering industry funds that they saw fit to support the initial basic studies from which the applied work has developed. We thank the following organizations in Australia for support of our projects: the University of Queensland, CSIRO (Aust.), the Australian Cattle and Beef Research Fund (now Meat Research Fund), the Rural Credits Development Fund of the Reserve Bank of Australia, and the University of Sydney. In Canada much support has been received from the University of Alberta, the National Research Council of Canada, the Alberta Department of Agriculture, the Alberta Agricultural Research Trust, and the Alberta Cattle Commission. In the early stages of this work a great deal of assistance was received from individuals with sufficient foresight to realize the need for anatomical assessment of progress in beef cattle breeding. The late Dr N. D. S. May set up the first project in the subdepartment of Veterinary Anatomy in the University of Queensland and it was while one of us (Rex Butterfield) was employed as a research student that a great deal of support was received from University and CSIRO personnel. Many of the early dissections were carried out in the facilities of CSIRO Meat Research Laboratories and Dr A. Howard and Mr L. G. Brownlie in particular provided considerable assistance to the foreign project in their midst.

Professor John Francis did much to win support for the project as

the work proceeded and Dr J. Rendel, Mr H. G. Turner, Mr John Kennedy and Mr R. Hayman, all of CSIRO, gave valuable encouragement and assistance in obtaining animals and in many other ways.

Mr J. Turton and his staff of the Commonwealth Bureau of Animal Breeding at Edinburgh gave us unstinting assistance during the writing of the manuscript and we express our gratitude.

This book was written in the era of change to metric measurements in many parts of the English-speaking world. We have therefore used metric units wherever possible. In some cases, however, to convert existing data into metric equivalents would have made it awkward to interpret (such as 100 lb intervals between slaughter weights), and so some non-metric units are used.

We hope that those who read this book may find some useful information, much intellectual stimulation and a modicum of pleasure. If it provides food for thought and a spur to further enquiry our efforts will have been well rewarded.

ROY T. BERG Professor of Animal Genetics University of Alberta REX M. BUTTERFIELD Professor of Veterinary Anatomy University of Sydney

1 Cattle growth and beef production

'Beef from dairy herds is beef.' (Edwards, 1965)

INTRODUCTION

The discussion in the following chapters will deal with the growth of the tissues, muscle, fat and bone. The proportions of these tissues in the carcass at slaughter are the most important aspects of composition to the consumer and therefore largely determine the economic worth of the carcass. The major objective in attempts to influence carcass composition is to have a high proportion of muscle combined with a desired proportion of carcass fat and a minimum of bone.

There are several major production trends operating at the present time which should result in increased production and improvement in the economic efficiency with which beef is produced. There are significant efforts to use cattle which gain more rapidly, and to use cattle of larger mature size. These efforts are paralleled by the trend towards less fat. Large size and late fattening make possible the slaughter of animals at heavier weights without excess waste fat. Slaughter weight, sex, shape, nutrition and breed can all affect carcass composition and are the major factors in the hands of the producer of beef in his attempt to alter carcass composition.

Although our purpose is to show how carcass composition can be modified, or improved if you wish, such an enterprise cannot be studied sensibly in isolation from the series of events which form the long and intricate chain in the production of a beef carcass. The beef cow, the manufacturing unit in the process, must be highly efficient in walking, grazing, breeding and surviving—all aspects of function. Whatever the carcass composition we wish to produce it must be compatible with the efficiency of these processes. Therefore we will consider growth and body composition in relation to their possible effects on function.

If the desired carcass composition for any market can be obtained by using the most efficient functional processes then the cost of production will be at a minimum. Any departure from this principle will result in the production of beef at higher costs.

CHOICE OF SLAUGHTER WEIGHT IN RELATION TO GROWTH PHENOMENA

Slaughter weight has a large influence on carcass composition but it cannot be considered independent of breed, sex and nutritional history. After reaching puberty, animals grown on a positive plane of nutrition tend to reach a stage where muscle growth slows up relative to fat deposition. Thus within a given breed and sex, heavier animals tend to be fatter. The rate of fattening and amount of fat deposited is influenced by plane of nutrition, maturity, breed and sex of the animal as will be shown later in this book. Fat is the most variable tissue in the carcass and excess fat is the major factor contributing to low saleable cut-out from a carcass. Therefore, slaughter weight should coincide with the point of maturity where fat is at a desirable or optimum level. It is difficult to tell on the live animal exactly when this stage has been reached. However, fat level is undoubtedly the most important factor in making decisions on the marketing and slaughter of animals. We must recognize that the economics of specific situations may make it advantageous to carry animals to levels of fatness which are quite wasteful with respect to carcass cut-out. Payment for edible meat content, rather than live or carcass weight, would put the economics of feeding to excess fat levels in proper perspective, as the unit price for edible beef would give a true indication of what the market is prepared to pay for each classification or type of beef. Currently this information is hidden in most countries in the host of variables which go to make up live and carcass weights.

In animals which are well advanced in the fattening stage, muscle growth is very slow, and this, coupled with the energy cost of depositing fat and the high maintenance costs of a heavy animal, results in very low biological efficiency for muscle growth at this stage. This growth will also be economically inefficient for supplying most markets.

As carcass weights increase over a range of slaughter weights there is a trend for an increase in the muscle to bone ratio as muscle continues to grow faster than bone. This increase is quite slow, about 0.03 change in muscle to bone ratio for each 10 kg increase in carcass weight (Berg and Butterfield, 1966) and is probably thus not of great economic importance within the reasonably narrow range of optimum carcass weights seen in any one market.

We may conclude that, in terms of any specific market, there is an ideal stage of developmental maturity at which to slaughter any animal regardless of sex or breed. This compositionally ideal slaughter point is therefore determined by the economics of each particular market, and is most simply indicated by the amount of fat on the carcass. Too little fat may be undesirable from the point of view of eating quality; too much reduces the percentage of saleable meat due to trimming.

THE RELATIONSHIP OF SHAPE TO GROWTH PHENOMENA

Traditionally, shape has been considered to influence the proportion of meat to bone and the proportion of high-priced cuts. More particularly, the general shape achieved by the more common British breeds of beef cattle has been claimed as the ultimate, and the term 'conformation' has been largely used as being synonymous with shape. Doubt has been cast on the concept of the perfection of the British breed shape by reports such as those of Butler (1957) who showed Brahman cattle to have as good, or better, proportions of high-priced cuts as Herefords; of Cole *et al.* (1964), who showed dairy cattle were equal to beef cattle in proportions of high-priced cuts; of Luitingh (1962), who showed that wholesale cut percentages were mostly influenced by fat distribution; and of Butterfield (1963a, c), who showed that animals widely different in shape (e.g., Old-type Shorthorns, Brahmans and Poll Herefords) were very similar in muscle weight distribution.

The relationship between shape and the musculature is now under considerable scrutiny. If animals can be appraised at equal levels of fatness, or if the influence of fat can be properly discounted, animals

	Better shape	Poorer shape
Number of carcasses	12	12
Conformation score*	5.3	3.6
Bone %	15.0	15.8
Fat %	18.2	17.4
High priced cuts %	42.0	41.0
Lean in high priced cuts %	45.8	45.8
Eye muscle area (sq. cm)	52.6	48.3

 Table 1.1
 Comparisons of carcasses matched for weight and fatness but of different conformation

*on 7 point scale Source: Chamberlain, 1970, cited by Harrington, 1971. of thicker conformation will have thicker muscles and skilled butchers may be able to cut a higher proportion of high-priced cuts from such animals by extending the boundaries of these cuts. Small advantages have been shown in favour of animals with better (thicker) shape at similar fat levels (Table 1.1). Most of the differences can be attributed to greater muscle to bone ratios at given fat levels with no apparent differences of muscle-weight distribution over the carcasses.

Heavy-muscled animals, low in fat, have a high proportion of muscle and a low proportion of bone in their carcasses. The 'Culard' or double-muscled animal illustrates the epitomy of this effect. Selecting for thickness of muscle, independent of fatness, will move toward this type of animal and the possible effect on functional efficiency must be considered.

Within the range of normal cattle, ignoring the double-muscled animals, there does not seem to be any advantage for 'better shape' in the traditional conformation concept. Harrington (1971) reported Meat and Livestock Commission studies on shape and stated that

Better-shaped carcasses in traditional terms did indeed have a better meat to bone ratio, but only a marginally better muscle:bone ratio coupled with substantial disadvantage of fatness. There was no advantage in high-priced cut yield or distribution of lean meat; the greater thickness of loin of the good conformation carcass was not due to eye muscle depth, but to the fat overlaying it. The conclusion from these data, therefore, is that good shape *per se* was largely achieved by excess fat deposition, which overshadowed small advantages in meat to bone ratio.

Harrington (1972) in a further report compared Friesian and Charolais \times Friesian steers for carcass characteristics. These results are given in Table 1.2.

These data show that in spite of 'superior' conformation of the Charolais \times Friesian steers, there was virtually no difference in lean in the carcass or in percentage lean in the high-priced cuts relative to that in low-priced cuts. The greater eye-muscle area in the Charolais crossbreds was related to a slightly higher lean: bone ratio in this group but no important differences in lean meat cut-out.

In this section we have so far tended to play down the effects of shape as a commercially important entity. Undoubtedly this is necessary if we are to clear away the show-ring inspired concepts which have dominated the beef cattle world for a long time. Shape does have a marked influence on the selection of animals in a large section of the industry, and will probably continue to do so for some

_	Friesian	Charolais × Friesian
Number	50	49
Carcass weight lb	484	507
% kidney fat	3.5	3.4
% carcass fat (ex Kidney fat)	18.4	19.6
% bone	16.1	14.8
% lean	63.8	63.6
Lean: bone ratio	4.0	4.3
Eye muscle area (sq. cm)	58	66
% wholesale cuts—Loin	9.3	9.5
Rump	7.1	7.2
Top side	22.5	22.9
Fore rib	5.0	5.1
% lean in high-priced cuts	47.8	47.7

 Table 1.2
 Comparison of carcass characteristics of Friesian and Charolais × Friesian steers

Source: Harrington, 1972.

time to come. Whether this is necessary from a meat point of view is debatable, and we believe that selection on productive criteria is more likely to lead to the functionally efficient animal which is needed to keep beef to the forefront. It may well be that selection for shape could be more effective if directed at such characteristics as ease of calving among groups of cattle already selected on growth criteria.

We recognize that many people will continue to select individual animals on appearance, either along with, despite, or in the absence of, performance records. Therefore it is necessary to make some comments on the factors which most influence the shape of live animals. The variations in skeleton are probably less important from a meat viewpoint than those of the other tissues and probably the most important aspect of the skeleton's contribution to shape is its total size. According to Riley (1971) important effects on fat distribution are also brought about by the relationships of the various skeletal components particularly in the more proximal parts of the hind limb.

The musculature exerts its main influence on the shape of cattle by virtue of variations in its amount, rather than by any differences in the relative size of muscles. And so a more muscular animal has some recognizable signs of this development in those areas of the body, such as the forearm where the muscle is not shrouded in fat.

However, as Brungardt (undated) has shown, visual estimates of muscle development may not have much significance. His conclusion that 'there are numerous optical illusions which trick the mind into this dilemma' can probably be applied to many of our efforts to 'eye-ball' cattle.

In the extreme muscle development of the 'Culard' most of the differences in shape of the animal are brought about by the total amount of muscle. However, some differences of distribution of muscle weight undoubtedly occur. The process of hypertrophy affects the muscle fibres and so those muscles which contain a high proportion of fibres to connective tissue, such as the big muscles of the hind leg, will become relatively larger than those muscles which contain relatively fewer muscle fibres and more connective tissue, such as the muscles of the shin and shank.

Fat exerts a major influence on shape. Although subcutaneous fat has the greatest opportunity to alter external appearances by its location immediately deep to the skin, the intermuscular fat undoubtedly exerts its effects also, mainly by a subtle shifting of the musculature (Harrington, 1971). Fat amount and fat distribution both have marked effects on shape and the distribution becomes much more important as the amount of fat rises. An excellent way to appreciate the effects of fat and its distribution on shape is to compare the shape of the 'Culard', which has virtually no subcutaneous or intermuscular fat, with a conventional animal in an advanced stage of fattening. It is immediately apparent that there is no 'depth in the flank' of the Culard. A large accumulation of fat in this area in the fatter cattle has been attributed with all kinds of virtues by show judges over the years, yet a simple study of the anatomy of the region indicates that this characteristic contributes nothing but waste fat. Similarly, the over-developed brisket of some breeds is seen to be only waste fat, as the 'Culard' has a very trim brisket.

For those who wish to pursue the concept of 'improvement' in shape the recommendations of Long (1970) are worth consideration.

We must try to assess the importance of shape in the future development of beef cattle. The current situation in the world scene of beef cattle should provide us with the answer to this question. All of the effort which has gone into the evolution of a beef-type animal is currently being thrown aside by wide sectors of the industry which are turning to animals which have had little or no selection for so-called beef characteristics. It seems that we have believed that we could retain the productive characteristics of a species whilst altering the basic structure to suit the whims of the fanciers. Undoubtedly, if we are prepared to husband a species of animal to the extent of helping it over all obstacles to survival, by assisting in conception, pregnancy, birth, suckling, and eventually all stages of feeding, then we can change the shape of that species in any measure we desire. The dog provides a perfect example of this phenomenon in its almost unlimited spectrum of perpetuated monstrosities, which survive under the patronage of doting breed societies. Many of these breeds would soon be extinct if placed into environments which demanded functional efficiency.

There is no limit to how much we can change shape by selection if we so desire. However, we have an animal which has evolved as a functionally efficient species, and if we wish to retain it in this form all efforts to change its shape must be made in the knowledge of what effect such changes will have on function. Will the animal be able to walk as well, reproduce as well, survive stress as well? There are clear indications that selection of cattle for muscle development will lead to problems with a great many functional characteristics. We should also take heed of what is happening in other species, such as the pig, where selection is capable of more rapid effects. The rise in transport mortality in pigs, between piggery and slaughter house, which has accompanied selection for muscle development, is a brightly flashing warning which the cattle industry should heed.

Selection for shape in the manner in which it has occurred under influence of the show-ring, along with unrealistic feeding regimes, has done a great deal of harm in recent years in increasing the incidence of arthritis and of dystocia among British breeds of beef cattle. It is an insult to the history of evolution for man to think he can lay down a set of ideals, springing mainly from ignorance of their implications, when dealing with a complex characteristic such as shape.

It seems that until we are fully aware of the problems, as well as the alleged advantages, which go along with any change in shape, we would do well to allow the animals to indicate to us by their performance just what shape is most functionally efficient.

It seems that, if we confine our selection for shape to the top few per cent of animals ranked on performance, we are unlikely to make many mistakes, provided that in reaching the peak of performance we do not provide any artificial props. For example, it would be wrong

to include in any such performance test an animal which has entered the world by assisted birth unless we are happy in our enterprise to be prepared to assist all future births.

SEX AND GROWTH PHENOMENA

Sex influences growth of body tissues and hence affects carcass composition and distribution of weight within the tissues. The most pronounced sex influence on carcass composition is achieved through the fattening process. Heifers tend to enter a fattening phase at lighter weights than steers, and steers at lighter weights than bulls. Therefore, the optimum slaughter weights are lighter for heifers and heavier for bulls than for steers. Also, the rate of fattening of bulls is less than heifers or steers and there is therefore a wider span of weights over which bulls may be slaughtered to achieve optimum fat cover.

The influence of sex on muscle growth also has an important effect on carcass composition. Sex differences in muscle weight distribution develop as the animals grow. Heifers and steers are not very different, but bulls increase proportionately more in forequarter muscles, which are usually somewhat lower in economic value than hindquarter muscles. However, if we are to take advantage of the ability of bulls to gain faster, convert feed more efficiently, to fatten later and to produce heavier carcasses without excess fat, we will probably have to accept something less than ideal in muscle weight distribution. Bulls also have higher muscle:bone ratios than heifers or steers at the same level of carcass fat. This is because bulls produce heavier carcasses at a given fat level and therefore they appear to have a more pronounced impetus for muscle growth than the other sexes. There does not seem to be any difference between heifers and steers in muscle:bone ratios at equal fat levels.

Sex significantly influences some management decisions. The producer can decide if it is possible to obtain the growth advantages of feeding entire males in his husbandry and market situation, and he must feed animals of each sex in a manner appropriate to their growth characteristics to achieve the best combination of slaughter weight and carcass composition.

BREED AND GROWTH PHENOMENA

The breeding of cattle is currently attracting more interest than at any time in history. Breeds are moving rapidly across previously impenetrable barriers. The forces which are lowering these barriers are mostly beyond the scope of this book, being largely concerned with the fulfilling of man's insatiable desire for novelty. The demand for large, rapid growing, highly muscled, efficient breeds has triggered an explosion spreading previously isolated breeds to all corners of the cattle breeding world.

Previously the spread of cattle breeds has been closely associated with the spread of man, and so the influence of British breeds of cattle has been world-wide. Notable exceptions to the failure of cattle to spread beyond the national and ethnic barriers of the countries of their origin are the British breeds in South America and the Holstein (Friesian) which has become the most important dairy breed in many countries and could even be ranked as the most important beef breed.

As political ties of the 'newer' countries with their homelands are weakening, so too are the beliefs that it is only by constantly returning to the genetic source of cattle breeds in the homeland for new 'blood' that the breeds can be maintained or improved. With the change of attitude, vast genetic resources are becoming available to the cattle breeder. The potential for both improvement and for disastrous alteration of existing cattle populations is great. Testing the many breeds and their crosses under many systems of production and in many environments will be most demanding. The challenge and opportunities are there, the rewards should be great and it is hoped that these will be obtained by the cattlemen and not only by the exploiters.

Reproductive efficiency is one of the most important measures of production and will have to be balanced against increased growth rate and muscle development obtained from the introduction of late maturing, large mature size cattle. Within the term reproductive efficiency we mean ability not only to conceive but also to produce a viable calf which is reared to slaughter weight. In different production situations reproductive efficiency may vary for each breed and, although a breed may produce a high turn-off of slaughter cattle under conditions of intensive husbandry, it may be an entirely different situation on open range with the insults of an extensive husbandry system. A calf which is born dead has a very poor growth rate, and any change to cattle of different carcass composition must be compatible with ability to rear a calf under the conditions of the enterprise in question.

Breed choice is of prime importance in attempting to meet the requirements of desirable carcass composition. There is no one

breed able to meet the ideal composition of all markets, any more than there is one breed best suited to the wide range of environmental conditions under which beef is produced. Breeds differ in the weight at which the fattening stage begins, and they probably also differ in the rate at which fat is deposited during this fattening phase. Since fat is the most variable tissue in the carcass and since it also represents the major waste in preparing a carcass for sale, it follows that breeds which are late fatteners, and/or slow fatteners, will be most desired under conditions of good nutrition so that heavy weights may be attained before slaughter is made necessary by increased fat. Early fattening breeds can be used where feed intake is restricted, or where they can be economically slaughtered at lighter weights or to meet special market demands.

For those markets where excess fat is a problem, efforts to reduce waste fat will be basic in breed selection. Cross-breeding the early fattening breeds with late fatteners will accomplish a large step in the desired direction. Complete substitution of late fattening breeds for the early fatteners will depend on whether suitably adapted examples can be found. Selection for a late fattening tendency within a breed will also be effective but usually much slower than can be accomplished by breed substitution.

Where late fattening, rapid growing, breeds such as the Friesian are already in widespread use, the next step in carcass composition alteration will be to improve the muscle yield relative to bone (i.e., muscle:bone ratio at any given level of fat). The muscle:bone ratio increases as the animal grows, and breed or strain comparisons should by made at the optimum fat level of the marketing outlet, as this will be the deciding feature for slaughter. When more is learned about factors which influence fat distribution it may be possible to modify this to advantage, and the 'predisposition to wastiness' of various cattle is already part of the appraisal of the system proposed by Long (1970). The partitioning of fat between the major depots may be a field for selection, as it seems some dairy breeds reach a desired level of intermuscular fat while still low in subcutaneous fat. This could result in minimized loss during trimming while achieving desired levels of intermuscular fat and probably also intramuscular fat. A similar advantage apparently also applies to bulls compared with heifers and steers.

Many breeds are classed as 'improved' in that they have had imposed on their basic abilities to survive and reproduce some added burden of supplying man's desires for either milk, meat or draft power. Breeds developed for milk production have been traditionally considered as not suitable for beef production. However, certain trends are bringing these breeds fully into the beef production arena, namely: increase in intensive production where the cow's potential for feeding several calves can be utilized; a trend towards faster gain, large mature weight and low fat carcasses, which are characteristic of the large dairy breeds; and an interest in beef direct from the dairy herd and from dual purpose breeds.

Rapid growth has been a major selection criterion in many beef breeds particularly in the last two to three decades. Some breeds had this characteristic well developed even prior to this selection trend. In general, rapid growth is compatible with economical beef production. It is associated with efficiency of feed conversion and with the trend to late fattening for more desirable carcass composition. Whether there are some negative relationships between extreme size and adaptability traits, such as fertility and survival, is not too clear.

Some conclusions of Brungardt in the undated publication previously mentioned indicate the complexity of the problem of making general statements regarding the relationships of growth and carcass composition as such relationships are conditioned by arbitrary decisions on the basis on which comparisons are made, e.g. constant age, or weight or grade (fatness).

- 1. At the same weights cattle with fast weight gains are more efficient than smaller, slower gaining cattle.
- 2. At the same grade cattle with rapid weight gain are almost as efficient as the smaller cattle.
- 3. Faster gaining cattle are approximately as efficient at their heavier weights as smaller cattle at their lighter weights.
- 4. Cattle selected for growth reach choice carcass grade or a compositional constant end point at significantly heavier weights. Thus evaluating cattle of different breeds and growth patterns at weight end points has less practical significance than composition or grade end points.
- 5. Using the Angus breed as a base (140 days feeding to Low Choice), the Charolais and Hereford breeds are approximately 43 per cent and 11 per cent respectively, later maturing (compositional maturity) breeds than the Angus.

In the chapters which follow we will attempt to demonstrate some of the many facets of biological growth which contribute to the fascination of the extremely important economic process of cattle growth.

2 Growth patterns of muscle, fat and bone

IN BRIEF Growth is often measured as live weight gain per unit time. Live weight is a commercially useful measure of growth only if it is highly predictive of the amount of desirable, edible product (essentially lean meat or muscle). Live weight can be misleading if the amount of fill is unknown, the amount of other non-carcass parts is variable and if the proportion of the carcass which is saleable is unknown. Carcass weight as an end point for growth is more useful than live weight. However the main problem with carcass weight (assuming standard definition and commercial practice) is one of assessing its yield of high value tissues and cuts. In order to obtain a clear picture of commercially useful growth it is thus necessary to look at the growth and relative growth of the tissues which make up the carcass.

Carcass composition as measured by the proportions of muscle, fat and bone changes as an animal grows. The patterns of tissue growth are influenced by several environmental and genetic factors. At birth there are about two parts of muscle to one part of bone in the carcass of a calf. Muscle grows relatively faster than bone in the post-natal period, so that the ratio of muscle to bone increases.

Fat makes up a small amount of the carcass at birth and it increases slowly until, given an adequate plane of nutrition, a fattening phase sets in and fat is deposited at an increasing rate. Fat is the most variable tissue in the body and manipulation of carcass composition by genetic or nutritional means depends largely on controlling the proportion of fat.

Under normal circumstances, weight at slaughter will determine the proportion of fat which increases along with body weight.

Genetic differences occur in carcass composition. Some breeds begin to fatten at light weights and others at heavier weights. The rate of fattening may also differ between breeds, but the major differences seem to be related to the time of onset of the fattening phase. Generally early maturing cattle have a lower mature size and they enter the fattening phase at lighter weights.

Breeds also differ in muscle measured as total muscle weight relative to bone weight. Breeds selected for body thickness or for draft usage generally exceed those selected for dairy character in muscle:bone ratio. Superior muscling occurs early in the post-natal period and breeds with high muscle:bone ratio remain superior throughout life, barring periods of weight loss. Genetic differences within breeds for muscling have not been as pronounced as differences between breeds, but, given sufficient numbers from which to choose, it is reasonably certain that genetic differences of practical magnitude will be found within normal cattle.

Sex influences carcass composition. Heifers mature at lighter weights than steers and bulls and reach the rapid fattening stage earlier. Provided that the

fattening phase has been reached, and under similar feeding conditions, heifers will be fatter than steers at given weights and steers fatter than bulls. Besides the difference in weight at which the fattening process begins, it appears that heifers fatten faster than steers and steers faster than bulls.

Differences between sexes in weight of muscle relative to weight of bone are influenced more by the criteria used to select them for slaughter than by direct sex-induced differences. Thus, at an equal level of fatness, bulls will be superior to steers in muscle:bone ratios because they will be heavier. There seems to be little difference between steers and heifers in a similar comparison. However, when compared at equal muscle plus bone weight, or statistically adjusted to equal weights, bulls and steers are similar in muscle:bone ratios. Thus the differences seem to be a manifestation of the bulls maintaining a more prolonged impetus for muscle growth whereas steers slow down and fatten.

Nutrition, particularly the level of intake of digestible nutrients (plane of nutrition), can affect carcass composition. Again the major effect is on the proportion of fat. A low plane of nutrition during the fattening phase will result in a lower proportion of fat, and a high plane in a greater proportion. It should be remembered that there is a strong tendency for an animal to achieve a certain carcass composition at a given weight and that it seems to be able to accomplish this over reasonably wide ranges in nutrition. This tendency has led some researchers to state that body composition is completely dependent on body size. There is sufficient evidence, however, that carcass fatness at a given body weight can be influenced by plane of nutrition.

A low plane of nutrition before the fattening phase begins has little or no effect on ultimate carcass composition provided that the animal is finished on an adequate plane.

Weight loss associated with starvation depletes all tissues, but the relative effect on fat is greater than on muscle, while bone resists depletion to a greater extent than muscle and fat.

Re-alimentation following weight loss tends to restore normal carcass composition. If the compensation period is long enough a normal state may be reached. However, at the same live weight the proportion of fat in carcasses of starved and then re-alimented cattle would usually be less than those on uninterrupted growth.

If the weight loss occurs in the early stages of growth before rapid fattening normally takes place, compensation will be complete and normal proportions of fat, muscle and bone will result for given weights, even though the external appearance of the animals may suggest extreme changes in composition. Similarly, holding animals at their birth weight for an extended period probably has no effect on their subsequent carcass composition following a period of normal feeding.

A hypothetical model is presented for the partition of nutrients to vital organs, maintenance, bone, muscle and fat. It is suggested that in the partition of nutrients for tissue growth priorities are relative rather than absolute. In animals on a positive energy balance, bone and muscle growth proceed together maintaining a genetically determined ratio. The amount of fat deposited will depend on how much surplus energy is available over maintenance and bone and muscle growth requirements. Under starvation (negative energy balance) the reverse process sets in with fat and muscle reserves, and to some extent bone reserves, being depleted to satisfy vital functions.

INTRODUCTION

Growth, according to Fowler (1968), has two aspects. The first is measured as an increase in mass (weight) per unit time. The second involves changes in form and composition resulting from differential growth of the component parts of the body. In studies of meat animals we are primarily concerned with the growth of the major tissues of the carcass which are muscle, fat and bone and with the proportions of these three major tissues in the carcass.

Age, weight, breed, sex, nutritional history and other factors influence the proportions of muscle, fat and bone at any particular stage of weight increase. In this chapter we will attempt to define the normal patterns of growth and differential growth and assess the influences of genetic and environmental factors on these patterns.

Gross live weight changes are relatively easily measured by expressing live weight gain per unit of time. Relative growth is more difficult to appraise since there is no reliable method available for obtaining quantitative measurements of body components or tissues in the live animal. The method we used in several studies of relative growth was serially to slaughter random samples of animals over a range in live weights followed by physical dissection of the carcass into its several tissues (Butterfield and May, 1966; Butterfield and Berg, 1966a).

In this technique, individual muscles were removed, trimmed of fat, severed from tendon at the last vestige of muscle and the weight recorded. The sum of all the 100 individual muscle weights of a side, and of some scraps of muscle, equalled total muscle weight. The 'scrap' muscle comprised vestiges of muscles damaged in the commercial dressing, such as the diaphragm and tail muscles, together with small unidentified fragments accumulated during dissection. Bones trimmed of fat and tendons were weighed in fourteen categories, being individual bones such as the femur, or groups of bones such as regional vertebrae, for example, the lumbar vertebrae. Fat tissues were dissected and weighed in three or four depot categories: subcutaneous, intermuscular, kidney and body cavity. Tendons and connective tissue were weighed separately. With data obtained in this way it has been possible to delineate the changes in the component

tissues as animals grow in size. Also, by comparing animals from different breeds, sexes and from differing nutritional treatments, it has been possible to assess the importance of these various factors in the relative growth of the component parts of the body.

NORMAL PATTERNS OF GROWTH

Live weight

A growth curve for live weight, in cattle under normal circumstances, follows the pattern shown in Fig. 2.1. From birth, given adequate



Fig. 2.1 A typical growth curve of cattle

nutrition, a calf will grow along a sigmoidal curve showing acceleration at about puberty and slowing down as maturity is approached. Animals are usually slaughtered near the end of their pubertal growth spurt between one-half and two-thirds of mature body size.

Live weight is used as a measure of total growth but there are several factors which could limit its usefulness as a measure of economic worth. If live weight is to be useful it must be as an accurate predictor of, first, carcass weight and, ultimately, edible portion of the carcass. Conditions prior to weighing can affect recorded live weight and thus its predictive value as a measure of carcass weight.

Animals may be weighed directly off pasture or from feeding yards after a period of restraint from feed or water or both, or after a period of transport for varying distances and under varying conditions. Obviously, if live weight is to be meaningful, some standardization of weighing conditions is necessary. Reid *et al.* (1968) found shrunk body weight (weighing after twenty-four hours without feed but with access to water) to be highly predictive of empty body weight (weight of body less the contents of the gut). Errors in recorded weights due to differences in fill can also be minimized by weighing several times on successive days and using the average weight so obtained, although this may not always be practical.

Carcass weight

From live weight to carcass weight, besides the loss in gut fill, a number of components are discarded including blood, viscera, hide, head and feet. Slight modifications are found in a commercially dressed carcass in various countries. It may be with or without kidney, kidney fat, pelvic fat, cod fat, udder fat, muscle portion of the diaphragm and the tail. De Boer *et al.* (1971), in a report on standardized procedures on the dressed carcass to the European Association for Animal Production, listed fourteen variations in the basic unit termed a carcass. Besides, the carcass may be weighed hot or cold, wet (washed) or dry, and shrouded or unshrouded. Again it is obvious that standardized procedures and definitions are necessary if meaningful comparisons are to be made.

The conditions of weighing, alive and as a carcass, as well as the dressing procedure, will influence dressing percentage or the ratio of carcass weight to live weight times 100. Dressing percentage is often a useless figure because it hides a multiple of variables. It must be precisely defined in terms of live and carcass weighing conditions and dressing procedures if it is to have any meaning.

Some procedures which influence dressing percentage are:

- 1. access to feed and water prior to weighing;
- 2. transport prior to weighing (Brännäng (1966) demonstrated that a short period of transport and yarding (one hour transport and half an hour waiting) increased dressing per cent by 1.4 per cent);
- 3. use of hot or cold carcass weight;
- 4. dressing procedure.

The major difference in dressing procedure in different countries is whether kidney and pelvic fat are removed or not. Since this fat is all on the hindquarter, and since it may comprise in extreme cases up to 6 per cent of carcass weight, leaving it on the carcass has resulted in some erroneous interpretations. Animals with a high proportion of kidney fat have been credited with high dressing percentages and also with a high proportion of hindquarter, considered a more valuable part of the carcass.

There are biological factors which affect dressing percentages and an understanding of their effects is necessary in interpreting live weight and carcass weights from experiments or in other comparisons.

Weight affects dressing percentage, as shown by Field and Schoonover (1967) in Table 2.1. The main increase in dressing percentage seems to occur between 100 and 400 kg live weight with little further change to 600 kg. Willis *et al.* (1968) showed no difference in dressing percentage for weight ranges from 350 to 430 kg.

Fat thickness mm	Live weight range (kg)	No. of animals	Dressing percentage (of starved live weight)			
2.11	91–135	3	51.4			
2.22	136-180	8	52.4			
3.22	181-226	27	52.4			
2.37	227-271	26	55.7			
3.19	272-317	64	56.3			
4.25	318-362	97	56.4			
5.47	363-407	52	57.8			
6.80	408-453	18	59.1			
9.57	454-498	26	58.8			
10.23	499-543	23	60.3			
8.74	544-589	10	59.9			

 Table 2.1
 Relationship between live weight, fat thickness and dressing percentage

Source: Field and Schoonover, 1967.

Fatness influences dressing percentage. If, at equal weights, one animal is fatter than another, it will usually have a higher dressing percentage. The extreme example of the effect of fatness is the high dressing percentage sometimes achieved by highly-fitted show steers. The data of Field and Schoonover (Table 2.1) could be interpreted as influence of increased fatness as easily as increased weight since the two factors increase together. The influence of fatness on dressing percentage is brought about by relatively more fat being laid down in the carcass as opposed to the non-carcass parts.

Tulloh and Seebeck (pers. comm.) put the situation clearly:

If you consider the three carcass components—bone, muscle and fat—and relate them to body weight by the exponential equation $y = ax^b$, then fat is the ONLY component contributing to increase in dressing percentage, because the 'b' value is approximately one for muscle, less than one for bone and greater than one for fat. Irrespective of carcass composition, the offal components taken together, have a 'b' value of less than one; therefore, they

contribute (in a negative way!) to higher dressing percentage as body weight increases.

The nature of the diet can have a marked effect on dressing percent. Butterfield *et al.* (1966) showed calves at 4 weeks had a reasonably high dressing percentage of 55.2. By 8 weeks of age, on rations containing roughage, the dressing percentage dropped to 51.4 and continued to drop till at 22 weeks the average was 46.1 per cent. This was despite the fact that live weight doubled during this time. However, in a subsequent experiment Butterfield *et al.* (1971) showed that calves fed on a milk diet with a wide range of intake levels increased in dressing percentage throughout the experiment. The results of the two experiments are plotted in Fig. 2.2 where level of feeding is ignored and the mean value at each slaughter weight is plotted. The different patterns are undoubtedly due to the different physical nature of the diets, one containing a high proportion of roughage (lucerne, cereal chaff and bran) and the other only milk.



Fig. 2.2 Effect of diet on dressing percentage of calves. x = calves fed on milk only; • = calves fed on milk and roughage Source: Butterfield *et al.*, 1966, 1971

That nature of the diet is also of considerable importance in older cattle was shown by Callow (1961). Preston and Willis (1969) demonstrated a decrease of 3.8 per cent in dressing percentage of Brahman bulls on high forage diets compared with others on concentrates. This was a particularly valuable demonstration as the bulls were of almost identical live weight and as far as can be assessed by the excess fat trim, of very similar fatness.

	ad lib. molasses urea with		
	forage ad lib.	grain <i>ad lib</i> .	
No. of bulls	48	107	
Live weight (kg)	384	389	
Excess fat percentage	8.0	9.0	
Dressing percentage	52.0	55.8	

Table 2	.2	Dres	sing	perc	œnt	of	Bra	hman	bulls	fed	ad	lib.	mo	lasses
urea plu	ıs ei	ither	ad Īi	b. fc	rag	e or	ad :	lib. g	rain					

Source: adapted from Preston and Willis, 1969.

Sex may affect dressing percentage. In his study of monozygous twins, Brännäng (1966) showed that bulls had a higher dressing percentage than their steer twins when kidney fat was removed at slaughter, whereas the body of literature which preceded his work, and which was based on carcasses which included kidney fat, showed that there were no differences between steers and bulls. Such advantage due to leaving the kidney fat in the carcass may accrue to heifers as well as all other earlier-maturing types of animals.

The advantage of bulls over steers in Brännäng's study was achieved despite the heavier hide of bulls at the same age (750 days). This could be regarded as due to his steers being only 90 per cent of the live weight of the bulls; however, his steers had considerably heavier thoracic, abdominal and kidney fat (about 9 kg more) and therefore it seems that the dressing percentage of the steers would be lower than that of the bulls at equal weights.

There are many reports of genetic differences in dressing percentage. Brahman \times Hereford had superior dressing per cent to Hereford in several comparisons (Black *et al.*, 1934; Carroll *et al.*, 1955; Butler *et al.*, 1956a, b; Damon *et al.*, 1960; Cole & Ramsey, 1961; Hewetson, 1962). This difference, which is probably of the order of 2 per cent when kidney fat is included in the carcass, may be even more with it removed, as Hewetson (pers. comm.) believes that Brahman cattle have lower kidney fat at the same levels of general fatness.

The Angus is quoted as being superior in dressing percentage to the Hereford by Powell *et al.* (1961) and Seebeck and Tulloh (1966). The latter authors also showed the Shorthorn to be superior to the Hereford.

In a large number of comparisons quoted by Preston and Willis (1970) Charolais has a higher dressing percentage than numerous other breeds. This was achieved despite lower fat levels in the Charolais.

Breed comparisons of dressing percentage can be commercially meaningless unless the underlying cause for any difference is known. If one breed is fatter than another it may have a higher dressing percentage, but the extra fat may have to be trimmed off, which makes increased dressing percentage in this case a liability. Dressing percentage figures which include kidney fat with the carcass are also misleading since such fat is of little commercial value.

On calculations which include kidney fat, the traditional beef breeds have a higher dressing per cent than dairy breeds, according to Preston and Willis (1970). It seems probable that the mature size of the animal, rather than its classification as dairy or beef type, may be more related to dressing per cent.

Branaman *et al.* (1962) showed a significant 3 per cent advantage for beef cattle at an average non-significant 2.3 per cent higher level of carcass fat, and this suggests an advantage for the beef cattle. They suggested, as did Pearson (1966), that it is a major advantage of the beef type and it is therefore important that the situation should be clearly defined. If, as is commonly held, dairy cattle have more kidney fat than beef cattle, then the advantage to the beef breeds should be even greater after the removal of kidney fat. The most common statement is that beef cattle have a higher dressing percentage which is largely offset in terms of meat yield by the extra fat of the beef cattle. However, as the major criterion for selection of slaughter cattle is the level of fat, and particularly the level of subcutaneous fat, it seems pointless to compare these two types other than at the same level of fat.

Other factors which might influence dressing percentage could be the relative proportion of non-carcass parts. Charolais crossbreds compared with Herefords were shown by Berg (1964) to have a higher dressing percentage as a result of a lighter hide. Newman and Martin (1971) have shown the same advantage for Charolais crossbreds v. Simmental crossbreds. Whether size of other non-carcass parts, such as head, feet and viscera, can be decreased to enhance dressing percentage is worthy of study. With present knowledge we must conclude that carcass weight, live weight and dressing percentage are inadequate descriptions of value in a beef animal.

Carcass components

As will be shown, the carcass is an extremely variable commodity. It should be considered as merely a step in the process along the chain from live animal to edible meat, not as Callow (1948) stated: 'The carcass is the most important unit in meat studies, since it finally settles the value of the meat animal both for the farmer and the butcher.' We predict that this settlement will more and more be based on measures or estimates of edible saleable product obtainable from the carcass, as is already done in the Argentine with beef and in Canada with pork. The carcass contains edible and inedible components, the largest among the inedible portion being the bones. There is also a big difference in value among the edible parts. Excess fat, although edible, is of little or no value in most markets today. Some parts of the carcass also command higher prices because of their particular characteristics. Thus it is necessary and desirable to look at the major carcass components separately and together, and to try to understand their growth and relative growth, so that we may be better able to aim at production of carcasses with higher proportions of the more valuable, at the expense of less valuable, components.

Muscle, fat, bone and connective tissue are the major components of the dressed carcass. Muscle is the most important tissue because it is most desired by the consumer and a superior carcass for any market has a maximum amount of muscle, a minimum of bone and an optimum amount of fat which varies according to consumer desires. Carcass growth rate and that of the component tissues—muscle, fat and bone—are depicted in Fig. 2.3 relative to live weight. These data are for beef steers from shortly after birth to 450 kg live weight.



Fig. 2.3 Growth of carcass and carcass tissues relative to live weight

From Fig. 2.3 it can be seen that there is a strong relationship between carcass weight and live weight, and that the muscle makes up the major part of the carcass. Due to the early development of bone and later development of muscle the ratio of muscle to bone at birth may be as low as 2:1. The growth patterns of the tissues show bone growing at a steady, but slow rate, and muscle growing relatively fast, so that the ratio of muscle to bone increases. Fat comprises a relatively small amount of the carcass at birth, but eventually its growth rate increases so that it approaches, and occasionally in very fat animals surpasses, muscle tissue in absolute amount.

The same data are shown in Fig. 2.4 plotted as percentages relative to total carcass weight. Bone percentage decreases slowly and continuously as weight increases.

Muscle comprises a high percentage at birth, rises slightly, and begins to decrease in percentage as the fattening phase takes over. So it can be seen that first muscle and then fat has the major influence on carcass composition, whereas bone at no stage exerts a dominant role in the determination of relative proportions of the three major tissues.

Bone obviously must reach a level of development during ante-natal life which allows it to function efficiently at birth, and it is therefore classed as an early developing tissue. Muscle needs to function at birth, but at nowhere near the ultimate peak of efficiency of the young adult animal; it therefore has an intermediate degree of development at birth compared with bone and fat. Apart from the requirements in the first day or so of life, the fat tissues are the least essential of the three tissues early in life and therefore are the latest developed.

These patterns of growth have been shown by many workers, including Haecker (1920), Callow (1948) and Berg and Butterfield



Fig. 2.4 Percentage of muscle fat and bone in a typical carcass during growth
(1968). The problem of expressing them in some manner which, while being simple and clear, also embraces all the relevant changes of biological importance, is constantly with us. Huxley (1932) studied growth of parts of the body relative to the whole by use of the allometric equation of $y = ax^b$ (where y = size of the organ or part, x = size of the rest of the body, and b = the growth coefficient of the organ or part). This equation was found by Huxley to give a reasonable quantitative description of many organ-to-body relationships. The use of the equation is based on the assumption that relative changes in component parts during growth are more dependent on the absolute size of the whole rather than on the time taken to reach that size.

In our comparisons the growth coefficient 'b' represents the ratio of the percentage post-natal growth of 'y' to the whole 'x' and it therefore enables relative maturity to be expressed. The size of 'b' is high when 'y' represents a late maturing tissue, and low when 'y' represents an early maturing tissue.

The allometric equation was used to compare the growth of muscle, fat and bone relative to muscle plus bone by Elsley *et al.* (1964) for sheep and pigs, and by Berg and Butterfield (1966) and Mukhoty and Berg (1971) for cattle. Calculated on this basis, the growth coefficient for bone in beef cattle was found to be low (less than 1.0), for muscle intermediate (although greater than 1.0), and for fat high (generally from 1.5 to 2.0). These coefficients substantiate that during post-natal growth, considered in its entirety, bone grows at a low impetus rate, muscle is intermediate and fat grows at a high impetus rate. There will be occasions, such as in early post-natal life, when the growth rate of muscle will exceed that of fat and therefore a 'b' value for this phase would be greater for muscle than for fat.

GENETIC INFLUENCES ON RELATIVE GROWTH OF MUSCLE, FAT AND BONE

Genetic differences can be observed between breeds and between strains within breeds. Generally we look first for major differences of an inherited nature between breeds, since breeds are expected to have more or less stabilized around a certain norm of development. If breed differences prove to be important we might then try to find genetic differences within breeds to ascertain if a breed could be shifted in a desired direction by selection. Even without marked breed differences it may be possible to find within-breed genetic variation.

When appraising relative growth of the tissues-muscle, fat and



Fig. 2.5 Growth of tissues relative to cold carcass weight of Hereford and Friesian steers

Source: Royal Smithfield Club, 1966



Fig. 2.6 Growth of carcass fat relative to growth of muscle plus bone in Hereford and Friesian steers Source: Royal Smithfield Club, 1966

bone—a certain baseline or control dimension has to be chosen. In Fig. 2.5 data from Hereford and Friesian steers, slaughtered at up to 24 months of age, are plotted relative to the carcass weight.

In the early stages muscle, fat and bone followed similar growth patterns relative to carcass weight, for the two breeds. However, the Herefords started the fattening phase at lighter carcass weights than the Friesians and thereafter the Friesians had relatively more muscle and bone in their carcasses and less fat than the Herefords.

Fat deposition can, perhaps, best be compared relative to the fat-free weight of the carcass. This is shown for the same data in Fig. 2.6.

This figure clearly indicates that the Hereford steers fattened at lower muscle plus bone weights than did the Friesians.

Lohman (1971) compared four breeding groups for fatness at four weights. Their data are shown in Fig. 2.7. It is obvious, and expected, that the Angus fattened at lighter fat-free weights than did Holsteins, with Angus \times Holstein and Charolais \times Angus intermediate in fattening patterns.

Similar breed differences in fattening are shown in Fig. 2.8 where the data of Hayman and Gardiner (1972) for Shorthorn, Sahiwal, and Friesian crossbreds are plotted. These data indicate the Shorthorn is an early fattener (which is no surprise), the Friesian is a late fattener and the Sahiwal (an Indian milking breed becoming popular in Australia as a beef producer) is intermediate.



Fig. 2.7 Weight of fat relative to carcass weight in different breeds and crosses Source: Lohman, 1971





Source: Hayman and Gardiner, 1972

The lines which depict fattening in Figs 2.6 and 2.7 seem to run parallel for Hereford and Friesian steers. However, they do not run parallel for the breed comparisons in Fig. 2.8. It is therefore not clear if the rate of fattening differs between breeds or if the differences of fatness at any time is due to time of onset. To test whether breed groups differ in their rate as well as in the onset of fattening, growth coefficients ('b' values) were calculated among several breed groups, within sexes (Mukhoty & Berg, 1971). Significant differences in 'b' values were found between breed groups of bulls, steers and heifers which indicated genetic differences in the rate of fattening or, more precisely in the proportionate increase in fat relative to muscle and bone. Therefore, it can be concluded that genetic differences may occur in both earliness of fattening relative to weight or size of animal and also in the rate of fattening relative to increase in weight of muscle plus bone through the fattening phase.

Berg and Mukhoty (unpublished) examined the same data with respect to changes in percentage of fat relative to muscle plus bone weight. In this study breed groups did not differ significantly in regression of percentage fat on muscle plus bone weight, but did

differ in percentage fat adjusted to a common muscle plus bone weight. This analysis leads us to the conclusion that breed differences in percentage fat resulted mainly from differences in onset of the fattening phase rather than the rate of fattening once this phase had begun.

Breed influences on fat growth have been considered relative to muscle and bone growth. In order to appraise relative growth of muscle and bone it is probably desirable to look at each relative to the other.

Muscle and bone show a high relationship (correlation) because they are both components of increased size.

There is a body of opinion in the pure breeding industry which holds that there is some unbreakable link between the weight of bone and the weight of muscle. The 'weight' of bone is usually assessed by visual appraisal of the cannon bones, which procedure has been shown by Kauffman *et al.* (1970) to be extremely inaccurate. They concluded that among slaughter steers of similar weight and wide differences in muscling, the bone may be heavy or light, large or small, and dense or porous with no particular association with the amount of muscle.

It is possible that the relationships between muscle and bone may be influenced by genetic or environmental means. The data of the Royal Smithfield Club (1966) for muscle weight v. bone weight of Hereford and Friesian steers, are plotted in Fig. 2.9.

It is clear that the Herefords have more muscle relative to bone at all stages than the Friesians. The slope of the line (increase in muscle relative to bone) also appears to be steeper for the Herefords but this was not tested statistically. Berg and Butterfield (1966) and Mukhoty



Fig. 2.9 The relationship of muscle to bone for two breeds *Source*: Royal Smithfield Club, 1966

and Berg (1971) found no difference in growth coefficients for muscle among breed groups. However, Mukhoty and Berg (1971) found significant differences in weight of muscle at standard muscle plus bone weights. Using the same data and regressing muscle on bone rather than on muscle plus bone, Berg and Mukhoty (unpublished) found breed differences in rate of muscle growth relative to bone. It therefore appears that the use of bone as a base line gives a more sensitive test than using muscle plus bone, and this seems to be logical, as incorporation of the large proportion of muscle in both the dependent and independent variable tends to reduce the sensitivity of the test. Another example of this will be seen in later information on muscle growth patterns (Chapter 4).

Another way of examining muscle-bone relationships is to look at muscle-bone ratios over increases in animal size. The data of the Royal Smithfield Club (1966) are plotted in Fig. 2.10.

The superiority of the Hereford steers in this measure over the Friesian steers is quite apparent. Berg and Mukhoty (unpublished) found significant breed differences in muscle-bone ratios before and after adjusting to standard muscle plus bone weights.

As cattle are selected for slaughter primarily according to fatness, and even selection at certain weights is largely due to prior knowledge of the likely level of fatness, there is a good reason why comparisons



Fig. 2.10 Muscle: bone ratios relative to total muscle plus bone weight from Hereford and Friesian steers

Sources: Royal Smithfield Club, 1966; Berg, 1968a

of muscle weight to bone weight should be carried out at equal levels of fatness. Such comparisons give a great deal of information about the composition of the carcass for all three major carcass tissues.

Breed differences in regression of muscle on bone and in muscle: bone ratios indicate genetic influences in the relative growth of these tissues. These genetic differences in muscle:bone ratio are accentuated in commercial practice by the slaughter of animals at different weights. The range which might be experienced can vary from about 4.1 for Friesians and perhaps other dairy types, to as high as 6.8:1 for doublemuscled animals of the Charolais breed (Dumont & Boccard, 1968). Brännäng (1966) concluded that variation in muscle-bone ratio could largely be attributed to genetic differences since differences between his identical bull/steer twin pairs accounted for 69 per cent of the variation in this trait. Thus the amount of muscle relative to bone should be amenable to selection.

SEX INFLUENCES ON RELATIVE GROWTH OF MUSCLE, FAT AND BONE

Numerous reports indicate that at equal weights or ages heifers produce fatter carcasses than do steers. What has not been so clearly demonstrated is whether the pattern of fattening differs between sexes, for it is important to the relative value of these two types of animals that a generalization should not be made which, although perhaps applicable in the later stages of fattening, may be quite incorrect at light weight.

The general statement that bulls are more muscular than heifers or steers also requires clarification, for again, a general statement which does not make it clear that the comparisons are made at specified weights or levels of fatness could be misleading.

Under conditions of good nutrition bulls grow faster than steers (Price and Yeates, 1969) and steers faster than heifers. Fig. 2.11 shows the general pattern of muscle, bone and fat growth relative to carcass weight for a group of bulls, steers and heifers treated alike and serially slaughtered to compare growth patterns and carcass composition among the sexes.

Weights per day of age from birth to slaughter for the same measures of growth are shown in Table 2.3.

Brännäng (1966) showed that castration depressed live weight growth by about 10 per cent and muscle growth by about 17 per cent in comparisons using monozygous twins. This compares to 7.5 per cent



Fig. 2.11 Patterns of muscle, fat and bone growth of heifers, steers and bulls Source: Berg and Fukuhara, unpublished

	Bulls	Steers	Heifers
Number	12	22	12
Age	361	383	398
Actual weights (kg)			
Live	386.1	376.9	345.8
Carcass	215.6	194.4	196.4
Muscle	146.2	123.6	107.8
Fat	47.8	61.2	62.2
Bone	27.8	25.6	22.0
Weights per day of age (g)			
Live	1,070	984	869
Carcass	597	508	493
Muscle	405	323	271
Fat	132	160	156
Bone	77	67	55
Muscle: bone ratio	5.1	4.8	4.9

 Table 2.3
 Growth of bulls, steers and heifers

Source: Berg, unpublished.



Fig. 2.12 Growth of tissues in heifers steers and bulls. A. Fat relative to muscle plus bone. B. Muscle relative to bone Source: Berg, unpublished

and 20 per cent respectively in the above table. All of the live weight advantage of bulls over steers in Table 2.3 was the result of increased muscle, while only half of the live weight growth advantage of steers over heifers was in muscle.

The fattening pattern for each sex group can be seen from Fig. 2.12A where fat is plotted against fat-free (muscle plus bone) weight.

Heifers and steers had more fat than bulls by the time they reached

the second slaughter point after birth, which corresponded to about 225 kg live weight. Heifers and steers separated in fattening pattern at a later stage. Differences in fatness between the sexes seem to be manifested by a combination of time of onset of the rapid fattening phase as well as the rate of fattening. Fattening relative to muscle plus bone growth appears to be curvilinear with the sharp rise occurring earlier in heifers than in steers and in steers earlier than in bulls. It is clear from Fig. 2.11 why heifers reach an optimum level of fatness at lighter weights than steers and why steers precede bulls in this characteristic. This is substantiated by Suess *et al.* (1969) who found heifers at 386 kg live weight to be similar in composition to steers at 455 kg live weight. This sort of information is vital to the proper utilization of sexes and breeds in any situation.

The influence of sex on the relationship of muscle to bone is not entirely clear. Bulls often have a higher percentage of muscle in their carcasses, but this can be explained by the fact that they have less fat. A similar result occurs when comparing steers and heifers. Also, bulls have higher muscle-bone ratios (see Table 2.3). This might be because they have heavier muscle, having progressed further along a normal differential growth pattern with muscle growing proportionately faster than bone. When muscle is plotted against bone for the data of Table 2.3 we see that there is very little indication of any differences between the sexes when compared at similar stages of development of muscle and bone (Fig. 2.12).

Similarly, Mukhoty and Berg (1971) found no significant difference between the sexes in growth coefficients for muscle, or for bone, and that the sexes were similar in amount of muscle and bone when compared at the same muscle and bone weight. Berg and Mukhoty (unpublished) studied the regression of muscle-bone ratio on muscle plus bone weights for the same data. Regressions were similar for the three sexes and muscle-bone ratios adjusted to common muscle plus bone weights were also similar among sexes.

Brännäng (1966) found that at the same fat level, and therefore different muscle plus bone weights, bulls had higher muscle-bone ratios than steers. The main difference between the sexes then comes back to the fact that impetus for fattening supercedes impetus for muscle growth at lighter weights in heifers than in bulls, with steers intermediate. Bulls reach higher levels of muscle relative to bone probably only because they are capable of a more prolonged impetus for muscle growth before heavy fat deposits are laid down.

NUTRITIONAL EFFECTS ON RELATIVE GROWTH OF MUSCLE, FAT AND BONE

Two major nutritional effects will be examined. The first will be the effect of plane of nutrition above maintenance and the second will be the effects of weight loss and compensation in relation to relative growth of muscle, fat and bone.

Plane of nutrition

That plane of nutrition affects live weight or carcass weight gain per day is well known and needs no documentation. What must be considered is the influence of plane of nutrition on relative tissue growth. Callow (1961) slaughtered animals from four planes of nutrition (Table 2.4) and found a significant difference in the percentage of fat in the carcass; those on the high plane in the final feeding period had fatter carcasses than those on the moderate plane. Hendrickson *et al.* (1965) performed a similar experiment with similar results (Table 2.4).

Treatment	High- high	High- moderate	Moderate- high	Moderate- moderate	Sig. level
(a).					
Wt. of carcass (kg)	347.3	329.2	308.7	338.7	
% muscular tissue	55.2	59.2	56.5	58.7	*
% fatty tissue	30.6	25.5	29.0	26.2	*
% bone	11.8	12.8	12.3	12.7	
Muscle-bone ratio	4.7	4.6	4.6	4.6	
(b).					
Wt. of carcass (kg)	242.9	236.5	236.5	242.0	
% muscle [†]	55.8 ^{ce}	58.4°	57.3°	60.3	*
% fat [†]	31.9°	27.4	29.5°	25.9	*
% bone†	13.8°	14.9	14.3°	14.7	*
Muscle-bone ratio	4.0	3.9	4.0	4.1	n.a.

 Table 2.4
 Comparison of two studies of the effect of plane of nutrition on carcass composition

*P < 0.05

†Estimated from rib dissection

n.a.-not analysed.

Means with the same superscript do not differ at P < 0.05

Sources. (a) Callow, 1961; (b) Hendrickson et al., 1965.



Fig 2.13 Effect of plane of nutrition on fat deposition relative to muscle plus bone weight *Source*: Guenther *et al.*, 1965

The influence of plane of nutrition on fat deposition relative to muscle plus bone growth is illustrated from the results of Guenther *et al.* (1965) in Fig. 2.13 and from Waldman *et al.* (1971) in Fig. 2.14. Guenther *et al.* fed half-sib Hereford steers from weaning (W) on two planes of nutrition, high (H) and moderate (M). Body composition was estimated at the start and as the experiment progressed. Waldman *et al.* used Holstein steers and started their experiment at birth. Their 'moderate' plane was designed to result in 60 to 70 per cent as much gain as the 'high' plane group which were self-fed. Composition was estimated from formulae based on rib cut dissection.



Fig. 2.14 Growth of fat relative to muscle plus bone on two levels of energy intake

Source: adapted from Waldman et al., 1971

Both sets of data illustrate more rapid fattening relative to muscle plus bone weight on the high plane of nutrition and thus how it is possible to control the level of fat relative to non-fat by altering the plane of nutrition.

There is some question about whether plane of nutrition will affect the amount of muscle relative to bone. Callow (1961) found no significant difference in muscle-bone ratios from four different planes of nutrition (Table 2.4). Although the data of Hendrickson *et al.* (1965) were not statistically analysed with respect to muscle-bone ratios, their results seem to be similar to Callow's (Table 2.4).

The data of Guenther et al. (1965) for muscle relative to bone is



Fig. 2.15 Growth of muscle relative to bone on high and medium planes of nutrition

Source: adapted from Guenther et al., 1965



Fig. 2.16 Growth of muscle relative to bone on high and medium energy diets

Source: adapted from Waldman et al., 1971

plotted in Fig. 2.15 and that from Waldman *et al.* (1971) in Fig. 2.16. In the first case there seems to be some influence in that muscle relative to bone from the high plane is greater than from the moderate plane. From the data of Waldman *et al.* (1971) however, muscle relative to bone is essentially identical for the two treatments. There may be some other explanation for the apparent differences in the results of these two experiments. Taylor (pers. comm.) has drawn our attention to unpublished results of T. Jackson of the Edinburgh School of Agriculture which indicate that muscle will grow relatively faster than bone depending on the protein:energy ratio of the diet. With high protein and low energy, bone grew relatively faster than muscle (and fat least of all) compared with the results for low protein and high energy.

Weight loss and compensation

The phenomenon of compensatory growth tends to assure that a certain final size is reached. Composition, within limits, may be influenced by final weight through the phenomenon of compensatory growth. Certain physiological factors associated with the growth curve, such as sexual maturity, are probably more influenced by weight than by age.

Lawrence and Pearce (1964) wintered steers on three planes of nutrition for a 168-day period, following which they were allowed good pasture and were slaughtered at a fixed weight. The relevant data from their experiment are shown in Table 2.5. There is an indication.

Plane of nutrition	High	Medium	Low	Sig. level
No. of steers	12	12	12	<u> </u>
Carcass weight (kg)	274.2	271.3	271.5	
Composition (predicted				
from 10th rib dissection)				
% muscle	54.2	53.6	55.3	
% dissectible fat	27.5	28.0	24.3	
% bone	15.3	15.3	16.6	*
Muscle : bone ratio	3.55	3.49	3.33	n.a.

Table 2.5	Effect of	plane of	nutrition	and	compensation	on	carcass
compositio	n in beef	steers			-		

* significant at P < 0.05

n.a.: not analysed

Source: adapted from Lawrence and Pearce, 1964.

that composition was affected in that percentage of bone was higher in the low plane group and percentage fat slightly lower, though not significantly so. The muscle:bone ratio favoured the uninterrupted group but this was not tested statistically. However, the differences in this work are so small that we must be extremely careful in assessing them as they are based on predictions from rib cuts. It is doubtful if the accuracy of the predictions is within the range of variation of the differences shown.

Butterfield *et al.* (1971) fed calves, to grow at three rates, on different levels of a milk diet from birth. The highest plane group had uninterrupted growth, as did the medium group, whereas the third group was held at its birth weight for 72 days before being allowed to grow normally. Slaughter and tissue dissection took place at seven fixed weights from 44 to 88 kg live weight. At these equal slaughter weights there was no difference in carcass composition (percentage dissectible muscle, fat and bone) between the calves from the three different planes of nutrition. This indicates that within quite wide



Fig. 2.17 Effect of starvation and recovery on tissue growth from half-sib Poll Hereford steers: C_1 and C_2 = control groups slaughtered at two weights after normal growth; S = group slaughtered following weight loss; R = group slaughtered following weight loss and recovery *Sources:* Butterfield, 1966a; Berg, 1968a

limits of growth rate, body composition is related to the body size reached. These results were achieved in the period before fat deposition would become important and should be interpreted in that light. They do not necessarily preclude the possibility that greater fat deposition can be achieved by the use of high energy feeds *ad libitum* or a lesser proportion of fat can be achieved by low energy and restricted feeding as mentioned earlier, but probably there is a fairly wide range of nutritional levels which will result in equal carcass composition at equal carcass weights.

The relative growth of bone, muscle and fat is altered under weight loss. The depletion of fat is most rapid and the degree of involvement of muscle and bone depends on the severity and length of time on the regime. Butterfield (1966a) combined weight loss and re-alimentation using 23 Poll Hereford half-sib steers. The data on tissue weight are plotted in Fig. 2.17.

It would seem that muscle loss and gain followed a completely normal pattern relative to muscle plus bone weight. The absolute amount of bone following weight loss did not drop to a level corresponding to that found in a normal carcass of the same weight, but it did seem to make near normal recovery on re-alimentation. Fat was markedly depleted under weight loss and in the recovery period of the experiment did not reach the expected level relative to the controls. Although the loss of fat to muscle seems greater when considered on the basis of percentage loss (70 per cent v. 21 per cent) the actual amounts of each tissue lost were very similar, as can be seen in Table 2.6. There was a slightly greater loss of muscle, 11.3 kg, compared with a fat loss of 9.6 kg.

Treatment	Muscle kg	Fat kg	Ratio of muscle gain or loss to fat gain or loss
Uninterrupted growth (C1-C2)	+ 16.8	+ 9.8	1.71
Semi-starvation (C1-S)	- 11.3	- 9.6	1.18
Recovery (S-R)	+ 18.2	+ 6.5	2.80

Table 2.6Composition of weight change in muscle and fat during
uninterrupted growth (C1-C2), semi-starvation (C1-S) and recovery (S-R)
of Poll Hereford steers

Source: Butterfield, 1966a.

This apparent contradiction arises, of course, from the fact that there was a greater amount of muscle present than fat, before weight loss commenced.

It appears that, if weight loss is imposed on reasonably fat steers, there is about equal weight of both muscle and fat used up in the loss of about 16 per cent live weight and there is only a small actual weight loss from bone. However, further weight loss from the carcass would have to come increasingly from the muscle tissue, as the fat tissues sink to an insignificant proportion of the remaining carcass.

Re-alimentation or compensation results in an increase in muscle towards a point of normal muscle-bone relationship, while the amount of fat tissue will reach the same level as uninterrupted controls only if a long enough period of compensation is involved. This process would probably be speeded up on a high energy intake. Butterfield (1966a) attempted to demonstrate this but was thwarted by repeated digestive disturbances when trying to feed high energy diets to previously semistarved steers.

Allden (1970), in his excellent review, summarized the position as follows:

The current evidence does not support the concept of Hammond and his co-workers that the form of an animal and the development of the musculature in particular can be manipulated by nutritional means. An animal whose growth has been retarded will be of similar shape to its 'normal' counterpart of similar weight, thus conforming with Huxley's allometric equation. But when feed conditions are so favourable that precocious fat development occurs, or so severely restricted that growth of bone continues at the expense of other tissues, the shape of an animal may be altered, though usually to a minor degree.

A MODEL FOR CONTROL OF CARCASS COMPOSITION

Hammond's well-known model showing how the tissues in the body compete for the nutrients in the blood stream (Hammond *et al.*, 1970) requires some modification in light of current knowledge. If the Hammond model is followed it implies that during growth on a low plane of nutrition bone has priority over muscle and therefore the result of low plane growth would be the production of animals of low muscle: bone ratio. This fitted the conclusions drawn earlier from work such as that of McMeekan (1940), but the re-analysis by Wallace (1948), and more recently by Elsley *et al.* (1964), have shown that this is not in fact true. Rate of growth does not affect muscle:bone ratio.

It would also be useful if a model could be constructed which allowed

for the phenomenon of the 'overflow' of the surplus nutrients into fat depots. High energy intake will affect the level of carcass fat at a given body weight and particularly if the feed intake is on a very high plane. This is the basis of McMeekan's recommendations which are so widely used in the feeding of pigs.

The model should also allow for the role of the musculature and the skeleton in providing nutrients during body weight loss.

Our model should incorporate the following principles:

- 1. Vital organs will have first claim on available nutrients for both maintenance and growth. The more vital the organs, for example brain, the higher priority they will have for growth and, indeed, the most vital will show minimal retardation by inadequate nutrition and only critically low levels will impair function.
- 2. Muscle and bone growth proceed at the same relative rates to each other irrespective of the rate of growth as long as positive growth is maintained. Protein:energy ratio of the diet may alter the relative rates somewhat.
- 3. The proportion of muscle to bone is altered during body weight loss. Relative rate of depletion may be affected by intake of protein as well as energy.
- 4. Fat growth relative to muscle and bone growth is dependent on the level of energy intake. A high level of energy intake produces more fat relative to muscle and bone.
- 5. The loss of body weight depletes fat, muscle and bone. It is not a selective depletion of fat.

Fig. 2.18 shows a model which allows for the partition of available nutrients on positive energy balance and also for depletion of tissues in negative balance. Plane of nutrition is indicated as height in the intake tube depicted at the left. If the level is considered as producing pressure the influence on the various tissues, both positive and negative, can be visualized. Relative priority of tissues for nutrients is depicted by their height. Thus if there are only small amounts of nutrients available the pressure is low and nutrients can be visualized as flowing into vital organs and meeting maintenance requirements. There would be insufficient nutrients (height in intake tube or pressure) to bring about any growth in bone, muscle or fat.

On a plane of nutrition which provides for slow growth (depicted by a horizontal line on the model) muscle and bone receive nutrients required for their growth but there would not be an overflow into



Fig. 2.18 A model of priorities for nutrients during growth at any rate or during body weight loss

fat depots. It is probable that muscle growth would not be at a maximum rate, unless there is some fattening, as depicted by the 'medium plane' horizontal line. Under such circumstances muscle and bone growth would be near maximum but fat deposition would be restricted.

A high plane of nutrition, such as *ad libitum* feeding of a high quality ration, would result in surplus energy going to fat deposition since all other requirements are met.

The model will also account for depletion of tissues from undernutrition. If fat depots are relatively full, they will be preferentially depleted—nutrients flowing from this depot to maintenance and vital organs. Depletion of muscles proceeds along with fat depletion in weight loss. The demand on muscle tissue becomes greater as fat stores are depleted until, when all fat stores are gone, survival depends on utilization of muscle tissue stores to maintain vital functions. Bone shows less depletion under weight loss conditions but some depletion is inevitable (i.e., assuming a negative pressure in the model there would be little repair of normal wear and tear). The depletion of bone would be greater under severe and prolonged weight loss. In our model under weight loss there would be loss from all tissues (because of negative pressure) and not selective depletion of fat until it is all used up, followed by depletion of muscle and then bone, as is sometimes suggested.

Growth, relative growth and weight loss should be considered as dynamic processes with changes occurring in relation to feeding and maintenance demands brought about by activity. There would at times be an overflow into fat, at others only sufficient to meet the vital requirements with periods where stores would be used for vital requirements.

In any one animal it could be visualized that it changes several times per day from one to another of the situations set out above, according to feed intake. An animal on *ad libitum* feeding would be more stable than one on once-a-day feeding. The situation during infrequent drought feeding would be one of fleeting periods of high blood level of nutrients with some repletion of body reserves, balanced by longer periods when the body stores were providing the nutrients.

The maturity status of different animals as determined by sex and heredity can be accommodated by considering that requirements for bone and muscle growth are satisfied and the surplus energy flows into the fat depots. As has been suggested earlier in this chapter, the division of nutrients for muscle and bone is not different for bulls v. steers, for example, but bulls retain an impetus for selective muscle and bone growth longer than do steers. Fattening is thus delayed in bulls since their nutrients are selectively used for muscle and bone growth.

3 Changes in the chemical composition of cattle during growth

IN BRIEF The major chemical components of the body are water, protein, fat and ash. Maturity, reflected by an increase in the proportion of fat, is accompanied by a decrease in the proportion of water and protein in the body. The range in percentage fat in the empty bodies of cattle can be from less than 2 to nearly 50 per cent. Water content can vary from approximately 80 to 40 per cent and protein from 20 to 12 per cent. Bodies of calves are high in water and low in fat. Protein, ash and water percentages decrease with age and fattening. As animals grow there is a decrease in water concentration and corresponding increases in protein and ash in the fat-free body. The decrease in water to protein ratio is most marked in the first year of life but continues to drop slowly into old age.

In the young animal about 50 pounds of water are stored in the empty body for each 100 pounds increase in live weight. In older animals this may drop to about 40 pounds. About 15 pounds of protein and 3 pounds of ash are stored for each 100 pounds increase in live weight and only a small decrease in these amounts is seen for older animals unless excessive fattening is taking place. The amount of fat stored per 100 pounds live weight increase is quite low in the calf and high in the latter stages of a fattening steer's growth. From 6 to 36 pounds of fat per 100 pounds gain have been reported. These changes in storage of the major chemical constituents result in an approximate range of 25 to 50 pounds of dry matter stored for each 100 pounds increase in live weight for a calf at the one extreme and a heavy fattening steer at the other.

The chemical composition of muscles in a steer of more than one year of age approximates 74 per cent water, 21 per cent protein, 4 per cent fat and 1 per cent ash. The amount of fat in muscle varies with the general level of fatness in the body. The percentage of fat also varies widely among different muscles being quite low (in the neighbourhood of 2 per cent or less) in shin and leg muscles and high (up to 13 per cent) in muscles of the rib, loin and abdominal wall.

The amount of chemical fat in the fat tissues varies with the depot and the age and fatness of the animal. The kidney fat depot has the highest percentage of chemical fat (in the neighbourhood of 90 per cent in a fat animal) and thus less water and protein than subcutaneous or intermuscular fat which contain approximately 70 per cent of fat in a fattened steer. Young animals and thin animals have lower chemical fat percentages in the various depots. Within a fat depot a great deal of variation is associated with location, for example in subcutaneous fat extremes have been reported of as low as 30 per cent fat from the foreshin to more than 80 per cent fat from the loin of fattened steers.

Body weight exerts a strong influence on carcass composition of animals on positive growth no matter how fast that growth might be. Some experiments support this concept, but others indicate that rapid growth brought about by a high plane of nutrition results in a higher proportion of fat in the body at given weights compared to slower growth on a lower plane of nutrition. Energy intake is the most important nutritional consideration but deficiencies in other nutrients may have some influence on body composition. Low levels of protein in the diet have been shown to result in increased proportions of fat in the carcasses of sheep slaughtered at specific live weights.

There is a parallel between growth patterns of chemical components—water, protein, fat and ash and those of physically separated muscle, fat and bone described in Chapter 2. Approximately 50 per cent of the body water and protein are in the musculature and a slightly higher proportion of the total chemical fat occurs in the fat depots, so that muscle growth is reflected in water and protein accretion in the body, and chemical fat parallels changes in the fatty tissue depots. However, since not all protein is found in muscle and fatty tissues contain various levels of fat, there is a great need for more studies of carcass composition by physical dissection followed by chemical analyses of the dissected tissues to establish the true relationship of results from the two methods.

INTRODUCTION

In the last chapter we have described the growth patterns of the major tissues of the body muscle, fat and bone. Such separation provides a useful end point for assessing carcass composition in terms of general commercial values. It is known that muscle tissue contains some fat as well as protein, water and ash, and that fat tissue is not all chemical fat but has protein and water as well. Therefore it seemed important to examine the patterns of growth and development of chemical constituents of the body and the tissues and to relate these patterns to those of the physically separated constituents described in Chapter 2. In so doing we rely heavily on the work of others who have painstakingly analysed whole bodies, tissues and depots into their major chemical components. Since few experimenters have done chemical analyses following complete physical dissection of carcasses. direct comparison of the two methods is not possible. However, we will attempt in this chapter to carry the comparisons as far as available data will allow in the hope that researchers in the future will fill whatever gaps remain.

CHEMICAL COMPOSITION OF THE BODY

Much of the information on body composition has been obtained from chemical analyses of whole bodies or of carcasses. Chemical composition of whole bodies has been used as a major criterion of animal response to various influences, particularly nutritional treatments.

In this way it has been possible to quantify what the animal does with the chemical nutrients of the feed in building up its body. This approach is useful from the point of view of understanding overall metabolism and growth, but it does not reveal the distribution of the nutrients to the edible and inedible parts of the body, which is important from an economic point of view, nor does it indicate the distribution of the nutrients to or within the various tissues—muscle, fat and bone—within the carcass. Nevertheless it is very valuable in understanding the whole picture of growth to examine growth of chemical components along with the growth patterns of physically separated muscle, fat and bone demonstrated in Chapter 2.

The major chemical components of the animal body are water, fat, protein and minerals or ash. Garrett (1968) credited an early German worker (Von Bezold, 1857) with indicating that morphologically similar animals had similar chemical composition. He credited two other Germans (Henneberg, 1881; Pfeiffer, 1887) with the observation that a reduction in water content (percentage) accompanied the fattening process in farm animals. According to Garrett, the concept that once the fat content of the body is known the chemical composition is obvious, was concluded by Murray (1919) based on the classic work of Lawes and Gilbert (1859, 1861). Later Murray (1922) and Moulton (1923) confirmed that the relative fatness of animals of the same species does not influence the composition of the fat-free body, and also that the water content of the fat-free body decreases slightly with age.

Maynard and Loosli (1962) listed the chemical composition of the bodies of several species as follows (Table 3.1).

Such values seem to imply some constancy in chemical composition for a species. However, a great deal of variation exists as reported by Reid *et al.* (1968) who reviewed results of chemical determinations on

	Water	Protein	Fat	Mineral
Steer	54	15	26	4.6
Sheep	60	16	20	3.4
Hog	58	15	24	2.8
Man	59	18	18	4.3

Table 3.1 Percentage of gross composition of bodies of several species

Source: Maynard and Loosli, 1962.

large numbers of animals in several species. These are shown in Table 3.2.

]	Range in er composi	npty body ition %	
Species	No.	Age range (days)	Water	Fat	Protein	Ash
Cattle	256	1-4,880	39.8-77.6	1.8-44.6	12.4-20.6	3.0-6.1
Sheep	221	90- 895	29.6-73.8	4.9-46.6	10.7-19.5	1.7-5.8
Pigs	714	1- 923	30.7-80.8	1.1–61.5	8.3–19.6	1.3–5.6

 Table 3.2
 Range in chemical composition of bodies of cattle, sheep and pigs

Source: Reid et al., 1968.

There are obviously very large variations in chemical composition of bodies of animals within a species. In the remainder of this chapter we shall attempt to describe the patterns of chemical component growth in the bodies of cattle, to examine external factors which might have some influence on these patterns and on ultimate chemical composition of the body and of the carcass, and to relate chemical composition to physically separated tissues—muscle, fat and bone.

PATTERNS OF GROWTH OF THE CHEMICAL COMPONENTS OF THE BODIES OF CATTLE

As animals grow and develop, the concentration of water decreases and that of protein and ash increases in the fat-free body before reaching values which are fairly constant for the species. The point in time when the fat-free composition becomes reasonably constant was called 'chemical maturity' by Moulton (1923) who judged that this occurred at an age equal to 4.0 or 4.5 per cent of the total life expectancy.

However, Spray and Widdowson (1950) found that 'chemical maturity' varied with the chemical constituent being studied. They found potassium concentration in rats rose for 30 days whereas calcium concentration rose for 100 days.

Reid *et al.* (1963) reported that the concentration of water declined and that of protein and ash increased markedly to about 400 days of age in cattle, after which changes were smaller and more gradual but continued to at least 5,000 days of age. However, the variation of water, protein or ash is much less when considered on a fat-free dry basis, that is the protein: ash ratio is fairly constant and is given by Reid *et al.* (1963) as 80.3 ± 1.7 per cent: 19.7 ± 1.7 per cent for protein and ash in fat-free dry tissue of cattle. Thus, although the concept of chemical maturity is an oversimplification, it is quite useful for most practical purposes.

One of the most extensive studies of the body composition of the ox was done by T. L. Haecker at the University of Minnesota in the early part of the present century. Beginning in 1908, Haecker, recognizing the need for fundamental knowledge on body composition in relation to feed consumed, launched a research project to analyse chemically the carcasses of steers at 100lb intervals to 1,500lb live weight. Ten years later, having fed 189 steers and individually recorded their weekly feed consumption and weight changes, and having completely analysed the total bodies of 63 steers, Haecker began to write his results which were published in the 111-page Bulletin No. 193 of the University of Minnesota Agricultural Experiment Station in 1920. Haecker's experiment represented a massive effort and showed a commendable persistence and dedication.

Haecker's results included steers from 100 to 1,500lb live weight and we will use these data extensively to help describe patterns of chemical growth in cattle. Haecker gave full credit to two studies on body composition of cattle which preceded his. He referred to Lawes and Gilbert of Rothamstead, England, who in 1849 made chemical analysis of 'a fat calf 9 or 10 weeks old, which had been fed on fattening food but had been grown rather than fattened, and a moderately fat ox about 4 years old, fed on fattening food'. The second study reported by Haecker was by W. H. Jordan, then Director of the Maine Agricultural Experiment Station, who on 1 September 1893 began experimental feeding of 4 high-grade Shorthorn steer calves weighing on average 292 lb. After 17 months on feed two were slaughtered, one weighing 870 lb, the other 958 lb, and ten months later the other two were slaughtered, one weighing 1,290 and the other 1,307 lb. Jordan's experiment was planned to study the effect of rations widely different in nutritive ratios (19 per cent v. 10 per cent protein) on the rate of growth and composition of the bodies of the steers. Complete and detailed records on feed consumption, feed analyses and live weight gains were kept. The bodies of the animals, except the skin and hair, were submitted to chemical analyses. This experiment, like Haecker's which followed, showed the keen desire of nutritional scientists, then as now, to try to understand how food was used in the growth of animals.





Two statements by Jordan as quoted by Haecker are most worthy of note since their basic premise is still important today. The first was: 'The kind of growth caused by the two rations, viz; the portions of water, protein, fat and ash, was not materially different with steers of the same size.' The second statement was: 'With steers fed the same time, the composition of the entire bodies, the proportion and composition of the carcasses and the proportions and composition of the edible parts were practically alike.' More will be said of these statements later after we look at constituents stored in cattle bodies during growth.

Haecker's body composition data for steers slaughtered from 100 to 1,500 lb live weight are plotted in Fig. 3.1. These represent total components of the empty body less the contents of the intestinal tract and include blood, skin and hair, offal, feet and head.

Relative to live weight, water is the major component of the body; it increases steadily as an animal grows. Protein shows a fairly steady increase relative to live weight, as does ash. The amount of chemical fat increases at an accelerating rate, slowing somewhat in the heavier animals represented in Fig. 3.1. The similarity of this figure to that for dissected tissue growth (Fig. 2.3) will be immediately apparent.

In Table 3.3 are shown the percentages of the chemical components

Live weigh	t	Water	Protein	Fat	Ash	Water: protein ratio	Protein: ash ratio
(lb)	No.	%	%	%	%		
100	5	71.84	19.89	4.00	4.26	3.61	4.67
200	4	70.43	19.14	6.01	4.42	3.68	4.33
300	4	65.72	18.77	11.19	4.30	3.50	4.37
400	5	65.79	19.31	10.56	4.34	3.41	4.45
500	5	62.90	19.15	13.73	4.22	3.28	4.54
600	3	61.20	19.40	15.04	4.36	3.15	4.45
700	4	60.35	18.60	16.58	4.48	3.24	4.15
800	3	58.44	18.80	18.52	4.24	3.11	4.43
900	3	54.10	17.66	24.08	4.16	3.06	4.25
1,000	4	52.03	17.11	26.91	3.95	3.04	4.33
1,100	3	47.77	16.38	32.03	3.82	2.92	4.29
1,200	3	47.96	16.02	32.32	3.70	2.99	4.33
1,300	2	47.93	15.79	32.50	3.78	3.04	4.18
1,400	1	47.76	16.15	32.58	3.51	2.96	4.60
1,500	1	43.48	15.72	37.59	3.21	2.77	4.90

 Table 3.3
 Chemical components of the empty body of steers of varying live weight

Source: Haecker, 1920.



Fig. 3.2 Composition of steers from 100 to 1,500 lb, as per cent of empty body weight *Source*: Haecker, 1920

in the empty body from Haecker's data. The same figures are plotted in Fig. 3.2. From 100 lb calves to a 1,500 lb steer, the water content of the empty body decreased from 71.84 to 43.48 per cent; protein decreased from 19.89 to 15.72 per cent; fat increased from 4 to 37.59 per cent; and ash decreased from 4.26 to 3.21 per cent respectively. Thus it is apparent that a large part of the variation in body composition is related to weight in normal growing cattle. Bodies of calves are high in water and low in fat while those of older fattened animals are the reverse. Protein percentage drops slightly as fattening proceeds and ash also assumes a slightly smaller proportion of the total in the heavier animals.

The negative relationship of water and fat content is obvious. The relationship of fat to protein content is not so apparent. The influence of fat on protein per cent is more apparent from data of an early study of Moulton *et al.* (1922). They reported protein per cent in the empty body dropped from 19.74 to 12.26 for animals from 3 months to 48 months of age on *ad libitum* feed. For animals over the same age range, fed for growth, the drop in protein per cent was only from 19.44 to 17.96; and for animals fed for 'restricted' growth, protein per cent did not drop, remaining at near 20 per cent of empty body weight throughout. Thus the drop in protein per cent was closely related to the fatness achieved on each treatment.

Water: protein ratio is also shown for Haecker's data in Table 3.3. It has been suggested as an index of chemical maturity (Bailey *et al.*, 1960) and, although the ratio drops more quickly from 100 to about 500 lb live weight, it continues to decrease slowly in line with the suggestion of Reid *et al.* (1963).

Protein to ash ratio is also shown in Table 3.3 and it is reasonably stable showing no consistent trend.

A further insight into the storage in the body of the various chemical components can be obtained from Haecker's data in Table 3.4 which gives the number of pounds of each component stored in the empty body per 100 lb live weight gain from an initial weight of approximately 100 lb to the final weight of each slaughter group.

About 50 lb of water was stored in the body for each 100 lb increase in live weight up to 500 lb. Thereafter slight decreases occurred in the amount of water stored until it dropped to about 40 lb per 100 lb of live gain in the heavy steers. The amount of fat stored per 100 lb live weight gain showed a continuous increase as the animals grew, from 6 lb for the first 100 lb gain to 36 lb per 100 lb in the animal slaughtered at 1,500 lb. Protein stored per 100 lb of gain increased slightly from just over 13 lb for the first increment to nearly 16 lb in the intermediate

Final weight (lb)	Water (lb)	Protein (lb)	Fat (lb)	Ash (lb)	Total dry matter (lb)
200	50.16	13.35	6.06	3.36	22.77
300	50.36	14.58	11.93	3.44	29.95
400	51.41	15.41	10.26	3.52	29.19
500	50.10	15.67	13.22	3.47	32.36
600	47.62	15.54	13.89	3.52	32.95
700	48.33	15.20	15.39	3.73	34.32
800	48.09	15.83	17.34	3.59	36.76
900	43.78	14.73	24.35	3.40	42.48
1,000	43.71	14.72	25.78	3.44	43.94
1,100	39.99	14.22	31.28	3.34	48.84
1,200	41.80	14.28	31.53	3.32	49.13
1,300	41.96	14.29	27.92	3.21	45.42
1,400	40.22	13.90	30.49	3.02	47.41
1,500	37.17	13.86	36.21	2.81	52.88

 Table 3.4
 Chemical components stored in the empty body per 100 lb live gain from initial to final weight

Source: Haecker, 1920.

weight ranges and then dropped back to about 14 lb for the heavy weight groups. A similar trend to that for protein was shown for ash, only on a lower general level.

It is interesting to note that in the increment from 100 to 200 lb live weight, 22.77 lb of dry matter were stored in the empty body, while for the increment from 1,400 to 1,500 lb, 52.88 lb of dry matter were stored. This points out the fallacy of looking at feed conversion on a live weight basis.

DISTRIBUTION OF CHEMICAL COMPONENTS AMONG THE TISSUES OF THE EMPTY BODY

The chemical components of the body—water, protein, fat and ash, make up varying fractions of the organs and tissues. Total chemical composition gives a gross picture of what the body contains but falls short in providing any insight into the chemical composition of the various organs or of the major tissues—muscle, fat and bone. Fortunately the early workers (Haecker, 1920; Moulton *et al.*, 1922) did their chemical analyses separately for some organs and tissues before combining the results for the body as a whole. More recent data obtained by grinding and homogenizing the whole body provide rather limited possibilities for interpretation by those who may be interested in the distribution of chemical components among tissues.

Haecker's chemical analyses were done on flesh (fat and muscle), bone, cartilage and tendons, blood, skin, and edible and inedible offal. For our purposes we will take bone, cartilage and tendon as bone; Haecker's flesh plus bone can then be equated to a commercial carcass. Fig. 3.3 shows a breakdown of the distribution of protein, water and fat in the empty body for animals at selected intervals from Haecker's experiment.

In the 100 lb calves (Fig. 3.3 top), 42 per cent of the protein is found in the muscle and fat and 27 per cent is found in the skeleton while the remainder (31 per cent) is found in non-carcass parts of the empty body. The percentage of the protein in the muscle plus fat rises to 58 per cent in the 1,500 lb steer while the per cent of the protein in the skeleton decreases to 16 per cent and in the non-carcass to 26 per cent. The percentage of protein found in the carcass stays fairly constant from 100 to 1,500 lb live weight at between 70 and 74 per cent of the total.

Water percentage (Fig. 3.3, middle) follows a similar pattern to protein except that the amount of water in the skeleton drops more



Fig. 3.3 Distribution of the chemical constituents in the empty body of cattle *Source*: Haecker, 1920

markedly, comprising 20 per cent in the 100 lb calves to 7 per cent in the skeleton of the 1,500 lb steer. The proportion of the total water found in the carcass rises slightly from 65 to 70 per cent from 100 to 1,500 lb animals.

The distribution of fat in the body changes quite markedly as animals grow (Fig. 3.3, foot). The percentage of the total fat found in the skeleton is higher than that from the muscle plus fat tissue in the 100 lb calves (47.5 ν . 30.5 per cent respectively). However in the carcass of a 1,500 lb steer only 5 per cent of the total fat is found in the skeleton and 69 per cent is found in the muscle plus fat tissues.

The proportion of the fat in the non-carcass tissues did not change greatly, increasing from just over 20 per cent to about 25 per cent of the total as the animals grew from 100 to 1,500 lb.

It is obvious from these figures that the distribution of the chemical

constituents in the body changes as an animal grows and fattens. These factors would have to be considered in attempting to relate the total chemical composition of the empty body to proportions in the edible parts.

CHEMICAL COMPOSITION OF THE TISSUES Chemical composition of muscles

Brännäng (1966) chemically analysed muscles of identical twin steers and bulls. His results are shown in Table 3.5.

					-
	Water	Protein	Fat	Ash	
Bulls	74.09	20.64	3.25	0.96	
Steers	72.90	20.33	5.64	0.94	
Manage -					

 Table 3.5
 Average percentage composition of muscles from bulls and steers

Source: Brännäng, 1966.

Johnson et al. (1973a) obtained levels for chemical fat of the musculature varying from 2.66 per cent in an animal with 12.3 per cent total dissectible fat to 7.26 per cent for one with 35.1 per cent total dissectible fat (Table 3.6). There was a high correlation between the fat of the musculature and total dissectible fat. Brännäng (1966) found a similar high relationship and the regression of chemical fat of the musculature on total dissectible fat of the carcass was similar for steers and bulls. Both groups of workers showed considerable variation in the percentage of fat in different muscle groups. Johnson et al. (1973a) found differences were greater for animals which were fatter (Table 3.6). Muscles of the distal limbs (standard muscle groups 2 and 6) had the least fat and muscles around the spinal column (group 3) and of the abdominal wall (group 4) had the highest percentages of fat. Average intramuscular fat was 5.14 per cent for an average dissectible fat level of 22.4 per cent, a figure quite comparable to Brännäng's steers (Table 3.5).

Garrett and Hinman (1971) determined the fat content in muscles from four locations from steers and heifers of choice and good grades. Muscles of the chuck (Infraspinatus and Serratus ventralis) varied from 6 to 13 per cent of chemical fat; muscles of the back (Longissimus dorsi), rump (Gluteus medius) and round (Semimembranosus and Adductor femoris) had a range of 3 to 6 per cent fat. Fat content of muscles was higher from 'Choice' than from 'Good' carcasses. Fat percentage was related to marbling score and to a lesser extent to

Wt	of total			W	eight of in	itramuscu	ılar fat (?	∕₀ total we	ight) in		
0188 (%	of wt	Standa	rd muscle	group:							Total side
of carc	carcass)	1*	2	3	4	5	6	7	8	9	muscle
	12.3	1.60	1.53	2.45	5.51	2.25	1.34	3.47	2.89	4.58	2.66
	13.0	3.19	2.45	2.94	7.04	2.26	1.75	3.44	3.30	5.62	3.50
	15.1	3.92	2.29	3.95	6.35	3.18	2.58	4.97	5.67	8.09	4.09
	15.5	1.59	1.93	3.36	7.67	2.26	2.13	4.18	3.94	7.32	3.35
	19.6	3.70	3.29	5.94	10.62	2.89	3.61	6.10	6.73	10.19	5.71
	21.0	3.09	2.80	5.37	10.48	7.39	2.77	6.11	7.09	9.33	5.17
	22.7	3.43	2.56	6.84	7.87	4.84	2.71	5.85	4.56	7.45	5.15
	28.9	4.88	3.97	8.09	10.71	5.25	2.43	7.27	6.34	8.41	6.58
	31.4	5.39	3.37	9.24	12.43	7.00	2.72	9.04	7.35	9.24	7.57
	31.9	4.82	3.17	7.92	10.44	6.26	2.30	6.22	5.17	8.25	6.25
	35.1	4.26	2.95	6.54	12.22	4.75	3.54	10.05	8.12	11.65	6.47
ean	22.4	3.63	2.76	5.70	9.21	4.39	2.54	6.06	5.56	8.19	5.14

 Table 3.6
 Intramuscular fat content of the standard muscle groups of 11 Angus steer carcasses

* for detail of standard muscle groups see Chapter 4 Source: Johnson et al., 1973a.

Yield Grade. Comparable muscles from heifers averaged 0.5 to 1 per cent higher in fat than from steers of the same quality and yield grade.

Callow (1962) reported a range of from 1.3 per cent fat in the muscles of the foreshin in a Friesian steer up to 11 per cent fat in the loin muscles of a Shorthorn steer. Intercostal muscles showed higher percentage of fat in all studies than those quoted, but fat associated with these muscles is very difficult to separate physically.

Thus the musculature is not uniform in chemical composition and this is particularly influenced by the general level of fatness of the carcass.

Chemical composition of fatty tissues

Brännäng (1966) analysed fat from the various depots for bulls and steers. These results are given in Table 3.7.

Depot		Bulls		-	Steers	
	Water	Protein	Fat	Water	Protein	Fat
Subcutaneous	24.24	9.19	66.65	17.23	6.10	76.69
Intermuscular	24.93	7.20	68.16	22.71	6.57	70.94
Kidney	7.08	1.46	91.66	5.48	1.11	93.39
Mesenteric	17.24	3.38	79.43	14.71	2.75	82.68

 Table 3.7 Percentage chemical composition of fat from various depots of bulls and steers

Source: Brännäng, 1966.

The chemical composition of the various fat depots is thus variable. Kidney fat has the lowest percentage of moisture and protein and the highest percentage of fat. The fatter an animal gets the higher will be the percentage of chemical fat in each fat depot, conversely in thinner animals the percentage of chemical fat in each fat depot will be lower. Young calves at low fat levels have a low percentage of fat in the fat depots and correspondingly higher proportions of moisture and protein.

Reid (1972) cited work of Waters (1908) which showed that chemical fat in adipose tissue of cattle (separable fat minus kidney and offal fat) was influenced by plane of nutrition (Table 3.8). Adipose tissue from cattle on the lower plane of nutrition had considerably more water and less chemical fat than that from animals on the higher plane.

Regimen prior			
to slaughter	Water	Protein	Fat
	%	%	%
Full-fed	20.0	7.8	72.9
Maintenance	25.5	9.2	62.8
Sub-maintenance	42.4	13.8	37.7

Table 3.8Composition of adipose tissue

Source: Reid, 1972.

Callow (1962) reported a great variation in the percentage of fat within a depot depending on where it was located. He quoted variations in percentage of fat of subcutaneous tissue from 25.2 per cent (from the 'foreshin' of a Friesian) to 89.8 per cent (from the 'pelvis' of a Hereford); for percentage fat of the intermuscular depot the range was 29.5 per cent (from the 'foreshin' of a Friesian) to 82.7 per cent (from the 'pelvis' of a Hereford). His average for percentage fat in subcutaneous tissue was 69.5, for intermuscular tissue was 67.7 and for kidney fat 94.2—values similar to those of Brännäng (Table 3.7).

RELATIONSHIP OF CHEMICAL COMPOSITION

TO PHYSICALLY SEPARATED TISSUES OF THE BODY

There is a definite parallel between growth patterns of chemical components—water, protein, fat and ash—and those of physically separated muscle, fat and bone described in Chapter 2. The chemical component showing the greatest variability is fat and its increase proportionately reduces water and protein in the body. This is the same effect as observed for physically separated fat in relation to muscle. Approximately 50 per cent of the body water and protein are found in the musculature and a slightly higher proportion of chemical fat is found in the fat depots of the body, so that muscle growth parallels water and protein accretion in the body and chemical fat relates to increases in the fatty tissue depot storage.

There is a school of thought which questions the relation of chemical and physical composition. Since not all protein is found in the musculature and fatty tissues contain various levels of fat, one can readily understand how a direct relationship may not exist. Reid (1972), in comparing data from an early Illinois study on three types of pigs, found chemical composition to be quite similar among the types while physical separation revealed one group (Chuffy) to have considerably

more fat than the other two. However, the two sets of data were not obtained from the same pigs so sampling error may have been involved. Conversely, when comparing chemical and physical composition of two groups of lambs, Reid (1972) reported very good correspondence, in that physically separated fat was 36.6 and 31.9 per cent of carcass weight, while chemical fat was 34.8 and 30.0 per cent respectively. Reid calculated correlations between carcass protein and dissected lean and between carcass ether extract and dissected fat for two groups of lambs. Both relationships were very high with relatively low residual coefficients of variation. Unfortunately little data of this sort are available whereby a direct relation between chemical and physical components can be determined, but it appears that similar though not identical conclusions should result from either end point in most studies of growth. There is a great need for more studies which would determine carcass composition by physical dissection followed by chemical analyses of the dissected tissues so that the true relationship could be established.

FACTORS INFLUENCING GROWTH PATTERNS OF CHEMICAL COMPONENTS OF THE BODY

Since the chemical composition of the body is reflected by proportions of physically separated tissues, one can conclude that the factors which were shown in Chapter 2 to affect the proportions of muscle, fat and bone would also influence the chemical composition in terms of water, protein, fat and ash. Major effects occur in fat deposition which then influence the proportion of other components. Genetic effects are observed in that some breeds are inclined to be early fatteners and others late fatteners; sex effects result from the fact that heifers fatten more readily than steers and steers are earlier fatteners than bulls. The influences on chemical composition brought about by nutrition have been studied to a considerable extent and these will be reviewed briefly.

Plane of nutrition effects on body composition

Haecker (1920) totally analysed carcasses of steers from lot feeding (concentrate feeding reported earlier in this chapter) and from steers reared on pasture. The latter were slaughtered from 600 to 1,200 lb live weight. A comparison of fattening under the two systems can be assessed in Fig. 3.4 where chemical fat is plotted against live slaughter weight. Fat level was higher in the lot-fed animals indicating a higher effective plane of nutrition compared with the pasture fed steers.


Fig. 3.4 Comparison of chemical fat in the empty body of lot-fed and pasture-fed steers *Source*: Haecker, 1920

Reid (1972) described an experiment with sheep where plane of nutrition, age at slaughter and slaughter weight were controlled. Two planes of nutrition were imposed, the lower of which was still sufficient to produce positive gain in body weight. Body composition results are presented in Table 3.9. The most important variable affecting body composition was empty body weight. Plane of nutrition affected the time taken to reach a certain body weight but did not seem to affect carcass composition. Age at slaughter also seemed to have little effect on body composition independent of weight effects.

Obviously, on the rations used, body composition followed a predetermined pattern relative to body weight from which neither plane of nutrition nor age of animal caused any major deviation. These results seem somewhat at variance with others reported in Chapter 2 and it is not possible to conclude that these different results occur because of chemical v. physical analyses.

Since the chemical composition of the tissues can vary, it follows that physical separation and weighing of the separate tissues may not tell the whole story. For example, a fat depot may, under certain circumstances, carry a large proportion of water and a low proportion of chemical fat and physical weighing would not detect this effect. It has also been held (Reid *et al.*, 1968) that there is a strong tendency

A minu - 1	Empty	Plane	Age		Body c	omposition	
no.	Body wt (kg)	or nutrition	at slaughter (days)	Water	Fat	Protein	Ash
				%	%	%	%
2	19.9	Low	270	61.5	18.5	15.6	3.9
1	28.2	High	270	57.4	24.4	15.0	2.9
3	28.7	Low	349	56.6	23.9	15.8	4.0
5	27.7	Low	381	54.5	27.7	14.3	2.8
8	31.8	Low	374	56.3	24.1	15.8	3.3
4	50.0	High	381	46.1	38.1	13.1	2.6
6	47.5	Low	583	46.1	38.5	12.6	2.7
7	58.3	High	374	46.2	38.4	12.8	2.4
9	56.0	Low	613	46.0	38.5	12.7	2.8

 Table 3.9
 Influence of age and weight on body composition of sheep fed two planes of nutrition

Source: Reid, 1972.

for body chemical composition to be controlled by empty body weight. This theory holds that the chemical components accumulate in the body as it grows in fixed patterns which are determined by the net amount of growth. If growth is slower the whole process is merely delayed in time and slow growth would be expected to result in exactly the same chemical composition as more rapid growth at the same empty body weights.

The data of Haecker (1920) plotted in Fig. 3.4 clearly indicate an exception to this presumed homeostasis as the slower growing steers on pasture had less fat in their bodies at given weight than the faster gaining steers fed in a lot. Also Pryor and Laws (1972) showed that steers which grew faster on a high level of wheat had significantly more carcass fat at similar carcass weights than steers which grew slower on a lower proportion of grain.

Influence of rate of growth, weight loss and re-alimentation on chemical composition of the body

The foregoing deals with situations in which positive growth is maintained. Weight loss may affect chemical composition in a different way than physical composition, particularly since it has been shown

that fat depots from thin animals contain more water and less fat than those from fatter animals. Also Farrell and Reardon (1972) reported that undernourished sheep had a significantly higher water content in the fat-free empty body than well-nourished sheep.

Reid (1972) described an experiment with sheep which was designed to test the effects on chemical composition of the body of (a) rate of growth, (b) weight loss, and (c) re-alimentation following weight loss. The plan of his experiment is shown in Fig. 3.5 and the results of the relevant comparisons are given in Table 3.10.



Fig. 3.5 Plan of experiment by Reid (1972) to test effect of rate of growth, weight loss and re-alimentation on chemical composition of the body

T 11 A 10	<u> </u>	^					•	•
1 able 3, 10	Composition	ot empty	bodies of	sheen i	reared	under	various	regimes
1 4010 0110	composition	or ompty	000100 01	uneep i	Loui ou			B

Treatment [†]	-	1	2	3	4	5	(6 + 7 + 8)	(9 + 10)	(11 + 12 + 13)
Empty body wt	kg	25.8	25.9	30.9	30.8	35.7	35.8	44.7	44.7
Water	kg	15.0	15.0	16.5	19.5*	20.7	21.5*	23.8	25.2*
Protein	kg	4.1	4.1	4.6	4.8	5.3	5.4	6.2	6.4*
Fat	kg	5.6	5.6	8.5	5.2*	8.3	7.5*	13.1	11.5
Ash	kg	1.0	1.2*	1.3	1.3	1.4	1.4	1.6	1.6

*significantly different at P< 0.05 to 0.001 †as shown in Fig. 3.5 Source: Reid. 1972.

The results he obtained were as follows:

- 1. At equal empty body weight, weight loss resulted in similar body chemical composition to continuous growth except the animals losing weight had a slightly higher level of ash (1 v. 2 in Table 3.10).
- 2. Re-alimentation following weight loss resulted in lower levels

of chemical fat and higher levels of water and protein than those maintaining positive growth or those on the down phase of a weight losing regime. There was no apparent effect on level of ash which seemed to be at exactly expected levels at all stages in this experiment.

These results on chemical body composition following weight loss and recovery are quite in line with those described in Chapter 2 where physically dissected tissues were used as the criteria.

Influence of protein level in the diet on chemical composition of the body

Little has been said to this point about nutritional effects other than plane of nutrition (energy intake) on body composition. Nutritional effects depend on rations adequate in other respects. Rations deficient in some important nutrient will have a marked effect on growth and could have effects on body composition. There is insufficient research information in this area to allow projection of what to expect from rations inadequate in ways other than for energy.

Protein is a major important nutrient and a deficiency in protein in the ration might be expected to influence protein levels in the body. It is quite possible, too, that animals with a higher continuous impetus for muscle growth, such as bulls, or late fattening breeds, may have a higher requirement for protein. Stated another way such animals might give additional response to higher levels of protein in the way of overall growth or increased muscle growth.

If the level of protein in the ration does not satisfy the complete requirements of a particular animal, will his response be merely to grow slower, resulting in similar body composition at given empty body weight? Or will there be a differential response in the tissues such that less tissue high in protein (predominantly muscle) will be produced and more fat will be deposited? Haecker (1920) quoted Jordan (1895) as finding no difference in body composition (chemical) in animals fed rations of 19 per cent v. 10 per cent protein.

Reid (1972), drawing from reports of Norton *et al.* (1970) and Andrews and Ørskov (1970), showed how low protein rations resulted in higher levels of fat in the carcasses of sheep. The results of Norton *et al.* are shown in Fig. 3.6 and those of Andrews and Ørskov in Table 3.11. Norton *et al.* used very young lambs and a 12 per cent protein ration resulted in a marked increase in the level of fat in the carcass



Fig. 3.6 Relation between the protein calories in the diet and the fat and protein content of the empty body weight: o-o = 12 per cent crude protein; $\bullet - \bullet = 28.5$ per cent crude protein; $\bullet - = 45.5$ per cent crude protein *Source*: Norton *et al.*, 1970

while a 28.5 per cent level seemed to result in only a slight difference from that of a 45.5 per cent protein level in the ration.

Andrews and \emptyset rskov, with heavier lambs, showed more fat deposited relative to live weight in those on the two rations of lower protein (10 and 12.5 per cent) than in those with 15 per cent or more of protein in the ration. Thus lower levels of protein in the ration seem to result in differentially more fat being deposited in the body than would be expected at the same body weights given higher levels of protein.

10	12.5	15	17.5	20
10	12.5	15	17.5	20
2.14	2.26	2.20	2.28	2.31
3.12	3.27	3.22	3.30	3.18
2.57	2.21	1.62	1.72	1.32
6.13	4.81	4.37	4.01	4.24
	10 2.14 3.12 2.57 6.13	10 12.5 2.14 2.26 3.12 3.27 2.57 2.21 6.13 4.81	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$

 Table 3.11
 Influence of dietary protein level on protein and fat content of sheep carcasses

Source: Reid, 1972.

4 Muscle growth patterns in steers

IN BRIEF The muscles of the calf at birth provide the mechanism by which it converts its limited energy stores into the mobility needed to supplement these stores and thus survive. The relative weights of the individual muscles in this complicated system are determined by the evolutionary experience of the species to meet the immediate needs of the new-born animal. Such needs are different from those of the adult bull. A transition must therefore take place in the relative weights of the muscles, in association with their overall increase in weight in the growing animal.

The stimuli and mechanisms which produce different rates of growth in different muscles are largely unknown, but it is suggested that the weight of evidence favours a strong influence of an evolutionarily acquired genetic pattern in ante-natal growth which is modified by function in the immediate post-natal period. Then follows a pre-pubertal and adolescent phase, when the relative weights of muscles alter little, and from which phase the steers and heifers do not emerge. The young adult male enters a maturing phase which adapts the musculature to the dual role of survival and reproduction with its attendant battles. This phase is undoubtedly stimulated by androgens, but the mechanism of selective action on muscles is unknown.

Mathematical procedures are useful, though limited, in describing the relative growth of muscles. We continually face the problem that the more simple the procedure adopted the better the representation of what happens in growth which can be produced, but the more difficult it is to display or discuss. For example, there is no better way to describe how a muscle grows in weight than to plot every weight, which can be recorded during growth, on a time scale, or some other scale—but such a procedure produces an indigestible, unwieldy bulk of data.

On the other hand, a single value such as an allometric growth coefficient ('b' value) misses out in recording fine detail but is a very useful tool for reducing the recorded information to a simple unit for comparison, tabulation and discussion.

The worker must choose the method or methods most suitable to the particular needs of his investigation, avoiding as much as possible the mathematical procedures which are not based on biological concepts and those, such as percentage increase, which rely heavily on the accuracy of the values chosen as a base for calculation. We find a combination of 'b' values and simple percentage values most useful for describing the growth patterns of muscles and muscle groups while realizing the limitations of our approach.

There is considerable justification for the use of methods of calculation which fix the break point, or points, in di- or multi-phasic patterns. Although it may be argued that biological changes do not occur at precise points but rather over a period of time or a range of weight, this is merely returning to the conflict of the

alternatives of having a simple linear pattern which can be easily discussed, or a curve which defies simple assessment by the non-mathematically inclined, which adornment embraces the majority of those interested in animal growth. The breakpoint itself may, in the growth patterns of some muscles, have a biological significance in pinpointing the onset of androgen production at effective levels far more accurately than does the external appearance of the animals. Such a built-in biological test could titrate effective levels of androgens more effectively than knowledge of blood levels.

The growth patterns of muscles discussed in this chapter show that, in general, large muscles grow proportionately faster than small muscles. There is often discussion regarding the relative growth rates of deep and superficial muscles of the body, and attempts to classify muscles in this way are frustrating for it is hard to decide if many muscles are deep or superficial. For example, are the digital flexors and extensors of the forelimb deep or superficial? There is no answer to this, and so it is suggested that a more practical approach is to classify muscles according to their relation to the skeleton.

Perusal of the muscle growth impetus classifications will show that, in general, the muscles most closely related to the skeleton are smallest and have the lowest growth impetus (the impetus rating of muscles being expressed relative to the rate of growth of the total carcass muscle). All of the low and low-average impetus muscles are closely related to the skeleton; some of the average impetus muscles are less closely related, such as the superficial pectoral and the long head of the triceps brachii. As we pass to the high, average-high and high-average groups the majority of the muscles have only minimal contact with the skeleton.

There is an obvious general conclusion that the muscles most closely related to the skeleton grow slowest and those most removed grow fastest. We can, therefore, think of the low impetus muscles closely related to the skeleton as the vital survival muscles and those of higher impetus, less closely related to the skeleton, as the muscles involved in productive work rather than survival.

Just as it is necessary to seek simple mathematical resolution of growth phenomena by lumping a great deal of data into a few simple figures, so is it also necessary to group individual muscles together into workable anatomical units, so that we may relate their growth to that of the live animal or carcass or total muscle. And just as we lose precision in mathematically lumping data together, so also do we lose precision by the adoption of groups of muscles as the unit of study. This is particularly so in the use of regional anatomical groups which comprise muscles of widely different growth patterns. The 'standard muscle groups' of Butterfield (1963a) have nevertheless proved to be useful and the functional units of Fowler (1968) will also play a part in our understanding of why and how the muscles in the various regions of the body grow on their characteristic patterns.

A great deal more precision in detecting differences in growth of muscles can be obtained by grouping them according to their growth impetus (Butterfield and Berg, 1966c), and this method will be useful in studying the full effects of stimuli such as occur at birth and during sexual maturation. It has already been used to demonstrate the effects of planes of nutrition on relative muscle growth.

The study of growth of muscles indicates that the muscular system is a complex of many units, the growth of each of which is conditioned by genetic and environmental influences. These influences may act in the evolutionary background of the species in determining a pattern for serial development of the musculature, or they may act in response to the day-to-day activities of the individual.

INTRODUCTION

The calf at birth is equipped with a set of muscles which have grown during ante-natal life in such a way that they are able to play their part in ensuring the survival of the new-born animal. The detail of this ante-natal growth is beyond the scope of this book; however, it is a phase of the life cycle which is assuming increasing importance in animal production as the slaughter age of many animals is declining.

If it is to survive, the new-born calf must be able to do two things in which the skeletal musculature is vital. It must walk, or even shakily run, with its dam and it must suck. To carry out these tasks it must have well-developed muscles in the distal parts of its limbs and in its jaws. Such muscles have been called 'early developing' muscles, in that they have completed a considerable part of their total growth at birth.

In contrast to the early developing muscles there are others which have little immediate function at birth and these have completed only a small part of their total growth. The muscles of the abdominal wall fall into this category, for the new-born calf has only minimal gut content and hence there is little weight for the abdominal wall to support. They are termed 'late developing'.

Between the extremes of early and late developing muscles there is a spectrum of development which has evolved to provide the animal with the maximum chance of survival in the vital immediate post-natal period. In this chapter we will pick up this spectrum as it exists in the new-born calf and follow the development of the muscles through post-natal period.

THE CAUSES OF DIFFERENTIAL GROWTH IN THE MUSCULATURE Hammond's theories

An outstanding feature of muscle growth is that it is accompanied by large developmental changes. Individual muscles grow at different rates. There must be causes for the changes in the proportions of individual muscles as animals grow; and it is interesting to re-discuss, after forty years, the three causes put forward by Hammond and to

reconsider the conclusions he reached in light of present knowledge. Hammond (1932) proposed three possible causes for changes in proportion of muscles with age as follows:

- 1. a change in the manner in which the various muscles are employed after birth (i.e., function);
- 2. the hereditary tendency for serial development;
- 3. a reaction to the changes in shape, and alterations in the relative proportions and angles of the different bones.

We would now not accept that muscle proportions do necessarily change with age, for, as shown by Butterfield and Berg (1966c) and Butterfield and Johnson (1971), the changes which are observed in muscle weights are quite independent of age and are highly total muscle weight dependent. In other words we proceed on a different baseline from Hammond. However, this does not prevent valid comparison of current thinking with that of Hammond.

Function and differential muscle growth

Our present knowledge leads us to believe that the change of function of muscles is a major factor in their growth rate relative to each other in the immediate post-natal period, and the evidence which Hammond used to discount this effect is not supported by modern total muscle dissection studies. Hammond stated that the relative changes of weight of some groups of muscles were just as great after as before five months of age, and as function did not change as much after as before five months, it could not be a major factor.

The coefficients of variation for the changes between growth impetus of muscle groups in various phases of growth in steers were presented by Butterfield (1963c) and these are set out later in this chapter (p. 93) and show that the maximum changes in muscle-weight distribution do occur in the early post-natal period—certainly before five months under any reasonable state of nutrition.

Hammond cautiously said that it would be unjustifiable to attribute all the changes to functional demands, and with this we agree, but nevertheless we believe that the evidence is in favour of function being a major factor in relative growth of muscles in the immediate post-natal phase, for the changes which occur in the relative size of the various muscles are so compatible with the changes in function which confront the new-born calf. Withdrawal of the functional challenge has been shown to inhibit the specific developmental changes which normally occur in the musculature. A demonstration of this is given in Chapter 5, where the effect of a fibrous diet compared with a milk diet is shown to influence the relative growth of the muscles of the abdominal wall. Irrespective of nutritional plane, calves on a fibrous diet developed relatively heavier muscles in the abdominal wall than those on a milk diet. The whole milk diet, being an abnormal diet in that the calves were denied any fibrous food, resulted in an abnormal retardation of growth of the muscles of the abdominal wall.

The most dramatic illustration of the effects of function on postnatal development of muscles is seen in changes of growth patterns of muscles with changes of function in the elephant seal (Bryden, 1969). Large changes in relative sizes of muscles were demonstrated in this species associated with changes of activity as the animals changed from aquatic to terrestrial habitat.

Heredity and differential muscle growth

With Hammond's second cause of differential muscle growth, the hereditary tendency for serial development, we are in substantial agreement. There seems little doubt that the experience of evolution has implanted in each species a basic plan of development which is completed in anticipation of functional demands, rather than in response to them in the current generation. The development represented in the new-born calf must be largely governed by a genetic template which ensures a viable structure to be then moulded by the environmental experiences in the pre-pubital stage. However we do not know how far this extends into post-natal life, for example, whether a young bull, completely removed from the opportunities to enter mock battle, will still go through the changes in muscle-weight distribution which we will later show are characteristic of the mature male. Is special 'exercise' necessary to stimulate this development?

Fowler (1968) pointed out that the stage at which form is most critical in the mammal is somewhere between puberty and early maturity. As the animal approaches maturity the stress of reproduction is superimposed on the animal's existing functional requirements. Fowler credits Darwin with saying that the most important part of the selection process occurs when animals are 'nearly grown up'. It is at this time that the competition for the right to reproduce is added to other functional requirements and it seems that, as this is the climax of the whole purpose of the existence of the individual, the

development of its major energy converting system, the musculature, should be centered about this event. It therefore seems highly probable that the concept of a genetic template should extend to this period of life also, and that its implementation is triggered by androgens and its fulfilment modified by functional demands.

The conclusions of Butterfield and Berg (1972), when discussing the role of various factors on muscle development, support the role of 'masculinity' in controlling adult muscle development in preference to fat and age which have been favoured independent variables on which developmental changes of the musculature have been assessed.

Influence of bone growth on muscle growth

Hammond's cause, that the changes of proportion of the muscles was a reaction to the changes of relative proportions and angles of the bones, does not gain a great measure of support from current knowledge, although it was favoured by him as a major factor. There would be justification for this theory only if there were in fact substantial change of those parameters of bone which would produce different functional demands on the muscles.

The growth of muscle relative to bones has been discussed recently by Stewart (1972) in studying the effects of tension on muscle growth, the contention being that increases in length of bones produce increases in passive tension on muscles, and therefore differential bone growth helps to explain differential muscle growth in the surrounding muscles. Stewart stated that 'although it is not suggested that passive tension is the sole factor or even the principle factor in stimulating muscle growth, it appears very likely that it does play a role, perhaps quite an important one in early development'. In support of this conclusion Stewart presented data from Joubert's (1956) ante-natal study on sheep and several post-natal studies (Hammond, 1932, in sheep; McMeekan, 1940, in pigs; Lohse *et al.*, 1971, in sheep; Bryden, 1969, in elephant seals).

A broad consideration which must place great doubt on the claim that there is a cause and effect relationship between the weight of bone and the weight of surrounding muscles is the relative distribution of muscle and bone weights in bulls and steers as shown by Brännäng (1966) working with identical twins. He showed that although there was a marked difference in the weight of muscle in the forequarter there was no difference in the weight of bone (Table 4.1).

	Forequarter		Hindquarter	
	Bulls	Steers	Bulls	Steers
Muscles as % of carcass weight	36.4	30.8	33.4	33.2
Bone as % of carcass weight	9.8	9.8	7.9	7.9

 Table 4.1
 Distribution of muscle and bone weight in monozygous twin bulls and steers

Source: Brännäng, 1966.

The claims regarding the changes in length of bones are largely supported by data handled by the method of percentage increase which tends to exaggerate differences. Fig. 4.1 shows the relative lengths of the femur and tibia of cattle from the dissection series of Butterfield (unpublished). The lengths recorded in each case are the functional lengths of the bone, that is, from proximal to distal articular surfaces. The functional lengths were taken because the greater trochanter of the femur changes its size relative to the length of the shaft of the femur as the animal grows, and the length of the whole bone is therefore no indication of shaft length. As can be seen, the functional length of the two bones is almost identical and variations are extremely small. The



Fig. 4.1 Relationship between lengths of femur and tibia of an heterogeneous collection of cattle (previously unpublished data)

difference in length of the two bones rarely exceeds a centimetre. The only part of the study where the majority of plots fall below the line (i.e., the femur is shorter than the tibia) is in the ante-natal period and in the immediate post-natal period, when the mean difference in length is about 0.5 cm. It is tempting to suggest that there may be a relationship between this small difference and changing relative muscle growth because they do occur at the same time. However, of the five one-dayold calves plotted, two are each side of the line and one is on it. There was no greater difference than 0.3 cm from equal length. As the calves on and above the line had already achieved their mature relative lengths, are we to believe that they should also have achieved their mature muscle weight distribution? Dissection of the musculature confirmed that they had typical new-born calf muscle weight distribution. Had they developed into normal adults, as they undoubtedly would have done, this would have been achieved without any differential passive tension due to differences in femur and tibia length.

It seems to be unrealistic to talk about the possible effect of the length of bones without also taking into account the angles of joints. It would take a minute alteration in angulation of joints to adjust for the differences in functional length of these bones. No data are available on angulation.

To group together muscles with widely scattered insertions and, as Stewart has done, call them muscles of the thigh as distinct from muscles of the leg, and to then relate each group to the growth of a particular bone, is sweeping with a very broad broom. For, whereas the adductor femoris muscle for example may be truly related to the femur, it seems that muscles like the biceps femoris which span both bones should be related to them both, if the answers to differential muscle growth were to be found in changes in bone length.

It is our opinion that it is of little importance to this discussion what happens to the weight of these bones. However, as Hammond used weight in developing his support for this cause, and as the weight of bone appears to have mystical qualities in traditional live animal assessments, it is well to note that the relative weights of the tibia and femur bore a relationship just as constant as did their length (see Fig. 4.2.)

In experiments with twin bulls and steers (Brännäng, 1971) there did not appear to be any consistent relationship between the measured differences in skeletal weight or length and the difference in growth



Fig. 4.2 Relationship between weights of femur and tibia of same heterogeneous collection of cattle as in Fig. 4.1 (previously unpublished data)

of associated muscles. The scapula and humerus were reduced in both length and weight by castration, yet the infraspinatus, supraspinatus and subscapularis muscles reacted in an irregular fashion. In one experiment the supraspinatus was retarded less than total muscle and in another it was retarded similarly to total muscle by castration. The infraspinatus muscle was retarded more in both experiments whereas the subscapularis was retarded less than total muscle in both experiments. These three muscles bear as close a relationship to bone as is found anywhere in the body due to their expansive origins on the scapula, yet their weights do not follow the bone weight.

On the other hand, the small (about 7 per cent) reduction in the height of the first to fifth thoracic dorsal spines in steers is associated with the general reduction of the weight of the dorsal muscles of the neck in the steer. However, the bones of the pelvis are both lighter and shorter in the steer and yet he has muscles in this area which are relatively just as heavy as in the bull. Hammond particularly emphasized the effects of length in the caudal part of the pelvis, but there seems to be little evidence to support any relationship between this length and differential muscle growth, as in Brännäng's data the length from the cranial edge of the os pubis to the caudal part of the os ischii was significantly reduced in steers, yet muscle development in the area was not.

A further factor which influences us against the acceptance of any overall causal relationship between growth in weight of muscle and bone is that surrounding any bone there are muscles of extremely

different growth patterns—for example, the sartorius and tensor fascia lata muscles were shown by Butterfield and Berg (1966a) to have 'b' values of 0.87 and 1.04 which were significantly smaller and larger than 1.0 respectively. Both these muscles have their origins on the os coxae and proceed distally along the femur.

In general those muscles which are more closely related to the skeleton and smaller have lower growth impetus than those which are more superficial. It does not seem likely that a causal relationship could be established between the increase in weight of a bone and the variety of different rates of weight increase of the muscles surrounding that bone. Many, including Stewart (1972) continue to rely on the alleged late relative development of the loin put forward by Hammond. It has since been shown by many workers (Luitingh, 1962; Butterfield, 1963a, c; Walker, 1963; Fourie, 1965; Lohse, 1971) that the alleged high impetus of post-natal growth attributed to the loin by Hammond was mainly derived from the high impetus of the muscles of the abdominal wall which he included in his 'loin'. The most careful studies of bone growth in the loin are those of Walker (1963) and Fourie (1965). However, Walker reported that the bones of the lumbar region grew at almost the same rate as total bone in cattle, and that the muscles of the lumbar region considered as a group also grew at about the same rate as total muscle. It certainly makes more sense to relate the growth of muscles in areas such as the loin, where they are closely tied to the vertebrae, to the growth of these vertebrae, as there is little change possible in angulation. However, there must surely be consideration, not of groups, but of individual muscles closely associated with the lumbar vertebrae such as the longissimus dorsi and multifidus muscles etc. A comparison of the growth patterns of these muscles will show that there is a variety of patterns of growth impetus in the muscles which could not fit any one pattern of bone growth. Similarly in the pelvic limb there are muscles in the thigh with a wide range of different growth patterns. If passive tension is a factor in the growth impetus, its effect must be extremely small relative to other factors, such as function, and also highly selective among muscles in some way which is not presently clear.

An interesting and most significant development in the relationship of bone weight to muscle weight has been revealed in the studies by Vissac *et al.* (1971) of the morphology of 'double-muscle' cattle in France. They have shown that these cattle have the greatest reduction of bone weight, compared with normal cattle, in the proximal part of the limbs, whereas in these same regions they have the greatest increase of muscle weight compared with normal cattle.

Although there could be some objection to the use of evidence from these animals which are unusual in many ways, this is certainly further support for the idea that the relationship between increases in muscle weight and increases in bone weight of a specific region are independent processes. Thus the proposal of Hammond is not compatible with the information on growth patterns which has become available since he suggested it—although even when preparing the cause he did point out, but did not justify, that individual sub-groups of muscles round a bone vary among themselves in their rates of growth.

Conclusions—causes of differential muscle growth

The available evidence supports a phasic variation in the influence of three causes on the variation in muscle growth rates.

PHASE 1 — The ante-natal phase

Is probably almost entirely under the influence of a genetic template which ensures that at birth the animal is capable of meeting the 'usual' environmental challenges to which the species has adapted throughout evolution. Muscle is probably stimulated by passive tension from skeletal elongation.

PHASE 2—The immediate post-natal phase

A phase of great change in relative muscle weight. Is largely completed during the doubling of the birth weight of the musculature but certainly continues in some muscles to a quadrupling of the muscle weight (Lohse *et al.*, 1971). This development is largely influenced by function and as the function of the pre-pubital quadrupeds within a species is remarkably uniform, so too is the development uniform. Where differences in function are produced (e.g., in muscles of the abdominal wall by different physical nature of the diet) then differences in rate of relative growth of muscles results.

PHASE 3—The pre-pubertal and adolescent phase

In which muscles of both the male and female grow at an almost uniform rate from a base which is the product of their genetic and functional adjustment. In this phase there is a large increase in size with little change in relative weights associated with little change in function.

PHASE 4 — The maturing phase

In which the relative growth of the musculature alters dramatically in the male to produce an animal which is capable of fulfilling the double role of survival and struggle for the right to reproduce. This phase is probably triggered by androgens to proceed along an hereditary pathway of development, supported by responses to function. In the steer this fourth stage is seen as a faint mirage of what would have been had castration not occurred, in that some slight change in the muscle weight distribution pattern of the type seen in bulls is found also in steers, but without the support of adequate sex hormone the full development is not achieved. In other words the musculature of the steer and also the female never matures. There seems to be little need to invoke causes other than heredity, changes of function, and sexual maturation to explain the observed changes in muscle weight distribution in cattle. Which is in line with the statement by Goss (1964) that the extent to which an organ expresses its potential for growth is determined by the physical requirements placed on it after having differentiated to the point of functional competence.

METHODS OF DESCRIPTION OF MUSCLE GROWTH PATTERNS

The growth of muscles may be measured by comparison of weights of the individual muscles of a series of animals slaughtered and dissected throughout the life span. A dissection technique for cattle was described by Walker (1961) and this technique is suitable for use by a large team. A technique which can be used by a lone worker or a small team was described by Butterfield (1963a, b) and in more detail by Butterfield and May (1966).

Having assembled a large amount of data from a dissection series the worker is confronted with the task of choosing, from among the mathematical methods available, that which best depicts the growth patterns. No one method, or indeed any combination of methods, can capture the full story of growth. In seeking mathematical methods best suited to depict the phenomena of growth we are torn between the need to present a completely accurate picture, and the need to have some simple value which can be easily understood and simply presented. If we are to have a workable body of data when dealing with large numbers of values for large numbers of anatomical entities such as individual muscles, we should use the most simple method available which will capture the most important aspects of the growth patterns. Methods of describing relative growth have been discussed by Pálsson (1955) and by Luitingh (1962). A method which compares the percentage values of weight of individual muscles or groups, relative to total muscle weight at various stages of development, is most useful in studies of the musculature, as a simple visualization of relative weights of muscles is possible from the percentage values. For studies of continuing growth this method suffers from the need for specific cut-off points at which comparisons are made. Huxley's (1932) growth coefficients can be used to provide a measure of proportionate change over a range of weight during growth.

We have found that by using combinations of percentage values of the entity to the whole at the start and end of some growth phase, combined with the growth coefficient or coefficients between these two points, that information is assembled which is workable, and it can be freely understood by the non-mathematicians who predominate among those interested in cattle. Thus in this chapter we will rely on these two methods.

Growth patterns of individual muscles of steers were first described by Butterfield and Berg (1966a) based on the dissection of 62 steers and 30 calves. They found the terms 'early and late developing' inadequate fully to describe the growth patterns and introduced a system of classification based on the rate of growth of the muscle expressed relative to the growth of total muscle. The muscles were classified according to relative growth impetus. By arbitrary division of the total span of the study into phases they were able to detect changes of growth impetus. If no change occurred the muscle was described as possessing a monophasic growth pattern, however, if a significant difference between phases was detected then it was described as a diphasic pattern. Schematic representation of the various growth patterns is shown in Figs. 4.3 and 4.4.

The system of classification is described as follows:

- *High impetus:* a muscle with a growth coefficient significantly greater than 1.0 and no significant difference among phases.
- Average impetus: a muscle with a growth coefficient not significantly different from 1.0 and no significant difference among growth phases.
- Low impetus: a muscle with a growth coefficient significantly less than 1.0 and no significant difference among growth phases.
- High-average impetus: a muscle with a growth coefficient significantly



Fig. 4.3 Schematic representation of monophasic growth patterns



Fig. 4.4 Schematic representation of diphasic growth patterns

greater than 1.0 in early life but not different from 1.0 in later phases of growth.

- Average-high impetus: a muscle with a growth coefficient not significantly different from 1.0 in early life, but significantly greater than 1.0 in later phases of growth.
- Low-average impetus: a muscle with a growth coefficient significantly less than 1.0 in early life, but not significantly different from 1.0 in later phases of growth.

A refinement of this method was introduced by Lohse *et al.* (1971) when classifying sheep muscles in which a system of overlapping growth coefficients was introduced. In this system the growth impetus up to and beyond multiples of total muscle weight at birth were calculated and tested for significant differences. This method allows more sensitive testing of changes of growth impetus although it still suffers to some extent from the arbitrary selection of phases.

The method of calculating a 'break point' for change of impetus introduced by Mellits (1968) and used extensively by Cheek (1968) has not yet been utilized in cattle studies, but could provide a useful tool particularly in detecting the smaller differences which will no doubt be sought in future work.

The problem of choice of a baseline on which to calculate muscle growth patterns was to select between various available parameters, such as age, live weight, carcass weight or total muscle weight. Although the original study of Butterfield and Berg (1966a, b) was based on cattle grouped into age phases, the analysis was carried out on a total muscle weight basis. Subsequently Butterfield and Berg (1966c) showed that the relationship between the weight of individual muscles and total muscle weight was extremely close, irrespective of age. It was therefore clear that the growth impetus of individual muscles should be determined relative to the weight increase in total muscle. As the major function of the musculature in cattle is to support the total weight of the animal and not just the weight of the musculature, there could be an argument for calculating muscle growth patterns on the basis of total body weight. However, the fortunate phenomenon of the muscle weight being a fairly stable 33 per cent of body weight in cattle (Callow, 1944) probably means that such a procedure would be little different to the present one, in which total muscle weight is used.

It is difficult to utilize the growth patterns of 100 individual muscles in consideration of weight, genetic, nutritional or other influences, and so it has been necessary to group muscles in various ways. The study of muscle groups defined on an anatomical basis, and called 'standard muscle groups' was reported by Butterfield (1963a, c) who developed growth patterns for muscles of steers by the simple comparison of the weights of the muscle groups as a percentage of total muscle.

The definition of the 'standard muscle groups' is:

GROUP 1—Those muscles of the pelvic limb which arise from the os coxae, together with the vasti and articularis genu muscles.

- GROUP 2—Those muscles which arise from the distal half of the femur, from the tibia, or from the fibula, excluding the vasti and articularis genu muscles.
- GROUP 3—The muscles surrounding the spinal column in the thorax and lumbar region.
- GROUP 4-Muscles of the abdominal wall.
- GROUP 5—The intrinsic muscles of the thoracic limb which arise from the scapula or proximal half of the humerus.
- GROUP 6—Those intrinsic muscles of the thoracic limb which arise from the distal half of the humerus, from the radius, or from the ulna.
- GROUP 7—The muscles of the thorax which are attached to the thoracic limb.
- GROUP 8—The muscles of the neck which are attached to the thoracic limb.
- **GROUP** 9—The intrinsic muscles of the neck and thorax.

'EXPENSIVE GROUP'—The combined groups 1-3-5.

Butterfield and Berg (1966b) continued the study of muscle groups by classifying the growth patterns of the 'standard muscle groups' in steers using the same allometric growth coefficient method of analysis as for individual muscles. Berg (1968b) used a combination of growth coefficients and percentages when studying the relative growth of the standard muscle groups in bulls, steers and heifers. Brännäng (1971) adopted a useful approach in comparing the relative muscle growth of twin bulls and steers. He expressed the weight of individual muscles and some groups studied in steers relative to bulls, and relative to total muscle weight. This is shown in Fig. 4.5. Brännäng described the difference as the effect of castration, thereby emphasizing that it is the bull which is normal and the steer which is modified by man. The figure shows the per cent reduction in the muscles of the steer compared to his monozygous twin bull. The dotted line indicates the reduction of the total musculature of the steer relative to the bull (about 7 per cent).

GROWTH PATTERNS OF INDIVIDUAL MUSCLES

On the basis of arguments set forth previously it seems to be a reasonable assumption that the pattern of post-natal muscle development in steers is largely determined by the modifying effects of function on the genetically established pattern of muscle growth. As Bryden



Fig. 4.5 The effect of castration on muscle weight both for the total muscle mass and for the different single muscles or muscle groups *Source*: Brännäng, 1971

(1969) has suggested, functional demand is of relatively greater importance than minor differences of heredity during post-natal development of the musculature, and Leche (1970) has extended this to imply that small breed differences are likely to be swamped by functional modifications.

Set out in this section is the classification of the growth patterns of individual muscles of steers adapted from Butterfield and Berg (1966a) together with discussion of the functions of the muscles which would lead to these patterns. They are classified by impetus groups as described above. Within the impetus groups the muscles are arranged in the standard muscle grouping.

The forty-four muscles with a low or low-average post-natal growth pattern are those which, having reached a relatively advanced stage in their growth at birth, then grow at a slower rate than the remainder of the musculature following birth. No study has been made of the

Low impetus muscles

(Within each standard muscle group the muscles are arranged in ascending order of growth impetus.)

	· · _ · · · · _ · _ · _	
		Muscle weight
		as per cent of
A notomical location		total muscle
(Standard muscle group)		500 lb corocco
(Standard muscle group)	Nama	(Duttorfield &
	Name	(Dutternett &
		May, 1900)
I. PROXIMAL HINDLIMB		
	M. gemellus	0.16
	M. sartorius	0.39
	M. obturator internus et ext	ternus 0.58
	M. rectus femoris	2.12
	M. vastus lateralis	2.59
	M. gluteus profundus	1.25
II. DISTAL HINDLIMB		
	M. tibialis anterior	0.12
	M. popliteus	0.29
	M. extensor digiti quarti	
	proprius (pedis)	0.25
	M. peroneus longus	0.10
	M. flexor digitorum	
	superficialis	0.44
	M. flexor hallucis longus	0.63
	Mm. extensor group	0.73
	M. flexor digitorum longus	
	(pedis)	0.20
	M. tibialis posterior	0.12
III. SPINAL MUSCLES		
	M. psoas minor	0.34
	M. quadratus lumborum	0.14
	Mm. multifidi dorsi	0.86
	M. iliacus	0.88
V. PROXIMAL FORELIMB		
	M. brachialis	0.48
	M. triceps brachii (caput	
	laterale)	0.65
	M. coracobrachialis	0.15
	M. teres minor	0.20
	M. supraspinatus	1.52

Anatomical location (Standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
VI. DISTAL FORELIMB		
	M. extensor carpi obliquus	0.02
	M. flexor carpi radialis M. flexor digitorum	0.11
	sublimis M flexor digitorum	0.36
	profundus	0.64
IX. THORAX and NECK	M. extensor carpi radialis	0.73
	M. multifidus cervicis M. intertransversarius	0.25
	longus M. longissimus capitis et	0.28
	atlantis	0.28
N = 32	Total	17.86
		Mean 0.56%
Low/average impetus muscl	8 \$	
III. SPINAL MUSCLES		
	M. spinalis dorsi	1.64
	M. iliocostalis	0.46

	M. iliocostalis	0.46
V. PROXIMAL FORELIMB		
	M. deltoideus	0.50
VI. DISTAL FORELIMB		
	M. extensor digiti terti	
	proprius	0.12
	M. extensor digiti quarti	
	proprius	0.21
	M. extensor carpi ulnaris	0.29
	M. flexor carpi ulnaris	0.15
VII. NECK TO FORELIMB		
	M. brachiocephalicus	1.46

Anatomical location (Standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
IX. NECK and THORAX		
	M. longissimus cervicis M. serratus dorsalis	0.32
	cranialis	0.13
	M. longus colli	0.32
	M. semispinalis capitis	1.55
N = 12	Total	7.65 Mean 0.64%

muscles of the head which, because of their essential nature for survival, would most certainly have a low post-natal impetus.

The low and low-average impetus muscles include those essential for the most elementary actions of locomotion (the flexors and extensors of the distal part of the limbs) and the deep muscles of the thicker parts of the body. Not only are they well developed at birth but they lose the least relative weight during periods of body weight decline (Butterfield, 1966a). These muscles are generally individually small, fibrous and non-fleshy. They make up about 33 per cent of the total musculature at birth and 25 per cent in a market weight steer (500 lb carcass).

It is tempting to suggest that the location and function of the low impetus muscles makes it extremely difficult for these muscles to grow. For example, the very deep muscles surrounding the hip joint, such as the obturators and the deep gluteal, are so tightly bound by their attachments that some physical restriction to their growth seems likely. The extensors and flexors acting on the carpus, tarsus and digits are very tightly bound by connective tissue which could impede their growth.

The fifteen muscles classified as average impetus may be expected to perform uniform functions throughout post-natal life. The demands placed upon them in the new-born animal relative to the activity of

Anatomical location (standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
I. PROXIMAL HINDLIMB		
	M. gracilis	1.40
	M. gluteus accessorius	0.28
IV. ABDOMINAL WALL	C C	
	M. serratus dorsalis	
	caudalis	0.12
V. PROXIMAL FORELIMB		
	M. triceps brachii (caput	
	longum)	3.13
	M. biceps brachii	0.67
	M. subscapularis	1.17
	M. tensor fasciae antibrachi	i 0.16
	M. teres major	0.46
VII. NECK TO FORELIMB		
	M. trapezius cervicalis	0.54
VIII. THORAX TO FORELIME	3	
	M. pectoralis profundus	3.72
	M. pectoralis superficialis	1.50
IX. THORAX AND NECK		
	M. transversus thoracis	0.21
	M. rectus thoracis	0.14
	M. obliquus capitis	
	caudalis	0.34
	M. scalenus ventralis	0.58
N = 15	Total	14.21 Mean 0.95%

Average impetus muscles

the whole musculature are probably little different from those found in the adult steer. Thirteen of the fifteen muscles of this classification occur in the forequarter and of these nine are associated with the proximal part of the forelimb.

It may be suggested that the calf at birth needs muscles in the proximal part of the forelimb which are capable of performing relatively as well as in the adult animal, for the new-born calf to suck its mother it needs some stability of the cranial end of the trunk. Observation of the stance of the new-born calf when suckling indicates that it can adopt a more stable position with its forelimbs than with its hind.

The group of eight muscles classified as high impetus might be expected to experience functional demands which increase with increased weight of the animal. Most of the muscles in the group are weight supporting, such as the ventral serrates which provide the most direct line of force for the weight of the trunk to the forelimb.

Anatomical location (standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
I. PROXIMAL HINDLIMB		
	M. tensor fasciae latae	1.36
IV. ABDOMINAL WALL		
	M. cutaneus trunci	1.63
	M. obliquus abdominis	1.(2
	internus	1.03
VIL NECK TO FORFLIND	M. rectus abdominis	2.13
VII. NECK TO FORELIMB	M. competers constralia	
	M. serratus ventrans	2 1 2
VIII THOPAY TO FORELIME		5.12
VIII. THORAX TO PORELIME	M latiesimus dorei	2.04
	M serratus ventralis	2.04
	thoracis	1 34
IX THORAX AND NECK	tilotaçis	1.54
M. MORAMO ALCK	M. splenius	0.77
N = 8	Total	14.02
		Mean 1.75%

High impetus muscles

The latissimus dorsi by its action in preventing flexion of the shoulder joint in the standing animal is also involved in supporting weight.

It is surprising that the deep pectoral muscle does not have a similar pattern and it is interesting to note that in sheep Lohse *et al.* (1971) reported high impetus in the growth of the deep pectoral in the immediate post-natal phase of growth.

The splenius is a muscle which has some weight supporting function in relation to the head; however, its high impetus growth in the steer is probably more related to its specialized function of fighting in bulls than to weight support. This will be discussed along with other sex differences in Chapter 5.

No special reason can be advanced for the high impetus growth of the cutaneous muscle other than its unrestricted location within the superficial fascia.

The two muscles of the abdominal wall which fall into this classification (the internal oblique and the rectus) play a major part in supporting the weight of the abdominal contents. Although it may simply be fortuitous that the other two muscles of the abdominal wall (the external oblique and the transverse) have high-average rather than high growth patterns, it could be suggested that their weight bearing function is less than that of the rectus and the internal oblique, each of which arise primarily from discrete origins.

It is also possible that more extensive study may reveal that there is little difference between the patterns of those muscles we have classified as high and those classified as high-average. Lohse *et al.* (1971) classed all the muscles of the abdominal wall of sheep as 'high impetus' except the external oblique muscle which was 'average-high' and this suggests that more extensive data in cattle may result in all the muscles of the abdominal wall being classified as high impetus.

the muscles of the abdominal wall being classified as high impetus. The high-average impetus group contains the luxury muscles of the body. They are luxury muscles functionally and also from the consumer's point of view. Included are the major fleshy muscles of the hind limb and loin and also two from the abdominal wall. They remain relatively light at birth—a fortunate occurrence for the ease of that event—and then enjoy a rapid growth spurt as soon as the intake of food after birth results in a gain of weight in the musculature. Butterfield and Johnson (1971), by holding calves at their birth weight for seventy days, showed that this relative increase in muscle weight of these muscles could be delayed.

These may be regarded as muscles, the full development of which

Anatomical location (standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
I. PROXIMAL HINDLIMB		
	M. biceps femoris	7.29
	M. gluteus medius	3.82
	M. semitendinosus	2.59
	M. semimembranosus	5.24
	M. adductor femoris	1.90
III. SPINAL MUSCLES		
	M. psoas major	1.70
	M. longissimus dorsi	6.55
IV. ABDOMINAL WALL		
	M. transversus abdominis M. obliguus abdominis	1.21
	externus	2.17
N = 9	Total	32.47 Mean 3.61%

High-average impetus muscles

is necessary for maximum locomotor performance, or in the case of those located in the abdominal wall, maximum visceral performance, but whose full development is not essential to survival. This applies equally in the new-born calf or in the animal subjected to severe body weight loss (Butterfield, 1966a).

These two average-high impetus muscles, one connecting the forelimb to the neck and the other connecting the forelimb to the neck and thorax, are muscles which, in the bull, could be expected to be involved in fighting. The average-high pattern in steers is probably a faint replica of the pattern in bulls. Brännäng (1971) showed that the rhomboid and ventral cervical muscles (which include the omotransversarius) were markedly affected by castration (p. 81).

Anatomical location standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
VII. NECK TO FORELIMB	······································	
	M. omotransversarius	.53
	M. rhomboideus	1.45
N = 2	Total	1.98 Mean 0.99%

Average-high impetus muscles

Unclassified muscles

Anatomical location (standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 500 lb carcass (Butterfield & May, 1966)
I. PROXIMAL HINDLIMB		
	M. quadratus femoris	0.07
	M. articularis genu	0.08
	M. vastus medialis	0.70
	M. vastus intermedius	0.70
IV. ABDOMINAL WALL		
	M. retractor costae	0.13
V. PROXIMAL FORELIMB		
	M. anconeus	0.10
	M. triceps brachii (caput	
	mediale)	0.10
	M. infraspinatus	2.02

Anatomical location (standard muscle group)	Name	Muscle weight as per cent of total muscle weight in 5001b carcass (Butterfield & May, 1966
IX. THORAX AND NECK	<u>.</u>	
	M. scalenus dorsalis	0.17
	M. rectus capitis ventralis	
	major	—
	Mm. intercostales	2.59
	M. rectus capitis dorsalis major	
	M. intertransversales colli	0.46
SCRAP MUSCLE		4.69
N = 14	Total	11.81
		Mean 0.84%

Thirteen muscles were not classified due to various factors. These are mostly very small muscles, or muscles in which the dissection involved some arbitrary separation such as the division between the medial vastus and intermediate vastus.

It is interesting that only one large muscle, the infraspinatus, grew in such a variable manner that it could not be classified.

Discussion of growth patterns

The size of muscles in the various classifications of growth patterns is of considerable interest, for it will be seen from Table 4.2 and from the individual values given alongside each muscle in the impetus groups above that there is a strong tendency for small muscles to grow proportionately slowly and large muscles to grow proportionately fast.

Why do large muscles grow faster than small muscles?

We believe that there is probably a very simple explanation to this question in that almost all small muscles contain a higher proportion of connective tissue than do large muscles and therefore a smaller proportion of muscle fibres. The potential for growth of muscle

		Mean weight of each muscle as % of total	Total weight of muscles as % of total muscle	Muscle weight relative to % of total muscle weight			
Impetus group N	N	muscle weight	weight	Grea N	ater than 1%	Less N	than 1% %
Low	32	0.56	17.86	4	12.5	28	87.5
Low-average	12	0.64	7.65	3	25.0	9	75.0
Average	15	0.95	14.21	5	33.3	10	66,2
Average-high	2	0.99	1.98	1	50.0	1	50.0
High	8	1.75	14.02	8	88.8	1	11.2
High-average	9	3.61	32.47	9	100.0	0	0.0
Unclassified	14	0.84	11.81	3		11	

 Table 4.2
 The relationship between muscle weight and growth impetus

fibres appears far to exceed that for connective tissues and therefore the muscles with a higher proportion of muscle fibres to connective tissue can be expected to grow faster. Support for this idea can be seen in the growth of the 'Culard' where the more fibrous muscles of the distal parts of the limbs are less hypertrophied than the fleshy muscles more proximally (Vissac *et al.*, 1971). This is further discussed in Chapter 5.

GROWTH PATTERNS OF ANATOMICALLY-DEFINED MUSCLE GROUPS

There are good reasons (p. 79) why it is necessary to group muscles into anatomical regions to look at the story of growth, although it must be recognized from the start that to group together a collection of such individual entities is immediately to invite imprecision. For, as has been seen in the previous section and in more detail in Butterfield and Berg (1966a), each muscle is an individual which grows according to a genetic pattern and the functional demands of the body in meeting its environmental challenges. Nevertheless, a good deal of trade in beef takes place in which anatomical regions are the article of commerce and it is important to know how the muscle mass in each of these regions grows relative to each another.

Fowler (1968) put forward the idea that we could regard some anatomical regions as functional units and showed the advantages of this approach in analysing the effects of nutritional treatments. Lohse *et al.* (1971), in reporting the growth patterns of muscles of sheep, contended that the growth patterns of individual muscles, within some anatomical regions, were so diverse that it was difficult to regard them as members of the same functional unit. The examples given by Lohse *et al.* fall into the regions which Fowler classified as 'intermediate' between his various functional units, and it is apparent that both schools of thought recognize similar difficulties.

This discussion highlights the differences in growth patterns of individual muscles within a group and it is a matter of concept whether a functional group should, or should not, contain muscles of different growth patterns. In this section we are going to deal mainly with groups of muscles which have only one feature in common—their anatomical location. Earlier work of Hammond used a technique of jointing of carcasses and the establishment of groups of muscle tissue on the basis of commercial 'cuts' of meat. While this method was valuable to describe growth changes in a commercially meaningful way, it also produced some misleading information. This was due largely to the utilization of anatomical terminology to describe butcher's cuts which exceeded the normal boundaries of the anatomical regions utilized in their naming. The outstanding example of this was the cut described as 'loin' which included a major part of the abdominal wall.

We have come to accept that, with small limitations, we can divide carcasses in two down the midline and use the data from one side as a sample of the whole (Butterfield, 1963a), but this is the limit of mutilation which can be accepted if we are to obtain the maximum yield of information from studies of the musculature. The process of breaking a carcass into any type of smaller unit immediately destroys the systematic structure.

In order that some standardization of procedure can be obtained in studies using anatomically-precise groups it is necessary that various workers use the same grouping procedure for comparative work. Butterfield's 'standard muscle groups' (1963a, b) have been used by several other workers in the common meat animals, to all of which they are readily adaptable, and by Bryden (1969) in elephant seals where some modification was needed due to the anatomical differences encountered. Butterfield (1963a, c) presented a classification of the growth patterns of these standard muscle groups as 'early, average, late and very late developing'. He expressed the growth of the weight of each group relative to the growth of total muscle weight in the form of an index as set out in Table 4.3.

Table 4.3 Relative growth of muscle groups from birth to four years in steers (relative to total muscle = 100)

N = 57 Standard m	nuscle group	
No.	Name	
6	Distal intrinsic muscles of foreleg	60
2	Distal intrinsic muscles of hindleg	70
5	Proximal intrinsic muscles of foreleg	90
-	Total muscle	100
3	Muscles surrounding the spinal column	100
7,8&9	Muscles of thorax and neck and those attaching	
	forelimb to trunk	103
1	Proximal muscles of hindleg	104
4	Muscles of abdominal wall	135

Source: Butterfield, 1963c.

From this work Butterfield suggested that the patterns demonstrated could be explained, at least in part, on a functional basis, and also that the period of greatest change in the proportions of the musculature was from birth to not more than 240 days. The coefficients of variation of percentage weight increases were shown to decline rapidly after this period (Table 4.4).

Days old	Muscle weight distributio in steers	
	Coeff. of variation $\%$	
0- 240	0.175	
241- 490	0.084	
491- 770	0.026	
771–1,020	0.039	
1,021–1,440	0.032	

 Table 4.4
 Coefficients of variation for per cent weight increase of muscles of cattle in age phases

Source: Butterfield, 1963c.

No mystical value should be ascribed to the age of 240 days, as it was merely the arbitrarily chosen age at which the first analysis after birth was carried out. This highlights the weakness of the method of analysis for, as will be later shown, many changes take place between such arbitrarily selected ages. However, this weakness in method should not in any way detract from the most important demonstration that the maximum amount of differential relative growth within the musculature occurs soon after birth.

The next step in this work was to use more sophisticated, although not necessarily more precise, techniques to analyse the data, and as with the individual muscles, the patterns of the groups were classified by Butterfield and Berg (1966b) using Huxley's growth coefficient. The system of classification was the same as that set out for the individual muscles (p. 77).

The two classifications using 'b' values and a direct comparison of percentages are set out in Table 4.5.

Muscle group	Growth coefficients 'b'	Direct comparison of percentages (Butterfield, 1963c)
1. Proximal pelvic limb	High-average or low	Late
2. Distal pelvic limb	Low	Early
3. Surrounding spinal column	Average	Average
4. Abdominal Wall	High-average or high	Late
5. Proximal thoracic limb	Low-average	Early
6. Distal thoracic limb	Low-average or low	Early
7. Thorax to thoracic limb	High	Very late
8. Neck to thoracic limb	Average-high	Very late
9. Neck and thorax	Low-average	Very late

 Table 4.5
 Growth patterns of standard muscle groups of steers using growth coefficients and percentage value

Source: Butterfield and Berg, 1966b.

The growth patterns of regional groups of muscles in steers have been discussed by Luitingh (1962), Walker (1963), Butterfield (1963a, c) and Butterfield and Berg (1966b).

In general muscle groups, like individual muscles, undergo a period of diverse growth rates immediately after birth, but by the time that the birth weight of the musculature has doubled they are mostly tending to grow at a similar average impetus rate. The distal muscles of the limbs and also the proximal muscles of the forelimb are better developed at birth than the remainder of the musculature and therefore grow slower than the remainder, at least in the immediate post-natal period.

The muscles of the proximal part of the pelvic limb, the muscles of the abdominal wall and those connecting the thorax to the thoracic limb, are relatively poorly developed at birth and therefore grow faster than average in the early post-natal period. It is worth noting here again that such a growth pattern in a group is the sum of all the patterns of the individual muscles which make up that group and many of these muscles have quite different patterns to the group as a whole. This is particularly so if the muscles concerned are relatively small. So we see in the 'proximal pelvic limb group' that the deep small muscles have different patterns, generally of low impetus, compared with the large superficial muscles which have an initial high impetus and which due to their size dictate the pattern of growth of the group.

The muscles surrounding the spinal column were believed to grow, as a group, at the same rate as total muscle throughout (Butterfield 1963a, b and Butterfield and Berg, 1966b). However, more evidence from Berg (1968b) (see Chapter 5) indicates that there is a slight increase in impetus following birth in this group in line with the growth pattern of its major individual muscle, the longissimus dorsi.

The three muscle groups from the cranial end of the carcass were originally described by Butterfield (1963a, c) as 'very late developing', however Butterfield and Berg (1966c) did not find any evidence for a late upsurge in relative growth impetus in these groups when analysing data by use of growth coefficients. More recent data of Berg and Mukhoty (1970) supported the upswing in the impetus growth of these groups at heavy weights and the implications of this will be discussed in Chapter 5.

It is apparent from the foregoing that the standard muscle groups grow on different growth patterns and that they may therefore exert a different effect on the external appearance of animals at different stages of the growth process. There is, therefore, a temptation to relate difference of external appearance in cattle to differences in relative muscle development. Butterfield and Johnson (1968) discussed this and concluded that, even though calves which appeared very different because of different rates of growth had different relative proportions in their musculature, these different proportions could not be incriminated in accounting for the external appearance. They
showed that the differences in appearance were not substantially altered by the recovery of normal muscle weight distribution.

The commercial importance of relative growth of anatomical regions is that, if it could be shown that there are various stages of growth when the more expensive areas of the musculature are relatively better developed than at other times, then this would obviously be an optimum time to slaughter animals to capture this advantage. There seems to be little justification for the pursuit of such a goal as there is no evidence at all of any increase in the proportional development of any muscles which would be commercially advantageous. Unfortunately, the suggestion of Hammond (1960) that the muscles of the loin increase relatively at about eighteen months has not been supported by dissection studies and there is no functional stimulus likely to precipitate such increase.

GROWTH PATTERNS OF IMPETUS GROUPS OF MUSCLES

It has been demonstrated that the greatest amount of differential growth occurs in the immediate post-natal period. This was shown by Butterfield and Johnson (1968) and their table is reproduced as Table 4.6. It can be seen that the number of muscles growing at a rate significantly different from total muscle drops markedly once the immediate post-natal period is passed (21 to 8). The percentage of

Phase	······································	1	2	3	4	5
Age range (days)		084	85-365	366-730	731-1,460	1,460 +
Muscles with 'b' values significantly different from 1.0	Number of muscles	21	8	6	6	3
	Percentage of total muscle weight (adult)	41.5	5.5	8.9	3.9	9.0

Table 4.6 The proportion of the musculature of steers with diphasic growth patterns whose 'b' values are significantly different from 1.0, in five age phases

Source: Butterfield and Johnson, 1968.

total muscle weight represented by muscles growing at a differential rate shows a proportionately greater decrease (41.5 to 5.5 per cent respectively).

As it became apparent that the greatest amount of differential growth of muscles occurred in the immediate post-natal period, so it also became apparent that the standard muscle groups were not suitable for studying the detailed effects within the musculature of such criteria as rate of growth. This was because the inclusion of muscles of different growth patterns in the same group was, to some extent, self-cancelling. For example, the grouping of two muscles of the same size with growth coefficients each similarly greater and less than 1.0 would result in a combined 'b' of 1.0 and a complete masking of differential growth.

For this reason Butterfield and Berg (1966c) adopted the procedure of grouping together muscles according to their known growth patterns so that any influence on growth which differentially affected any particular type of muscle would be clearly demonstrated by the reaction of that group of muscles. They used the muscles of known 'high-average' impetus to study the effect of slow and fast growth in young calves.



Fig. 4.6 Change in proportion of total muscle weight by the high-average impetus group of muscles *Source*: Butterfield and Berg, 1966c

The results are set out in Fig. 4.6 and illustrate the extremely rapid change which takes place in young calves in the proportions of the high-average impetus group of muscles.

This study, which is more thoroughly discussed in Chapter 5, demonstrated the value of classifying muscles by impetus groups. It was subsequently used by Butterfield and Johnson (1971) in a similar type of experiment in which they studied the effect of extremely severe nutritional insult on the entire carcass musculature (p. 123).

To date the method of using impetus groups in cattle has been confined to studies in young calves and it is probably in this area of rapid change that it will be of greatest value. However, Lohse *et al.* (1973) have used the method to examine the changes within the musculature of sheep recovering from semi-starvation, and it is apparent that the simple procedure of comparing the relative weights of impetus groups of muscles in normal sheep and those in a recovery stage is more sensitive than some biochemical procedures tested.

When studies of the changes in the musculature due to sexual maturation in bulls are undertaken there may be considerable promise in studying, as an impetus group, those muscles shown to respond to male hormone. This should be particularly useful for, as Brännäng (1971) has shown, the differential male development of neck muscles is selective and adjoining muscles may be quite differently affected. Study of anatomical groups will not reveal the effects clearly whereas grouping those muscles with similar impetus patterns should pinpoint the effects.

5 Factors affecting muscle growth patterns

IN BRIEF The major factors affecting muscle growth patterns can be grouped under the general headings of sex, nutrition, breed and function, and each of these plays a part in determining the muscle weight distribution in the carcass of an animal at slaughter.

The difference in rate of growth of individual muscles in bulls, steers and cows can be considered on the basis of the bull being the only 'sex' which fully utilizes the inate potential of the musculature to grow differentially. The steer and the female do not come under the influence of gonadal androgens which are required to complete the full patterns of muscle growth, both in amount, as shown in Chapter 2, and in relative growth, as shown in this chapter.

The rate of growth has no effect on the amount of muscle relative to bone at any given weight of muscle plus bone and it also has no effect on the relative weights of individual muscles. Fast or slow growth does not alter the proportions within the musculature when the comparison is made at the same total muscle weight. Therefore it is axiomatic that, in young calves during the period of maximum differential muscle growth, comparisons of fast- and slow-grown animals at the same *age* will reveal differences in muscle weight distribution.

Loss of weight from the musculature is differential in such a way that those muscles most vital for survival are least affected by muscle weight loss. These are muscles which are well developed at birth and are of low post-natal growth impetus. The net result of this phenomenon is that the musculature following weight loss achieves distribution of weight which approaches that of the new-born calf.

One aspect of weight loss from muscle which is not yet clear is the effect on the high impetus, androgen stimulated muscles of the neck of the bull. There is some evidence that these muscles are not as severely affected by weight loss as the other muscles of high post-natal growth impetus. Fighting no doubt remains as a vital survival function in the mature male, even in periods of muscle weight loss, and retention of massive muscles of the neck may therefore reduce the capacity of a bull to survive in drought to a level below the steer and cow, the muscle resources of which are concentrated in locomotion and grazing.

On regaining weight the musculature quickly returns to its normal proportions, as would be expected of such a vital system. From a meat production point of view it is obvious, therefore, that a period of weight loss and recovery has no effect on the proportions of the total muscle tissue located in the various parts of the carcass, providing recovery is complete.

Breed plays a minor role in relative growth within the musculature and therefore in muscle weight distribution. Extensive study of conventional beef breeds, some dairy breeds and some crossbreds from the draft animals of Europe have failed to reveal any differences of muscle weight distribution of sufficient

magnitude to be of commercial importance. It may be that, in line with their utilization as draft animals, some of the European breeds will be shown to have different muscle weight distribution, but this has yet to be demonstrated.

Double-muscling (muscular hypertrophy) is a condition which has now been shown to cause differences in relative growth of muscles and the more fleshy muscles of the proximal parts of the limbs of these animals have been shown to be larger relative to the fibrous muscles more distal on the limbs.

Partial manifestation of the phenomenon of double-muscling in an animal will influence the muscle weight distribution. This means that studies of a breed in which there is a high incidence of this condition may be influenced by doublemuscling, even though it may not be apparent on visual inspection of the individual animals being studied. Therefore differences revealed in muscle weight distribution in a breed in which double-muscling is common should be viewed in this light.

There is little evidence on which to base discussion of the effect of exercise on the relative growth of muscles of our meat animals, as it appears that the minimal exercise enjoyed by the penned calf is adequate to stimulate normal muscle growth. The usual activities of cattle seem to be sufficiently alike that small variations do not exert any detectable effects on the relative growth of the muscles.

INTRODUCTION

In the previous chapter we have dealt with the basic growth patterns of muscles of steers. As will be shown in this chapter, the patterns of steers are less complete patterns than those of bulls. It is because of the persistence of castration as a general husbandry practice that we have found it simpler to work with steers than with bulls.

The patterns of growth of muscles may be influenced by a variety of factors, such as sex, rate of growth of the animal, the loss and gain of body weight, the deposition of fat within the musculature and the changes of function brought about by different activities. In this chapter we look at these factors and how they modify the basic muscle growth patterns of steers and thereby influence the muscle weight distribution attained.

THE EFFECT OF SEX ON GROWTH PATTERNS OF MUSCLE GROUPS

The standard muscle groups

The muscles of bulls have growth patterns which are different from those of steers or heifers, and indeed, as mentioned in the previous chapter, the musculature of the steer and cow do not proceed beyond an adolescent stage. The androgenic effect of the male hormones appears to be necessary to complete a full pattern of muscle development (Butterfield and Berg, 1972). Berg (1968b) presented the comparative growth patterns of bulls, steers and heifers as percentages which the standard muscle groups represented of total muscle at various weights. The calves in this study ranged from twelve to twenty-seven days old and therefore the patterns do not include the very early changes which occur in the new-born calf. However, for the purposes of this section our emphasis is on the more mature stages of growth when sex-influenced changes occur. The results of Berg (1968b), extended by unpublished data from four additional bulls and one fat cow, will be used as the basis for comparing sexes in muscle weight distribution. Results of other studies will be included for comparison.

The studies from which tabulated information is drawn, and details of how it is used, are listed below.

1. Berg (1968b).

A study involving Shorthorn-crossbred cattle.

Bulls (B), steers (S) and heifers (H), slaughtered serially at 3 weights for each sex. Data from 4 calves (C) are used as a starting point. Each point on the figures represents an average of 4 animals, except that for the heaviest steers, which is an average of 2.

la. Berg (unpublished).

Dissection data of 3 bulls of heavier weights than those above. These bulls were self-fed the same ration as the bulls in (1) and are plotted as 'B' to indicate a further stage in the differentiation of muscles in the bulls. Their average total side muscle weight was 115 kg. Data from a mature bull (5 years old) in good condition are included also as 'B' to indicate mature muscle weight distribution. His total side muscle weight was 194 kg. Data from a mature fat cow with a total side muscle weight of 95 kg are also included and plotted as 'H'. This cow was a dry 5-year-old, and had been self-fed on high concentrate ration for four months before slaughter.

2. Berg and Mukhoty (1970).

A study which compared the muscle weight distribution of 63 bulls (Hereford, Shorthorn cross, Crossbred, Holstein and Jersey), 85 steers (Hereford, Shorthorn cross, Crossbred, Brown Swiss Cross and Holstein) and 22 heifers (Hereford and Shorthorn cross). In this study and the two preceding ones half carcasses were totally dissected into individual muscles, weighed, and the data assembled into 'standard muscle groups' and presented as percentages of total muscle weight.

3. Brännäng (1971).

A study of monozygous twin bulls and steers, slaughtered at equal weights (455 kg) and then totally dissected. The weights of the muscles are presented assembled into eight groups which, although not strictly comparable with the 'standard muscle groups', are sufficiently similar for some comparative purposes.

- Butterfield and Berg (1966b). A study in which the growth patterns of the 'standard muscle groups' were classified on data from the dissection of 92 heterogeneous calves and steers.
- 5. Ledger (1966).

A study of 46 'improved' Boran steers from 1.5 to 5.5 years old, which were totally dissected. His results are assembled into four muscle groups which, although not readily comparable to the 'standard muscle groups', are useful for some comparisons.

Details from each of the above studies are tabulated in the format as set out in Fig. 5.1 for each standard muscle group. When subject to reference in the text, the above studies are indicated by number, for example, Brännäng (3),—Ledger (5), etc.

GROUP I-The proximal muscles of the pelvic limb

The initial phase of high impetus for this muscle group seen in new-born calves (Butterfield, 1963a, c) is not apparent in Fig. 5.1. The pattern for all three 'sexes' is one of 'low' impetus resulting, as the muscle weight becomes heavier, in a decrease in the percentage which this group represents of total muscle weight. The effect in the bulls is most marked and, as will be shown later, this is an effect which is associated with the transfer of muscle weight to the cranial end of the animal. The decline in the proportion of muscles in the upper hind leg is not in line with eye assessment of cattle in which the hindquarter appears to become relatively larger in older animals. It probably does so, but not under the influence of increasing proportion of muscle, but rather of both intermuscular and later subcutaneous fat. The statement of Hammond (1932), that much of the apparently increased muscular development of 'improved' breeds is due to deposits of intramuscular fat, is possibly applicable in this situation.

The best understanding of the shifting proportions of growing male cattle, in which this muscle group is heavily involved, can be obtained by careful study of the information given by Brännäng (1966) and set

Berg (1968b) (1), Unpublished	l (1a)	
† 'b' 1—Bulls 0.85 ± .01 †† 'b' 2—Bulls 0.84 ± .03	Steers 0.91 ± .01 Steers 0.90 ± .03	Heifers 0.85 ± .01 Heifers 0.93 ± .06
Weight of muscle group as a to of total muscle 31 35 35	50 100 Total muscle (kg)	—————————————————————————————————————
Muscles of 'proximal pelvic limb' as % of total muscle weight	Bulls28.4Steers29.6Heifers31.5	Berg & Mukhoty (1970) (2)
'Hip and thigh' group as % of total muscle weight	Bulls27.3Steers28.0	Brannang (1971) (3)
Growth pattern for steers	High-average or High-low	Butterfield & Berg (1966b) (4)
Regression of lean of 'hind leg joint' on total lean of Boran steers	-0.031	Ledger (1966) (5)

[†] 'b' 1 = Growth coefficient for all animals joined by solid line.

 \dagger b' 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.1 Statistical information relating to the growth of 'standard muscle group' no. I—The intrinsic muscles of the proximal part of the pelvic limb

out in Table 5.1. It should be noted that Brännäng's figures are relative to the weight of the *carcass* and hence react quite differently to those of Berg (1968b), which are relative to total muscle weight.

Brännäng's data show that, as a percentage of carcass weight, the bulls had the same amount of hindquarter muscle as steers; this is, of course, the commercially important aspect of this bull ν . steer comparison. We will later return to this aspect when considering the growth patterns of the muscles of the forequarter.

3. Brännäng (1971).

A study of monozygous twin bulls and steers, slaughtered at equal weights (455 kg) and then totally dissected. The weights of the muscles are presented assembled into eight groups which, although not strictly comparable with the 'standard muscle groups', are sufficiently similar for some comparative purposes.

- Butterfield and Berg (1966b).
 A study in which the growth patterns of the 'standard muscle groups' were classified on data from the dissection of 92 heterogeneous calves and steers.
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A study of 46 'improved' Boran steers from 1.5 to 5.5 years old, which were totally dissected. His results are assembled into four muscle groups which, although not readily comparable to the 'standard muscle groups', are useful for some comparisons.

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The best understanding of the shifting proportions of growing male cattle, in which this muscle group is heavily involved, can be obtained by careful study of the information given by Brännäng (1966) and set

Berg (1968b) (1), Unpublished	(1a)	
† 'b' 1—Bulls 0.85 ± .01 †† 'b' 2—Bulls 0.84 ± .03	Steers 0.91 ± .01 Steers 0.90 ± .03	Heifers 0.85 ± .01 Heifers 0.93 ± .06
Weight of muscle group as a " of total muscle 22 24 25 24 24 24 24 24 24 24 24 24 24 24 24 24	50 100 150 Total muscle (kg)	<u>————————————————————————————————————</u>
Muscles of 'proximal pelvic limb' as % of total muscle weight	Bulls28.4Steers29.6Heifers31.5	Berg & Mukhoty (1970) (2)
'Hip and thigh' group as % of total muscle weight	Bulls27.3Steers28.0	Brannang (1971) (3)
Growth pattern for steers	High-average or High-low	Butterfield & Berg (1966b) (4)
Regression of lean of 'hind leg joint' on total lean of Boran steers	-0.031	Ledger (1966) (5)

t 'b' 1 = Growth coefficient for all animals joined by solid line.

 $\dagger \dagger \bullet 2$ = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.1 Statistical information relating to the growth of 'standard muscle group' no. I—The intrinsic muscles of the proximal part of the pelvic limb

out in Table 5.1. It should be noted that Brännäng's figures are relative to the weight of the *carcass* and hence react quite differently to those of Berg (1968b), which are relative to total muscle weight.

Brännäng's data show that, as a percentage of carcass weight, the bulls had the same amount of hindquarter muscle as steers; this is, of course, the commercially important aspect of this bull ν . steer comparison. We will later return to this aspect when considering the growth patterns of the muscles of the forequarter.

	Forequarter		Hindquarter	
	Bulls	Steers	Bulls	Steers
Muscle % of carcass weight	36.4	30.8	33.4	33.2
Fat % of carcass weight	5.8	8.9	4.8	7.5
Bone % of carcass weight	9.8	9.8	7.9	7.9

 Table 5.1
 Distribution of tissues relative to weight of carcass

Source: Brännäng, 1966.

The relative decline in proximal hind limb muscle weight in steers and heifers, although smaller than in bulls, is probably also brought about to a small degree by a relative increase in the rate of growth of muscle of the cranial end of the animal and, particularly in heifers, by increase in the weight of the abdominal wall. Group I, being the largest of the standard muscle groups, shows the influence of the changes of impetus in the other groups to a greater degree than the smaller groups, when plotting percentage values of total muscle weight. A large part of the low impetus of this muscle group can be explained by increasing fatness. Butterfield (1963c) showed that this group is depressed as a proportion of total muscle weight by increasing percentage total dissectible fat.

The growth coefficients ('b' values) are significantly less than 1.0 for all three sexes, and it seems that the most suitable classification for the growth pattern of the proximal muscles of the pelvic limb for all sexes is 'high-low', which is one of the alternative patterns originally suggested in steers (3). The 'high' phase is passed soon after birth and is not demonstrated by these data.

It now seems probable that all 'sexes' grow on 'low' impetus patterns from about double their birth weight. However, as the three studies (1, 2, 3) in which steers and bulls are compared give larger values for steers than bulls, when this group is expressed as a percentage of total muscle, it seems that the group grows on a lower impetus relative to total muscle growth in bulls than in steers. Also, the two comparisons involving heifers (1, 2) indicate that this muscle group in heifers grows at a higher impetus than in either the bulls or steers.

GROUP II—The distal muscles of the pelvic limb

Fig. 5.2 shows that this small group of muscles has a 'low' impetus pattern of growth throughout and that there is no sex effect on this

pattern. The most suitable classification of the growth pattern for all sexes is a monophasic 'low' impetus pattern. This agrees with the pattern previously allocated for this group in steers (4) and with the fact that the gastrocnemius, the only muscle from this group listed in the twin study (3), was the same percentage of total muscle in bulls and steers.

Berg (1968b)(1), Unpublished (1a) $^{+}$ 'b' 1—Bulls 0.82 + .02 Steers $0.83 \pm .02$ Heifers $0.82 \pm .02$ $^{\dagger \dagger}$ 'b' 2—Bulls 0.92 \pm .03 Steers $0.90 \pm .03$ Heifers $1.05 \pm .06$ Weight of muscle group as a % of total muscle 200 100 150 Total muscle (kg) Muscles of 'distal Bulls 4.3 Berg & Mukhoty 4.3 (1970)(2)pelvic limb' as % Steers Heifers 4.3 of total muscle weight M. gastrocnemius as Bulls 2.2 Brännäng 22 % of total muscle weight Steers (1971)(3)Butterfield & Berg Growth pattern for Low (1966b) (4) steers Not applicable Ledger (1966) (5)

 \dagger 'b' 1 = Growth coefficient for all animals joined by solid line.

 \dagger t'b' 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.2 Statistical information relating to the growth of 'standard muscle group' no. II—The intrinsic muscles of the distal part of the pelvic limb.

GROUP III-The muscles surrounding the spinal column

Fig. 5.3 shows that this important group of muscles appears to follow a 'high-average' pattern of growth which varies from the 'average' classification previously allocated on the basis of studies of steers (4). However, it is doutful if the high impetus phase continues as far as Fig. 5.3 indicates, since this phase results largely from the growth of the biggest individual muscle in the group (M. longissimus dorsi), the high impetus phase of growth of which terminated by eighty-four days in the study of Butterfield and Berg (1966b).

† 'b' 1—Bulls 1.02 ± .01 1† 'b' 2—Bulls 0.97 ± 02	Steers 1. Steers 1.	$02 \pm .01$ $01 \pm .03$	Heifers 1.06 ± .02 Heifers 1.10 ± .06
Weight of muscle group as a 2, of 11 751 1041 muscle 14 14	H-HH B-S-B- S-B-B-		B
	50 1(Tota)	00 15 muscle (kg)	0 200
Muscles 'surrounding	Bulls	12.1	Berg & Mukhoty
spinal column' as %	Steers	12.3	(1970) (2)
of total muscle weight	Heifers	12.1	
M. longissimus dorsi as	Bulls	6.2	Brännäng
% of total muscle weight	Steers	6.3	(1971) (3)
Growth pattern for steers	Average	;	Butterfield & Berg (1966b) (4)
Regression of lean of 'loin joint'* on total lean of Boran steers	0.0017		Ledger (1966) (5)

Berg (1968b) (1), Unpublished (1a)

t'b' 1 = Growth coefficient for all animals joined by solid line.

t†'b' 2 = Growth coefficient for all animals joined by solid line except calves (c).
'Loin' includes abdominal wall.

Fig. 5.3 Statistical information relating to the growth of 'standard muscle group' no. III—The muscles surrounding the spinal column.

Growth coefficients shown in Fig. 5.3, with the calves omitted from the analysis, indicate that the bulls and steers had clearly settled to average impetus growth and the large standard error on the heifers is probably indicative of the change from high to average impetus for this phase also. The graphical data indicate that females may finish up with a higher proportion of their muscle weight in this important group; however, more evidence is needed.

The only indication from the bull v. steer twin data (3) refers to the largest muscle of this group, the longissimus dorsi, which is shown to be the same per cent of total muscle in bulls and steers.

When classifying the growth pattern of this group in steers, Butterfield and Berg (1966b) ignored the 'b' value calculated over the whole of their data, $1.01 \pm .004$, which was significantly greater than 1.0, in favour of the series of coefficients for each phase of their analysis which were not different from 1.0. It now appears that the best classification for all sexes is one of 'high-average' impetus, although the 'high' phase is not very pronounced and in steers and bulls is confined to the immediate post-natal period. In heifers the evidence indicates that the 'high' impetus phase may continue to a greater weight. There seems to be no readily apparent functional reason for a difference in heifers.

The evidence from the effects of weight loss in a later section of this chapter (p. 127) indicates that the growth pattern in steers is not different from total muscle.

It is best that an open mind should be retained regarding this group as further data could result in either an average or high-average classification.

GROUP IV—The muscles of the abdominal wall

In Fig. 5.4 muscles of the abdominal wall are shown to follow a 'high-average' pattern in bulls and steers and a 'high' pattern in heifers, although the value for the fat cow (H) indicates that females may also settle to an 'average' impetus. Both the 'high' and 'highaverage' classification agree with the alternative previously given for steers (4). This is a group in which variation is to be expected, for the muscles comprising the group are subject to a considerable array of functional stimuli, as pointed out in the last chapter. However, in the animals which were reared under uniform conditions (1), the variation within the sex groups is quite small, as evidenced by the standard errors on 'b' values. However, these do increase somewhat

Berg (1968b) (1), Unpublished (1a)

[†] 'b' 1—Bulls 1.08 ± .02 [†] † 'b' 2—Bulls 1.12 ± .05	Steers 1.10 ± .02 Steers 1.16 ± .05	Heifers 1.20 ± .03 Heifers 1.28 ± .08
Weight of muscle group as a X of 111 11 11 11 12 12 14 14 14 14 14 14 14 14 14 14 14 14 14	H B	B
	50 100 150 Total muscle (kg)	200
Muscles of 'abdominal	Bulls 9.7	Berg & Mukhoty
wall' as % of total muscle weight	Steers 10.9 Heifers 11.5	(1970) (2)
'Abdomen' group as %	Bulls 6.2	Brannang
of total muscle weight	Steers 6.5	(1971) (3)
Growth pattern for steers	High-average or High	Butterfield & Berg (1966b) (4)
· · · · · · · ·	Not applicable	Ledger (1966) (5)

t'b' =Growth coefficients for all animals joined by solid line.

 $\dagger \dagger \bullet b' 2 =$ Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.4 Statistical information relating to the growth of 'standard muscle group' no. IV—The muscles of the abdominal wal.

when the calves are omitted, but are still much smaller than the standard errors shown by Butterfield and Berg (1966b) in their analysis of heterogeneous steers with a variety of nutritional histories (4).

Although the 'b' values (1) are not significantly different between sexes, each of the studies available (1, 2, 3) gives the muscles of the abdominal wall of the steers as heavier than those of bulls at the same total muscle weight.

The influence of feeding a concentrate ration as compared with roughage is probably seen in the plot for the heavy cow (H) in Fig. 5.4,

where under the influence of four months of concentrate feeding the muscles of the abdominal wall have 'shrunk' relative to their expected proportions.

If the difference shown for heifers proves to be real, its explanation probably lies in greater functional demand. It may be that the total abdominal contents of heifers weigh more than steers and bulls due to earlier and larger fat deposits, or it may be an inbuilt preparation of the female for the advent of pregnancy. Heap and Lodge (1967) have shown that the weight of the muscles of the abdominal wall of sows increases during pregnancy, but we have no evidence relating such a phenomenon to the heifer.

The classification suggested for the abdominal muscles on present evidence is 'high-average' for bulls and steers and 'high' for heifers, Berg (1968b) (1), Unpublished (1a)

† 'b' $1-Bulls 0.98 \pm .01$	Steers 0.97 ± .01	Heifers 0.97 ± .01
^{††} 'b' 2–Bulls $1.00 \pm .02$	Steers $1.00 \pm .03$	Heifers 0.92 ± .04
15 15 15 13 13 13 13 14 15 15 15 15 15 15 15 15 15 15	B→S→B→S→	B
Arei tot	50 100 150 Total muscle (kg)	200
Muscles of 'proximal	Bulls 12.5	Berg & Mukhoty
thoracic limb' as % of	Steers 12.6	(1970) (2)
total muscle weight	Heifers 12.4	
'Shoulder' group as %	Bulls 6.1	Brännäng
of total muscle weight	Steers 6.1	(1971) (3)
Growth pattern for steers	Low-average	Butterfield & Berg (1966b) (4)
Regression for lean of 'foreleg joint' on total lean of Boran steers	0.0029	Ledger (1966) (5)

f'b' 1 = Growth coefficient for all animals joined by solid line.

 † t'b' 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.5 Statistical information relating to the growth of 'standard muscle group' no. V—The intrinsic muscles of the proximal part of the thoracic limb.

realizing that this muscle group can be greatly influenced by factors affecting weight of abdominal contents and that the level of impetus for the steers is probably higher than for the bulls.

GROUP V—The proximal intrinsic muscles of the thoracic limb In Fig. 5.5 all sexes tend towards a 'low-average' growth pattern, which agrees with the earlier classification for steers (4).

It is perhaps surprising that bulls do not follow a higher impetus pattern in this group, however, the 'b' values (1) clearly align the bulls with the steers. As is shown in Chapter 7, when comparison is made of muscle weight distribution of different species the visual impressions

Heifers $0.78 \pm .02$ Steers $0.84 \pm .01$ [†] 'b' 1—Bulls $0.83 \pm .02$ $^{\dagger \dagger}$ 'b' 2—Bulls 1.00 \pm .04 Steers 1.02 + .03Heifers 0.83 ± .06 150 200 Total muscle (kg) Muscles of 'distal 2.3 Berg & Mukhoty Bulls thoracic limb' as % Steers 2.4 (1970)(2)of total muscle weight Heifers 2.3 'Arm' group as % of Bulls 7.7 Brännäng total muscle weight Steers 7.7 (1971) (3) Growth patterns for steers Low-average Butterfield & Berg (1966b) (4) or Low -0.0029 Regression for lean of Ledger (1966) (5) 'foreleg joint' on total lean of Boran steers

Berg (1968b) (1), Unpublished (1a)

f'b' 1 = Growth coefficient for all animals joined by solid line.

 \dagger 'b' 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.6 Statistical information relating to the growth of 'standard muscle group' no. VI—The intrinsic muscles of the distal part of the thoracic limb.

of relative increase in the muscles of this area are seldom supported by dissection. The 'shoulder' group in the twin comparisons (3) is shown to be equal in bulls and steers and this further supports the concept that they follow similar patterns.

The low 'b' for the heifers (1), when analysed without the calves, probably again indicates that the heifers enter the phase of average impetus later than the steers and bulls, but this needs more evidence, since the spread of heifer weights is not great. The most suitable classification for all sexes appears to be that of 'low-average' impetus.

GROUP VI-The distal muscles of the thoracic limb

Fig. 5.6 shows that in all sexes the pattern for this muscle group tends toward 'low' or 'low-average', which were the alternatives suggested for steers (4). The present data go no further towards satisfying either one of the alternatives, but show that any differences between the sexes will be small. The 'b' values (1) with and without the calves support a 'low-average' pattern clearly for the bulls and steers; however, the value for heifers without the calves is indicative of continued 'low' impetus. This may be due to the narrow spread of data, as the fat cow brings the pattern back in line with the bulls.

In the twin comparisons (3) the muscles of our forearm group form about a third of the weight of the group called 'arm', which is not different between steers and bulls indicating a similar pattern. The comparison of the three sexes (2) indicates similar values for all. The most suitable pattern for all sexes appears to be 'low-average'.

GROUP VII—The muscles joining the thorax to the thoracic limb

In Fig. 5.7 it can be seen that there are no differences between the growth patterns for the sexes in group VII muscles. A common 'high'



Berg (1968b) (1), Unpublished (1a)

Bulls	10.5	Berg & Mukhoty
Steers	10.6	(1970) (2)
Heifers	10.3	
Bulls	22.3	Brännäng
Steers	20.4	(1971) (3)
High		Butterfield & Berg (1966b) (4)
+ 0.032		Ledger (1966) (5)
	Bulls Steers Heifers Bulls Steers High + 0.032	Bulls 10.5 Steers 10.6 Heifers 10.3 Bulls 22.3 Steers 20.4 High + 0.032

t'b' 1 = Growth coefficient for all animals joined by solid line.

 \dagger \dagger \bullet \bullet 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.7 Statistical information relating to the growth of 'standard muscle group' no. VII—The muscle connecting the thorax to the thoracic limb.

impetus pattern is indicated which is in agreement with the pattern previously allotted to steers (4). The 'b' values for the sexes are all significantly greater than 1.0 and not different from each other. No significant difference in the proportional weight of muscle in this group was shown between sexes (2).

It is not possible to make any useful comparison with information from the twin study (3), as those data include the remainder of the muscles of the shoulder girdle.

It seems quite clear that group VII possesses a 'high' impetus growth pattern and that it is not different between sexes. This is consistent with a weight bearing function, supporting the continuously increasing weight of the animal.

GROUP VIII—The muscles joining the neck to the thoracic limb

Fig. 5.8 shows that group VIII muscles tend to follow the pattern of 'average-high' impetus given for steers (4) and that of the bulls tend to have the highest growth impetus. The 'b' values (1) indicate no difference between the bulls and steers but a significant difference for heifers. The 'b' values without the calves show the bulls gaining impetus relative to both steers and heifers as they become heavier,

† 'b' 1—Bulls 1.09 ± .02	Steers 1.10 ± .04	Heifers $1.02 \pm .02$
†† 'b' 2—Bulls 1.28 ± .05	Steers 1.19 ± .08	Heifers 1.18 ± .07
roup as a 2 of roup as a 2 of t of a uscle t of a uscle	нв	B
3 α - 50	100 150 Total muscle (kg)	200
Muscles of 'neck to	Bulls 5.5	Berg & Mukhoty
thoracic limb' as %	Steers 5.4	(1970) (2)
of total muscle weight	Heifers 5.2	
'Shoulder girdle' group	Bulls 22.3	Brännäng
as % of total muscle weight	Steers 20.4	(1971) (3)
Growth patterns for steers	Average-High	Butterfield & Berg (1966b) (4)
Regression for lean of 'neck and thorax joint' on total lean of Boran steers	+ 0.032	Ledger (1966) (5)

Berg (1968b) (1), Unpublished (1a)

 \dagger 'b' 1 = Growth coefficient for all animals joined by solid line.

 \dagger \dagger \bullet \bullet 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.8 Statistical information relating to the growth of 'standard muscle group' no. VIII—The muscles connecting the neck to the thoracic limb.

however, the standard errors are large and the differences not significant.

In the twin comparison (3) two of the muscles from group VIII, the trapezius and the rhomboideus muscles, are included in 'shoulder girdle' and undoubtedly contribute towards the difference of almost 2 per cent demonstrated between bulls and steers; the bulls being the heavier. In comparison of percentages for the three sexes (2) no significant differences were shown, although the means differed in a manner supporting the other studies. The two individual muscles which are most affected by the onset of sexual maturity are the splenius

and the cervical rhomboid, the former of which is not a member of this group. In unpublished data from our dissection series and from the study of Brännäng (1971) the splenius is the muscle which increases most in *Bos taurus* bulls. As the hump of the *Bos indicus* is comprised of the cervical or thoracic rhomboid, according to breed, it is probable that the rhomboid may play a larger part than the splenius in these cattle. The only data available is from Brahman bulls of insufficient maturity to settle this point.

Ledger (1963), in talking of game animals containing very little fat, stated that the variance of the proportion of hindquarter to forequarter within a species is entirely a reflection of sex maturity differences.

This muscle group appears to fit a classification of average-high for all the sexes and with sufficient data it seems probable that it could be demonstrated that bulls will have significantly higher impetus than either heifers or steers.

GROUP IX—The intrinsic muscles of the neck and thorax

Fig. 5.9 shows a clear separation of the bull growth pattern from those of the steers and heifers. It is not possible from these data to suggest what happens in the immediate post-natal period when a 'low' impetus pattern for steers (4) was shown. However, in Berg's animals (1) the bulls entered a high growth impetus at some stage about 40 kg side muscle weight, whereas the steers and heifers continued on at an 'average' impetus. Butterfield (1963c) described this group in steers as being 'very late developing' on the basis of a percentage increase in heavy steers, and it is possible that the current data for steers does not extend to sufficiently heavy animals to detect such a late increase in impetus.

Exclusion of the calves from the calculation of the growth coefficients (1) accentuates the high impetus of the growth in the heavy bulls. The very heavy bull, not included in the analysis but plotted on the figure, demonstrates the type of end point suggested by the data of the lighter bulls.

Brännäng (1971) showed the differences between bulls and steers for the splenius and the semispinalis capitis muscles. There is little doubt as to the role of the splenius in the bull. It is the muscle which is largely responsible for the crest formation in the mature bull. Undoubtedly the muscles of this group, and particularly the splenius, are responsible for the differences between the twins (3) in the shoulder

† 'b' 1—Bulls 1.07 ± .01 †† 'b' 2—Bulls 1.21 ± .06	Steers $1.01 \pm .01$ Steers $1.06 \pm .03$	Heifers 1.02 ± .01 Heifers 0.97 ± .05
eight of muscle roup as a 's of 111 muscle 121 131 14 14 14	вв	B
<u> 5</u> 5 5	0 100 Totaj muscle (kg)	150 200
Intrinsic muscles of	Bulls 12.5	Berg & Mukhoty
thorax and neck as %	Steers 10.1	(1970) (2)
of total muscle weight	Heifers 9.0	
'Shoulder girdle' group	Bulls 22.3	Brännäng
as % of total muscle weight	Steers 20.4	(1971) (3)
Growth patterns for steers	Low-average	Butterfield & Berg (1966b) (4)
Regression for lean of 'neck and thorax joint' on total lean of Boran steers	+ 0.032	Ledger (1966) (5)

Berg (1968b) (1), Unpublished (1a)

t'b' 1 = Growth coefficient for all animals joined by solid line.

t t'b' 2 = Growth coefficient for all animals joined by solid line except calves (c).

Fig. 5.9 Statistical information relating to the growth of 'standard muscle group' no. IX—The intrinsic muscles of thorax and neck.

girdle group. Brännäng (1971) pointed out that the splenius is the muscle most affected by masculinity and that even closely related muscles are less affected or not affected at all.

The '3 sex' comparisons (2) showed that this muscle group was significantly larger in the bulls than in steers and heifers. The steers were also relatively heavier than the heifers.

It is the large variation in this group between the sexes which balances up the other, smaller, variations shown in other muscle groups. For example, the lighter muscles of the proximal hind leg and abdominal wall of the bull are balanced by the heavier intrinsic muscles of the neck and thorax, and to a small extent by the neck to the thoracic limb group. In the heifer the reverse applies for heavier muscles of the hindquarter and abdominal wall are compensated by lighter muscles of thorax and neck.

The steer assumes an intermediate position in the muscle weight shift. It can be clearly seen as a feminized male or a masculinized female. There seems to be justification for suggesting that the female reaches her mature proportions at a point in the whole growth story which is part way along the path of male development. The steer manages to proceed a little further than the heifer but does not attain bull proportions due to the removal of gonadal androgen which is necessary to produce the final changes associated with masculinity.

The 'expensive' muscles of the carcass

To divide the muscles into two groups which would have some relevance to trade prices for meat, Butterfield (1963c) combined groups I, III and V to form the 'expensive' part of the musculature, that is, the muscles of the proximal hindlimb, the loin and the proximal forelimb. There could be reasons, particularly in other places, to adopt other groupings in line with local trading prices and, indeed, Berg and Mukhoty (1970) used a grouping of only groups I and III as more indicative of the expensive muscles in Canada.

Using these two groupings, the differences between the bulls and steers of the Berg and Mukhoty study were:

Proximal hind limb plus muscle around spinal column plus proximal forelimb as % of total side muscle weight

Bulls 53.2	Steers 54.3	Heifers 56.1
	The values are significantly differen	t.

Proximal hind limb muscle plus muscle surrounding spinal column

Bulls 40.8	Steers 41.8	Heifers 43.6

The values are significantly different.

It is clear, therefore, that the use of bulls can reduce the proportion of expensive muscle, but this must be considered in the light of all the concurrent changes in the carcass and particularly in relation to the *amount* of muscle (see Brännäng, 1971).

General discussion of sex effects on muscle growth patterns and the resultant muscle-weight distribution

There seems little doubt that bulls are going to provide the greatest amount of beef from young animals in the future. Many countries already realize the potential production being lost by the archaic practice of castrating animals as routine. Brännäng (1969) reported that of 340,000 young cattle slaughtered in Sweden in 1968, 53 per cent were bulls and only 14 per cent steers. Yet in countries like Australia the mere mention of the word 'bull' to a butcher is to suggest that something inferior is being offered.

On the other hand, it is also presented to the producer in Australia that there is something inferior about heifers. Just what the alleged inferiority is supposed to be is difficult to determine. However, what certainly is not inferior is the proportion of high-priced muscle received in the bull at the same carcass weight or in the heifer at the same level of fat.

The most interesting table extracted from Brännäng (1966), which is reproduced as Table 5.1, shows that in steer and bull carcasses of *equal weight* the hindquarter muscle is the same weight, the forequarter muscle is heavier in the bulls, there is no difference in bone and the bull has less fat on both fore- and hindquarters. In effect this means that for the same price (presuming equal price per unit weight) the purchaser of a bull obtains the same amount of hindquarter muscle, more forequarter muscle and less fat all over. Forequarter muscle is worth more than most fat, and with the continuance of the current trend toward leanness there is little chance of this altering.

However, it is interesting that in game animals with little or no fat the influence of sex induced changes of muscle weight distribution is more important than in cattle, where the growth of fat on the heifer and steer virtually compensates for the muscle changes when consideration is made at equal carcass weights. Ledger and Smith (1964) pointed out the need for differential pricing of the game species according to sex because of the different percentage of the total muscle tissue found in the hindquarter. Whereas a mature male Uganda Kob has only 52.5 per cent of its total muscle weight in the hindquarter, an immature female has 61.2 per cent. This type of consideration could become more important in cattle if the trend towards leaner draft-type animals continues, when the compensating effect of fat demonstrated by Brännäng will disappear.

At Edinburgh three experiments, using Hereford × Friesians reared

on high energy diets, were carried out to investigate sex effects. In the first, bulls, steers and Russian castrates were killed at approximately 940 lb (Robertson *et al.*, 1967); in the second, bulls and steers were killed at approximately 924 lb (Robertson *et al.*, 1970); and in the third heifers and spayed heifers were killed at about 746 lb live weight (Hubard-Ocariz *et al.*, 1970). Data on dissectible lean in commercial joints from these experiments are set out in Table 5.2, which was supplied by Dr I. S. Robertson.

This table shows that, if bulls, Russian castrates and steers are killed at light weights, the differences in muscle weight distribution will be negligible.

There is no need for any concern to be expressed regarding the proportions of bull carcasses relative to steers if the slaughter weight is such that the changes associated with sexual maturity in bulls are avoided. Just what this weight is for particular breeds is not known with any certainty, but it can surely be assumed that the larger the breed the heavier the bulls can be before being subject to the changes

Carcass wt (lb)		Experiment I 523			Experiment II 520		Experiment III 415	
1.	Leg	2.88	3.19	3.34	3.34	3.53	3.77	3.64
2.	Round	24.43*	25.17	25.68	25.74	25.40	26.11	26.16
3.	Heugh	8.13	8.69	8.28	8.04	8.04	8.96	9.16
4.	Sirloin	9.78	9.85	10.07	9.36*	9.86	9.36	9.60
5.	Flank	5.52	5.60	5.77	5.04*	5.44	5.32	4.88
6.	Fine							
	End	4.12	4.18	4.17	4.80	4.73	4.49	4.53
7.	Crop	23.92*	22.59	22.61	21.63	21.00	20.52	20.93
8.	Brisket	7.56	7.90	7.13	7.93	8.05	7.42	6.96
9.	Neck	11.22	10.26	10.39	11.20	10.98	11.47	11.52
10.	Shin	2.44**	2.59	2.58	2.84	2.97	9.99	2.62

 Table 5.2 Dissectible lean in joints as per cent of total dissectible lean of bulls, Russian castrates (RC), steers, heifers and spayed heifers

* significant at 5% level

** just fails at 5% level

Source: from studies of Robertson et al., 1967, Robertson et al., 1970, and Hubard-Ocariz et al., 1970.

associated with their masculinity. The smaller the breed the lighter will bulls commence to transform into mature bulls.

This is not to say that the changes associated with maturity are necessarily undesirable, as the figures of Brännäng (1966) (Table 5.1) indicate that it is a matter of choice between fat and forequarter muscle, and it may well be that the forequarter muscle is an economically more desirable tissue.

There is little knowledge of the possible effect of spaying on muscle weight distribution and on theoretical grounds it would be expected that there should be no major effect. The growth patterns of muscles of heifers appear to be similar to steers (Berg and Mukhoty, 1970). It is therefore presumed that female sex hormones do not differentially affect muscle growth. The results set out in Table 5.2 indicate that spaying did not affect relative muscle growth in the series of Hubard-Ocariz *et al.* (1970).

There is no functional reason why the heifer should undergo any large changes of muscle weight distribution at puberty. Her passive sexual role at mating does not require any specialized development as she does not have to compete for the right to mate, particularly under conditions of equal numbers of the sexes. Even when man imposes a marked reduction in the number of males the short periods of oestrus ensure that competition between females is minimal.

It seems likely that the muscles of the abdominal wall become relatively heavier during pregnancy as they do in sows (Heap and Lodge, 1967) but there has been no work done on this in cows.

Of all the factors which influence muscle growth it is apparent that sex is a major consideration. The various aspects of sex influence on muscle growth can be best understood by considering the male to be the most perfect of the 'sexes' and the others to be striving to grow on the same patterns but failing due to the lack of gonadal androgen stimulation.

The bull is first a new-born calf with exactly the same primary problem, that of survival, as the heifer, so he is born with similar muscle weight distribution. He must then increase in size along with the heifer and with the less fortunate of his sex who are emasculated, and as there are no special problems, so his pre-pubital and early adolescent muscle growth is little different from the steer or heifer.

It is late adolescence with its struggle for the right to reproduce, which sets off in the bull a whole series of changes which are unnecessary for the heifers or for his emasculated contemporaries and which are aimed at producing the mature bull muscle weight distribution.

THE EFFECT OF RATE OF GROWTH ON THE RELATIVE GROWTH OF MUSCLES

The early post-natal period, during which the calf is doubling its birth weight, was shown to be the period of maximum relative change in weight of muscles by Butterfield (1963a, c), and it was therefore realized that during this period of maximum change the opportunity existed to study the effects of various rates of growth on relative growth of muscles.

Butterfield and Berg (1966c) showed that by grouping muscles of similar growth impetus that a clear picture could be obtained of the effect of the rate of growth on the changes of relative muscle weight.

Fig. 5.10, adapted from that paper, shows that the rate of growth of the musculature of two groups of calves was different and that the low plane calves therefore had considerably lighter muscle at each killing age.



Fig. 5.10 Effect of plane of nutrition on growth of muscle in calves. Source: Butterfield and Berg, 1966c.

In Fig. 5.11 it is shown that the high-average impetus muscles grouped together constituted a much smaller percentage of total muscle weight in the first twelve weeks in the low plane calves than did the same muscles in the high plane calves. Once the phase of high impetus ceased, that is when the low plane calves were about twelve weeks old and the high plane calves about six weeks, the muscles then represented a constant proportion of total muscle weight in both groups of calves.



Fig. 5.11 Effect of plane of nutrition on relative growth of high-average impetus muscles as a percentage of total muscle. Expressed relative to age *Source*: Butterfield and Berg, 1966c



Fig. 5.12 Effect of plane of nutrition on relative growth of high-average impetus muscles as a percentage of total muscle. Expressed relative to total muscle weight *Source*: Butterfield and Berg, 1966c

Fig. 5.12, which shows the same data on the basis of total muscle weight instead of age, indicates that the relationship was not affected by the treatment.

That this effect was a reflection of the changes which occurred in all of the muscles in this group is shown in the table from which the data were extracted (Table 5.3).

An experiment which carried this work further was reported by Butterfield and Johnson (1971). Fig. 5.13 shows different growth rates



Fig. 5.13 Mean live weight of calves on three planes of nutrition: high plane II, moderate plane III and low moderate plane IV: relative to mean birth weight = 100. Mean live weight = mean weight of surviving calves in each group determined at 10 day intervals. *Source*: Butterfield and Johnson, 1971

in three groups fed milk at different levels. The slowest growing group did not exceed their birth weights until seventy-two days old.

In this experiment the data were analysed by the use of growth coefficients and the results are set out in Table 5.4 for the analysis of six impetus groups of muscles.

The results show a very high degree of uniformity considering the extremes of nutrition to which the calves were subjected. The only muscles to show a significant difference between the treatments was the small group of low-average impetus muscles which represent only about 9 per cent of the total muscle weight. The effect of treatment on the external appearance of calves was marked and the calves on the lowest plane were typical of animals reared under very poor conditions. It is certainly levelling to our ideas on the visual assessment of live animals that such calves have the same relative development of muscles as calves which have been grown at a fast rate. This theme was developed by Butterfield and Johnson (1968).

As the muscles with diphasic growth patterns were primarily within the first phase of their patterns during this experiment, they could be grouped with the muscles of appropriate monophasic patterns and this has been done in Table 5.5, which shows no differences between feeding levels.

From this work it is possible to conclude that the rate of growth of muscle did not influence the relationship between the weight of individual muscles and the weight of total muscle throughout the

				Age	(weeks))	
	l-day-						
Muscle	old	old Groups					
	calves		4	8	12	15	22
Biceps femoris	6.6	L	6.5	6.9	6.9	7.6	7.6
		Н	7.0	7.2	7.2	6.9	7.3
Glutaeus medius	3.5	L	3.5	3.6	3.8	3.8	3.9
		н	3.7	3.8	3.7	3.8	3.9
Semitendinosus	2.1	L	2.3	2.2	2.2	2.0	2.3
		Н	2.5	2.5	2.4	2.3	2.3
Semimembranosus	4.9	L	5.7	5.8	6.1	6.1	5.5
		н	6.0	6.1	6.1	5.9	5.7
Adductor femoris	1.9	L	2.3	2.4	2.2	2.4	2.2
		Н	2.4	2.4	2.0	2.1	2.0
Psoas major	1.5	L	1.4	1.7	1.8	1.8	1.8
2		Н	1.7	1.7	1.6	1.6	1.7
Longissimus dorsi	5.6	L	5.9	5.8	6.7	6.2	7.1
e		н	6.3	6.4	6.4	6.5	6.4
Transversus abdominis	1.0	L	0.9	1.0	1.1	1.2	1.3
		н	1.2	1.2	1.1	1.3	1.4
Obliguus abdominis	1.5	L	1.4	1.7	1.9	2.0	2.0
externus	1.0	н	1.8	1.8	2.0	2.2	2.0
Rectus abdominis	1.5	T.	1.5	1.9	2.3	2.0	2.1
	1.0	н	1.9	2.1	2.2	2.4	2.2
Obliguus abdominis	1.0	ī	12	14	15	15	1.8
internus	1.0	H	1.4	1.5	1.5	1.8	1.9
		L	32.5	35.6	36.6	36.2	37.7
Total of 'High-average'			32.6	33.0	36.6	37.1	37.3
Impetus muscles as %	31.1 -						
of total half-carcass		н	35.9	36.4	36.4	36.7	36.6
muscle*			35.4	36.6	36.1	37.1	36.9
			20.1	20.0	2011		2012

Table 5.3 Individual muscle weights as percentage of total muscle weight in calves of different ages, grown on different growth patterns ('L and H')—each 'L' or 'H' value represents a mean for two calves

*a value for each L and each H calf is given *Source*: Butterfield and Berg, 1966c

phase of growth when such influence would be most likely to be effective. Although there is some danger in extrapolation beyond the weights and ages at which this work was carried out, it seems highly

Muscle growth impetus group	% of total muscle in day-old	Level of feeding					
	calf	High	Moderate	Low- moderate	Combined (all planes)		
		'b' values and standard errors					
Low	24	0.90 ± 0.06	0.91 ± 0.06	0.90 ± 0.06	0.91±0.03		
Average	16	1.00 ± 0.09	1.00 ± 0.09	0.98 ± 0.11	1.00 ± 0.05		
High	11	1.17 ± 0.14	1.08 ± 0.13	1.08 ± 0.11	1.12 ± 0.06		
Low-average	9	0.76±0.09*	0.92 ± 0.34	0.93 ± 0.09			
High-average	28	1.11 ± 0.07	1.12 ± 0.18	1.12 <u>+</u> 0.07	1.11 ± 0.05		
Average-high	2	0.93 ± 0.36	0.77 ± 0.32	0.97 ± 0.23	0.90 ± 0.15		

 Table 5.4
 Growth coefficients of impetus groups of muscles for calves on high, moderate and low-moderate levels of feeding

*high plane values significantly less (P < 0.05) than other two planes *Source*: Butterfield and Johnson, 1971.



Fig. 5.14 Muscle weight distribution index of Poll Hereford steers. The weight of 'standard muscle groups' as a percentage of the weight of total side muscle of semi-starved (S), recovered (R) and older control (C₂) groups, relative to younger control group ($C_1 = 100$) Source: Butterfield, 1966a

Muscle growth impetus group	% of total muscle in day-old	Level of feeding					
	calf (base line I)	High	Moderate	Low- moderate	Combined (all planes)		
High high- average	39	1.13±0.05	1.11±0.12	1.11 ± 0.07	1.12 ± 0.04		
average	33	0.87 ± 0.03	0.90 ± 0.08	0.91 ± 0.04	0.89 ± 0.02		

 Table 5.5
 Growth coefficients of combined impetus groups of muscles for calves on high, moderate and low-moderate levels of feeding

*all entries in the table are significantly different (P < 0.05) from 1.0, which indicates growth of the muscle group at a different rate to the total musculature, but there were no differences in either group due to levels of feeding

Source: Butterfield and Johnson, 1971.

probable that this finding would be applicable to all phases of growth, and the differences we may observe in the external appearances of animals which have grown relatively slowly cannot be explained in terms of different muscle weight distribution. It is more likely that these differences are attributable to different bone lengths and perhaps different fat deposition. Such animals would normally have longer bones and less fat at any given muscle weight. The influence of fat would be affected not only by the reduction of subcutaneous fat, but also by lower intermuscular fat, which, as Harrington (1971) neatly put it, 'subtly adjusts the relative muscle positions'.

The tendency for repetition of misleading statements in semiscientific publications makes it necessary to refer to the statement by Fraser *et al.* (1970).

'that a high level of nutrition and consequent high rate of gain in calfhood leads to the full development of the hindquarters and loin, so desirable in an animal destined for beef production. Conversely a low level of nutrition results in an animal with poorly developed hindquarters and little second thigh, in fact a 'dairy' type of beast.'

Such a general statement is very misleading and incompatible with research results.

It must be clear that the effects of slow growth are quite different to the effects of loss of weight, although these two situations are often confused in discussions of growth. The effects of body weight loss and subsequent gain on the musculature are discussed in the next section.

THE EFFECT OF MUSCLE WEIGHT LOSS AND RECOVERY ON MUSCLE GROWTH PATTERNS

The basis of this section is work reported by Butterfield (1966a) in which the effects of nutritional stress and recovery on body composition of some Poll Hereford half-sib steers was studied. During live weight loss of 57 kg in 64 days, steers which were about 600 days old lost 11 kg of muscle weight. During recovery of 125 kg of live weight in 207 days, their half-sib brothers gained 18 kg of muscle weight. It is with the changes in distribution of the muscle weight within these losses and gains that we are here concerned.

The information is set out in Fig. 5.14, in which the weight of the muscle groups is seen in comparison with the weights of the same groups in younger and older controls, reared on normal growth patterns without periods of weight loss.



Fig. 5.15 Growth of muscles of the abdominal wall of calves on two diets *Source*: Butterfield *et al.*, 1966, 1971

Muscle weight loss

The relative losses of the various groups are best discussed in comparison with the growth patterns of these groups set out in Chapter 4. It might be expected, in line with the statement by Hammond (1932), that 'during starvation it would appear that the organs with an early period of maximum growth can draw on, or have prior claim on, the nutrition of those having a later period of growth', that the principle could be extended to cover the musculature in the following way. Muscles of high growth impetus (b > 1.0) should be most affected by muscle weight loss; average impetus (b = 1.0) muscles should be affected to the same degree as total muscle, and low impetus (b < 1.0) should be less affected than total muscle.

The most convenient method of comparison, therefore, is to use the growth coefficients for steers given previously, to give an indication of the reaction of the groups which might be expected to muscle weight loss.

GROUP I-Muscles of proximal part of pelvic limb

The growth coefficient of 0.91^{**} is less than 1.0 and it should therefore be expected that this group would lose proportionately less weight than the total musculature.

Fig. 5.14 shows that this was so, although the difference was not significant. Many of the muscles in this group have individual growth patterns which do not comply with the patterns of the group as a whole and it is therefore to be expected that the effects of body weight loss on the group as a whole not be as clear cut as will be demonstrated by some other, more functionally uniform, groups.

GROUP II-Muscles of the distal part of the pelvic limb

This group, with a growth coefficient of 0.83^{**} and a low impetus classification, should be more resistant to weight loss than total muscle, and this is clearly the case, as shown in Fig. 5.14.

GROUP III-Muscles surrounding the spinal column

With a growth coefficient of 1.04** this group should react to weight loss a little more than total muscle. There is no significant difference in their proportionate weight loss. As pointed out earlier in this chapter, this group grows at a rate that is so close to that of total muscle that it may have an average impetus growth pattern rather than the high-average currently allocated to it. The weight loss information supports this contention.

GROUP IV-Muscles of the abdominal wall

This group has a growth coefficient of 1.10** and may be expected to

lose more weight than the remainder of the musculature. This is certainly the case and it is interesting to reflect on the direct functional causes of this phenomenon. This group is largely responsible for the support of the abdominal organs and the physical reduction in the weight of ingesta undoubtedly plays a large part in inducing the marked proportional loss from this group.

GROUP V-Muscles of the proximal part of the thoracic limb

With a growth coefficient of $0.97^{n.s.}$ this group may be expected to undergo weight loss on a similar pattern to total muscle. Just as the growth coefficient is slightly less than 1.0, but not significantly so, the resistance to weight loss is slightly greater than total muscle, but not significantly so.

GROUP VI-Distal intrinsic muscles of the thoracic limb

A growth coefficient of 0.84** fits this group to be protected from weight loss, and this clearly occurs, as shown in Fig. 5.14. This group is certainly the best example of the extreme of low impetus (early development) which is associated with muscles of vital importance to survival, and, just as they are essential to the new-born calf, so they remain an essential unit of basic mobility in the animal which is struggling to survive a period of body weight loss. As suggested by Lohse *et al.* (1971), these muscles are part of the essential elementary locomotion mechanism.

GROUP VII-Muscles attaching the thorax to the thoracic limb

A growth coefficient of 1.06** indicates that this group may be expected to lose relatively more weight than the musculature as a whole, and this is what happens.

As this group of muscles is mainly concerned with the support of the weight of the trunk, it is simple to visualize a marked reduction in function as a result of body weight loss, which in the case of these steers was 57 kg.

GROUP VIII—Muscles attaching the thoracic limb to the neck

A growth coefficient of 1.10**suggests that, if Hammond's principle extends to the musculature, and the considerations to date suggest that it does, then this group should lose proportionately more weight than total muscle. This does not happen and the reason is not clear. One possibility is that the muscles whose relative increase is made under the influence of androgens, do not follow the same principles during muscle weight loss as the remainder of the musculature. Some support for this is seen in the data from the dissection of a mature bull, which was slaughtered in what could be best described as very hard working condition (Butterfield, unpublished). This bull, despite the fact that his dissectible fat depots had fallen to only 1.8 kg on a side muscle weight of 90 kg, still retained the typical muscle weight distribution of a sexually mature bull. This probably means that, by retaining the need to fight, during drought the survival chances of the bull are diminished compared with the starved steer and female, which can mobilize more of their muscle resources for locomotion and grazing.

GROUP IX—The intrinsic muscle of the neck and thorax

A growth coefficient of $1.01^{n.s.}$ should lead us to expect that this muscle group would react to weight loss similarly to total muscle and Fig. 5.14 shows that there was no significant difference.

In summary it is clear that during body weight loss those regions of the musculature which are most essential for survival are least affected, whereas those which are less essential are most affected.

The degree of development of a muscle group at birth can therefore be used as an indication of its likely reaction to weight loss, for the whole process of loss from the musculature is accompanied by a tendency to revert to the muscle weight distribution of the new-born calf.

Considerably more work is needed, particularly in older animals and in bulls, to define the effect of weight loss on the muscles which enjoy high impetus growth at heavy weights under the influence of androgens.

The small amount of evidence currently available indicates that the process of reversion to juvenile muscle weight distribution, which is the main characteristic of the process in steers and presumably in cows, may not be so marked in bulls.

Muscle weight recovery

It is to be expected that any biological system should attempt to regain a state of normality following a period of stress which has altered its normal course of development. It is therefore not surprising to see in Fig. 5.14, that the re-alimented steers upon recovery regained their normal muscle weight distribution. No muscle groups were
different from those of the control animals in the proportion they comprised of total muscle weight.

This phenomenon of recovery is important in our assessment of live animals, for it is most likely that, even though these recovered animals may have identical muscle weight distribution, they will certainly look different from animals which have not passed through such a period of stress. In the particular study discussed here the animals had almost as much total muscle weight as they would normally have had at their slaughter weight. Had they been carried a little longer they would no doubt have completely recovered, and yet their external appearance was quite different from that of cattle which had not passed through such an experience. This indicates that muscle weight distribution has little influence on the external appearance of cattle and therefore it should come as little surprise that next we show that breeds of cattle, which look very different, have similar muscle weight distributions.

THE EFFECT OF BREED ON MUSCLE GROWTH PATTERNS

There has been some evidence for a very long time that there is little difference in the muscle weight distribution of breeds of cattle; however, the alleged lack of precision of the methods used to demonstrate this was always sufficient for doubt to be thrown on the validity of determinations. Little difference in the yield of high-priced cuts was found in the following comparisons: Beef and dairy cattle (Wilson and Curtis, 1893); 'Comprest' and conventional Herefords (Willey *et al.*, 1951; Stonaker *et al.*, 1952); British breeds and Brahman Crossbreds (Carroll *et al.*, 1955; Riggs and Maddox, 1955; Butler *et al.*, 1956a, b); Within the Charolais breed (Dumont *et al.*, 1961).

Butterfield (1963a, c) showed that there was considerable similarity in the muscle weight distribution of a heterogeneous collection of steers acquired from the Australian cattle population. These cattle came from diverse nutritional and environmental backgrounds and covered a wide range of age and fatness. They included purebred cattle of highly 'improved' breeds and others from a property known to have introduced no new bulls for at least seventy years, and on which the mating was completely random. There were *Bos indicus* and *Bos taurus* breeds.

Even from such cattle, widely diverse in so many features, there was a striking similarity in the relative weight of individual muscles and in the various groups of muscles. When the proximal muscles of the pelvic limb, those surrounding the spinal column, and the proximal muscles of the thoracic limb were grouped to form what were described as the 'expensive muscles' of the carcass, the differences between breeds were extremely small (Table 5.6). From this comparison has arisen the statement that 'irrespective of breed, 56 per cent of the muscle weight is in the expensive part of the carcass'.

This general statement, which is of course subject to a small amount of biological variation, has been used widely in extension for about ten years and the level of acceptance in the cattle industry is now high. Nevertheless there are still some breeders who cling to the illusion that they have materially changed the muscle weight distribution of their cattle, and that 'the scientists' have gone crazy (Snell, 1971). However, those who can accept that there is little variation between

	Breed										
		Poll Here- ford	Here- ford	Angus	3/4 Brahman	1/2 Brahman	Unimproved Shorthorn				
NC ani	mals	19	8	5	5	9	8				
'Sta	andard muscle										
1	Proximal hind	32 21	32 61	32 15	33.07	33 76	32.15				
2.	Distal hind	4.95	5.20	4.87	4.61	5.07	4.46				
3.	Spinal	12.18	11.94	12.20	11.76	12.07	12.30				
4.	Abdominal	9.90	9.69	10.50	9.20	8.85	8.65				
5.	Proximal fore	11.52	11.04	11.26	11.55	11.01	11.66				
6.	Distal fore	2.71	2.79	2.66	2.75	2.75	2.57				
7.	Thorax/leg	9.14	9.32	9.51	9.09	8.98	9.48				
8.	Neck/leg	7.03	7.06	6.61	7.64	7.00	7.42				
9.	Neck &										
	Thorax	9.59	9.66	9.66	9.70	9.84	10.61				
10.	Scrap	0.77	0.66	0.58	0.63	0.67	0.70				
11.	Expensive*										
	muscles	55.92	55.59	55.61	56.38	56.84	56.11				

 Table 5.6
 The weights of 'standard muscle groups' as percentages of the weight of total side muscle weight of six groups of steers of different breeds

*groups 1 and 3 and 5

Source: Butterfield, 1963c.

				Bulls					Steer	s		Hei	fers	G
Breed ¹	-	He	Shx	XB	Но	Je	He	Shx	ХВ	BSx	Но	He	Shx	Sex sig.
Number	of animals	13	12	22	8	8	11	22	32	14	6	10	12	
Age	(days)	461	361	430	386	407	402	383	434	404	480	365	398	
Live wt	(lb)	1,026	850	1,079	915	648	823	830	1,016	1,005	1,027	672	745	
Hot care	ass wt (lb)	615	515	652	511 ·	334	486	526	602	574	589	391	461	
Anatomi groups a muscle ²	cal muscle s % of total													
1. Proxi	mal hind leg	28.4	28.4	28.3	28.8	28.4	29.5	29.6	29.5	29.6	29.6	31.3	31.6**	
2. Dista	l hind leg	4.5	4.1	4.4	4.3	4.0	4.3	4.3	4.4	4.4	4.2	4.2	4.4	
3. Arou	nd backbone	12.4	12.4	12.6	12.1	12.1	12.3	12.3	12.3	12.2	12.3	12.2	12.1	
4. Abdo	minal region	9.8	10.0	8.8	10.9	10.6*	** 10.8	11.8	10.4	10.6	11.3*	* 11.7	11.4**	
5. Proxi	mal front leg	12.4	12.5	12.3	12.8	12.6	12.5	12.3	12.6	12.9	12.5	12.5	12.4	
6. Dista	l front leg	2.2	2.3	2.2	2.5	2.4	2.4	2.4	2.4	2.4	2.5	2.1	2.4	
7. Thora	ax to front leg	10.3	10.2	10.7	10.7	10.4	10.0	10.6	10.8	10.7	10.4	10.5	10.2	
8. Neck	to front leg	5.6	5.4	5.7	5.0	5.3	5.2	5.1	5.8	5.2	5.1	5.1	5.2	
9. Neck	to thorax	12.4	12.1	12.7	11.1	13.0*	** 10.4	9.5	10.4	10.3	9.4*	* 9.1	9.0**	•
Expe	nsive muscles ³	40.8	40.8	40.9	40.9	40.5	41.8	41.9	41.8	41.8	41.9	43.5	43.7**	
Expe	nsive muscles ⁴	53.2	53.3	53.2	53.7	53.2	54.3	54.2	54.4	54.7	54.4	56.0	56.1**	r
Hind	quarter	46.7	47.8	47.6	48.7	47.6	50.2	49.9	49.5	49.7	49.5	50.5	50.3**	k
Fron	t quarter	53.3	52.2	52.4	51.3	52.4	49.8	50.1	50.5	50.3	50.5	49.5	49 .7 **	•

 Table 5.7
 Distribution of muscle weight in breed groups of bulls, steers and heifers

¹He-Hereford, Shx-Shorthorn cross, XB-Hybrid and other crossbreds, BSx-Brown Swiss crossbreds, Ho-Holstein, Je-Jersey ²The totals do not sum to 100% since some muscle was weighed as scrap muscle and was not included in the anatomical groups ³Sum of muscle groups 1 plus 3 4Sum of muscle groups 1 plus 3 plus 5 **Differences statistically significant at the 1% level *Source*: Berg and Mukhoty, 1970 individual cattle, or between breeds of cattle, have cleared their minds of one of the supposed variables that has been hindering their progress for many years. Certainly those who are seeking progress in their industry are pleased to welcome any reduction in the number of selection criteria with which they must contend, as they well know that selection on large numbers of criteria ensures stagnation.

Since the above work with heterogeneous cattle much more interest has been displayed in the study of muscle weight distribution in all meat animals.

However, in cattle the major study has been in Canada, and Berg and Mukhoty (1970) published the results of muscle weight distribution studies on a variety of breeds and included 170 steers, heifers and bulls. The results of this study are set out in Table 5.7.

It is difficult to imagine how anyone, after studying results such as those in Table 5.7, could fail to be impressed with the degree of uniformity of muscle weight distribution in cattle of such diverse external appearance. There are only two muscle groups in which breed differences are shown in the above table and it is interesting to look at these. The muscles of the abdominal wall have been shown in other studies (see p. 138) to be altered by external influences, such as the nature of the diet, and it is therefore not surprising to find that there is a small difference between breed groups, and that variations of about 1.5 lb in the weight of this group are found.

The other group in which differences are found between the breeds is group IX, the intrinsic muscles of the neck and thorax, and these differences provide interesting comparisons. In the bulls the Jersey's are shown to be relatively heavier than the large type cattle and it seems that, even though of lighter weight, they had proceeded further towards compositional maturity than the heavier bulls. This line of reasoning is given further support in the steers, for here it is the large breed, the Holstein, which has fallen behind the others, suggesting that it is less compositionally advanced than the smaller breeds, even though heavier.

The above findings, although of little economic significance in consideration of breed differences, raise the possibility that, if breeds were to be compared at the same compositional age, their muscle weight distributions would be even more similar. This could be achieved by comparisons made at the same proportion of mature weight as suggested by Taylor (1968) rather than at equal weights.

The concept of similarity of muscle weight distribution, as

-			I	Experin	ment I					E	Experin	nent II		
London and Home County type cuts	Frie	sian	Heref Short	ord× horn	Ang Short	us × thorn		Frie	sian	Heref Short	ord× horn	Ang Short	us× horn	
Clod and sticking and fore and hind shin	21.9	0.4	22.3	0.4	21.6	0.4	n.s.	<u> </u>						
Clod and sticking								13.4	0.2	14.7	0.2	14.1	0.2	**
Fore shin								2.7	0.1	2.7	0.1	2.6	0.1	n.s.
Hind shin								5.0	0.1	4.8	0.1	4.6	0.1	*
Chuck	12.6	0.3	12.6	0.4	12.0	0.3	n.s.	14.6	0.4	14.4	0.3	14.0	0.3	n.s.
Brisket	6.5	0.3	6.3	0.3	6.3	0.3	n.s.	6.4	0.2	6.3	0.2	6.2	0.2	n.s.
5th, 6th, & 7th ribs	5.7	0.1	5.5	0.2	5.6	0.1	n.s.	5.4	0.1	5.1	0.1	5.3	0.1	n.s.
8th & 9th ribs	3.7	0.1	3.9	0.1	3.8	0.1	n.s.	3.6	0.1	3.6	0.1	3.6	0.1	n.s.
10th rib	1.8	0.1	1.9	0.1	1.6	0.1	n.s.	1.7	0.1	1.8	0.1	1.6	0.1	n.s.
Plate	1.3	0.1	1.4	0.1	1.3	0.1	n.s.	1.5	0.1	1.4	0.1	1.5	0.1	n.s.
Loin	6.4	0.1	6.4	0.1	6.6	0.1	n.s.	6.4	0.2	6.5	0.1	6.6	0.1	n.s.
Flank	7.5	0.1	8.7	0.1	8.4	0.1	+	7.6	0.2	8.0	0.2	9.1	0.2	***
Round	32.7	0.4	31.0	0.5	32.9	0.5	*	31.7	0.4	30.8	0.4	30.7	0.4	n.s.

Table 5.8	Lean meat in each cut as a percentage of total carcass lean in three beef 'breeds'
-----------	--

*P < 0.05 **P < 0.01 ***P < 0.001

n.s.—non-significant Source: Carroll and Conniffe, 1968.

demonstrated by individual muscle dissection, has allowed a reassessment of the precision of other methods of carcass assessment and Carroll (1972) by showing a very high degree of uniformity in the yields of muscle from cuts has produced a high level of confidence in his cutting procedures (see Table 5.8).

It would be foolish to extend this respectability to all methods of cutting, for it is wholly dependent on the skill and dedication of the workers.

The greatest contribution which the muscle weight distribution finding has made is to remove a variable from the assessment of live cattle and carcasses. We now know that there is no point in considering differences in relative size of muscles and can concentrate on the total amount of muscle. This principle has been adopted by Long (1970) in his system of live animal evaluation. It is impossible to determine if there has been any effect on the overall judging of cattle in shows or in selection of breeding stock; however, there are many astute breeders who are convinced of the validity and usefulness of the concept of uniform muscle weight distribution.

There are still among the scientific workers those who accept the concept of uniform muscle weight distribution, yet talk about differences in proportionate yields of cuts of beef as though caused by differences of muscle weight distribution. Preston and Willis (1970) stated: 'Although Butterfield concluded that there were no differences between breeds in muscle distribution, this is at variance with our own findings using commercial dissection procedures'. Their findings were set out in Table 5.9.

They then proceeded:

"We have shown that the Charolais is consistently superior to other Bos taurus and Bos indicus types and consider it possible that the qualities of this breed (a high proportion of edible meat *per se* and also a higher percentage of this in the more valuable parts of the carcass) are shared by other European breeds, such as the Limousin, Simmental and Piedmont.'

They also comment on the absence of these breeds from comparative carcass evaluation studies.

While the data given in the table reproduced here as Table 5.9 undoubtedly show an advantage for the Charolais against the other breeds there is no justification for the claim that this in any way demonstrated different muscle weight distribution. It may be that the Charolais and other Continental cattle do have differences in muscle weight distribution but the table does not demonstrate this.

No. of Bulls	Santa Gertrudis 8	Brahman 16	Criollo 16	Charolais 19	Sig. level
Carcass weight (kg)	225	228	235	235	
Dressing (%)	55.2ª	56.8ª	57.0 ^{ab}	58.0 ^b	*
Edible meat (%)	69.9 ^a	71.8"	74.8 ^b	76.4°	***
First quality (%) [†]	26.9°	27.6 °	29.8 ^b	32.1°	***
Excess fat $(\%)$	13.8"	11.5*	9.8 ^c	7.1 ^d	***
Bone $(\%)$	16.2	16.6	15.5	16.6	
Conformation index*	38.3ª	38.4	39.9 ^{<i>b</i>}	42.0 ^c	***
Meat/bone ratio	4.34°	4.36	4.94	4.60 ^{ab}	**

Table 3.7 The check of breed on cubic meat content of bun carea	Table 5.9
--	-----------

a, b, c, d means in the same row with the same letter do not differ significantly $^+$ first quality as per cent of total edible meat

*P<0.05 **P<0.01 ***P<0.001

Source: Willis and Preston, 1969b.

The differences shown in favour of the Charolais in Table 5.9 in yield of 'edible meat (%)' and yield of 'first quality (%)' could be explained in terms of reduced fat, and Preston and Willis were aware of this when they stated:

'The differences between breeds for this characteristic (cutability) are almost entirely due to variations in fatness, but they are none the less real in that, at the same carcass weight, an early maturing breed, e.g., Angus, will yield less edible meat than a later maturing breed, such as Holstein.'

Undoubtedly we will see over the next few years many studies in which the breeds which are slaughtered with a low level of fat will appear to be superior in yields of high-priced cuts. This will be brought about by two factors in normal cattle and three in double-muscled cattle.

In normal cattle, the fatter breeds will have more fat trim; and will also have proportionately less muscle weight in the proximal regions of the hind leg. This latter phenomenon which was reported by Butterfield (1963c) is still not understood, and is not due to differences in intramuscular fat deposition (Johnson *et al.*, 1973a). However, when comparisons of yields of high-priced cuts are made at equal levels of fatness it is unlikely that any breed will show an advantage unless it is entering the state of double-muscling. The third factor in these double-muscled cattle is some shift of muscle weight as observed by Vissac *et al.* (1971) into the thicker higher-priced muscles.

The largest study on other domestic species is that of Richmond and Berg (1971) in pigs, in which they showed that there is also a remarkable similarity in the muscle weight distribution of that species despite the extreme amount of pressure which has been exerted to change the shape of pigs. This will be discussed further in Chapter 7.

THE EFFECT OF FUNCTION ON MUSCLE GROWTH PATTERNS

The extent to which an organ expresses its potential for growth is 'determined by the physiological requirements placed on it after having differentiated to the point of functional competence' (Goss, 1964).

The (physical) requirements are described by Stewart (1972) as passive tension resulting from elongation and enlargement of the skeleton in pre-natal development and subsequently active tension which becomes more important in post-natal growth.

It seems that the functional demands placed on muscles by steers are very similar from animal to animal and breed to breed, for the differences in relative growth of muscles are small. It might be expected that a marked increased in activity should result in generally bigger musculature, yet this does not seem to be the case (see Chapter 2).

There are few examples of differences in muscle growth in animals induced by exercise so that it alters the basic genetic pattern of differential muscle growth within sexes. Butterfield (unpublished) exercised young calves by forcing them to jump low hurdles several times per day but was unable to induce any changes in the amount of muscle or muscle weight distribution when slaughtered at eight weeks compared with comparable calves reared in small pens with minimal exercise. Maybe the treatments were not sufficiently extreme, However, it does seem that the variation in activity normally met by the muscles of steers has little effect on relative growth of muscles. This experience in calves is not unique. When Rakušan et al. (1971) compared the pectoral muscles of pigeons after one group had been confined for a year and another group allowed to fly, the flying birds were 1.099 times as heavy, but their pectoral muscles were only 1.004 times as heavy (body weights 443 and 403 g; pectoral weights 22.1 and 22.2 g).

An example of an induced change is given in the data from the two calf feeding experiments of Butterfield *et al.* (1966) and Butterfield and Johnson (1971) which have been discussed earlier (p. 121). In the first experiment the calves were fed mainly on diets containing fibrous feed, such as ground grains and lucerne chaff, whereas in the second experiment the entire diet was milk.

When the data from the two experiments are compared it is clear that there are marked differences between the growth of the muscles of the abdominal wall in the two experiments (Fig. 5.15).

This is clearly a response to functional demand in that the added weight of ingesta plus the associated development of the digestive tract in the calves on the fibrous diet, required more work from the abdominal wall.

It is tempting to believe that the added visceral weight has produced an abnormally large response, whereas it may be just as true to say that the abdominal wall in the milk-fed calves had not received the necessary stimulus from physical requirements to make them express their full potential for growth. In young animals there must be an enormous reserve potential for muscle growth, and any specific muscle or group of muscles can be pushed towards its potential size more rapidly than total muscle by selectively increasing the functional demands made on it. Therefore, in the case of the muscles of the abdominal wall in the above example, it seems sensible to suggest that this is simply a case of different functional demand being met by different rate of progress along the path towards the maximum potential weight for those muscles.

It might well be that the differentially large muscles in abnormally active sites in young athletes, such as swimmers, have merely been induced to proceed further towards their mature size than the remainder of the musculature. In other words, they do not acquire bigger muscles than they were eventually to possess but they acquire them at lower total muscle weight.

That instances of variation within cattle of the same sex are so few surely indicates that the normal daily activities of cattle are not sufficiently diverse to produce marked differences. It seems clear that, if differences in muscle weight distribution are to be sought, they will be acquired by the encouragement of different types of activity from that in which cattle normally engage. It also appears that the overall rate of growth of the musculature is limited by the intake of 'nutrients' and genetic potential for growth rather than by exercise, for there is no evidence that cattle which are fed in confined spaces, such as feedlots, grow any less muscle than cattle at pasture, if these are considered at the same level of fatness. That cattle fed grain in feedlots tend to put on more fat on a high grain ration, as shown by Pryor and Laws (1972) and Davies (pers. comm.), than on a low grain ration indicates that the increased fatness of feedlot cattle (and therefore decreased muscle at the same weight) is due to factors other than exercise.

However, the effect of exercise on body composition of meat animals is an almost virgin field in which more information is required. The work of Skjervold *et al.* (1963), in which they induced abnormal exercise in pigs by feeding from elevated feeders, did not produce any higher proportion of ham muscles, but might have been expected to stimulate some other experiments in this area.

Heap and Lodge (1967) showed that the muscles of the abdominal wall in sows became relatively heavier during pregnancy, and Lohse (1971) produced a marked relative increase in the same muscles in a wether by feeding him lead balls; however, there is considerable need for further experimentation.

The impression which is gained from the relative performance of feedlot v. grazed cattle is that the effects of exercise in the differential or total growth of the musculature is minimal in slaughter cattle. Brännäng's (1971) data on the effects of castration on the muscles of the abdominal wall introduce a clear demonstration of the influence of function overriding any inbuilt growth pattern. For the muscles of the abdominal wall were less inhibited in their growth by castration than the total musculature, whereas their high impetus growth pattern clearly qualifies them for maximum retardation. There are two concepts emerging:

- 1. high impetus muscles which have special function in the bulls (e.g., neck muscles) are inhibited by castration, whereas high impetus muscles which do not have a special male function are not inhibited (e.g., abdominal wall);
- 2. inhibition by reduced food intake appears to show the reverse effect in that sex-induced high impetus muscles are not subject to proportionately large weight loss, whereas other high impetus muscles are.

An aspect of the possible effect of exercise on differential muscle

growth, which might well be investigated, is that exercise during puberty in males, when the muscle tissue is growing fastest, may be more effective in inducing change than the same exercise in pre-pubital or castrated males.

THE EFFECT OF HYPERTROPHY ON MUSCLE RELATIVE TO GROWTH

There is evidence that the phenomenon of the Culard, or doublemuscled, animal is associated with changes in the relative size of muscles (Vissac *et al.*, 1971; Hanset and Ansay, 1972), although Pomeroy and Williams (1962) and Butterfield (1966b) had earlier reported a close similarity on the basis of dissection of single animals.

The study of Hanset and Ansay, in which they compared the muscle weights of seven normal and seven hypertrophied animals at equal live weights, is a valuable demonstration of the anatomical detail of the phenomenon. The method of analysis adopted by them of comparison of muscles within regions, on the basis of the total weight of that region, produces the impression of more exaggerated changes than would be revealed by comparison on the baseline of total muscle weight; however, the method used helps to understand the phenomenon. Table 5.10 shows results extracted from Hanset and Ansay's paper.

Hypertrophy of total muscle weight		22%
Hypertrophy of the muscles of the forelimb		25%
		Degree hypertrophy
Muscle		(Culard/normal)
Infraspinatus		
(+ teres minor)		50%
Triceps brachii (caput later.)		31
Triceps brachii (caput long.)		
(+ tens. fasc. antibrachii)		29
Supraspinatus		29
Teres major		27
Subscapularis		23
Brachialis		20
Deltoideus		15
Biceps brachii		8
Muscles de l'avant-bras		7
(dont Flex. carpi radial)		
	Total	25%

Table 5.10 Comparison of individual muscle weights of Culard and normal cattle

Hypertrophy of muscles of hind limb		24% Degree hypertrophy (Culard/normal)
Biceps femoris		35
Glutaeus medius		25
Semitendinosus		25
Quadriceps femoris (groupe)		25
Semimembranosus		
(+ ad. femoris)		24
Sartorius		21
Tensor fascia lata		19
Gracilis		18
Soleus + Gastrocnemius		14
Muscles de la jambe (groupe) (dont Flex. digit. prof.)		13
Pectineus		11
Flex. digit. sup.		1
	Total	24%

Hypertrophy of muscles of thorax an	d loin	16%
Muscle		Degree hypertrophy (Culard/normal)
Latis. dorsi		30%
Longis. dorsi		19
Serratus ventralis (cerv. & thor.)		17
Pectoralis superf. (+ pector. prof.)		16
Psoas + iliopsoas		15
Rhomboideus		13
Splenius		10
Semispinalis capitis		6
Spinalis dorsi		5
-	Total	16%

Source: Hanset and Ansay, 1972.

The variation of hypertrophy can be considered in several ways. We might like to refer to it as a Centripetal gradient (Rollins *et al.*, 1969) which approximately describes the phenomenon but does little to explain why it should be that the muscles situated more distally are in general less affected than the proximal ones. There is one hypothesis which could explain the variation in simple terms and that is, that the degree of hypertrophy is common to all muscle fibres and, when measured by the weight of dissected muscles, is therefore inversely related to the amount of non-muscle fibre content of the muscle. This would be mostly connective tissue and, to a lesser extent, intramuscular fat, blood vessels and nerves.

Such an hypothesis seems to explain much of the variation recorded by Hanset and Ansay (1972) and is an extension to the musculature of the hypothesis put forward by Goss (1964) in regard to some visceral organs.

6 Fat: its growth and distribution in cattle

IN BRIEF Fat is the most variable carcass tissue both in amount and in distribution. Therefore it has the greatest influence on both the amount of each of the other tissues in a carcass at any particular weight and the proportionate size of the joints ('cuts'). Fat also exerts a considerable influence on the external appearance of both live animals and carcasses due to the shrouding effect of the subcutaneous depots and the bulging effect produced by the inter- and intramuscular depots. Unfortunately some of the sought after shapes in beef cattle have been heavily influenced by fat depots which are increasingly incompatible with high yields of saleable product, as consumers react against the purchase of fat at the prices associated with beef.

The acceptance of low-fat breeds in recent years has revolutionized the concepts of 'beef' animals, and breeds previously shunned as being of 'dairy-type' or draft animals are now dominating the beef scene in many parts of the world. However, most markets still require some fat; a few still require, and are likely to continue to require, a lot of fat; and animals in many environments still require fat depots to enable them to maintain their survival characteristics. We must therefore know how fat grows.

As with many areas in which research has been inadequate, the field of fat growth is often disposed of by generalizations. It is often said that there is an order in which fat is deposited and that subcutaneous fat is the last. As shown recently and set out in this chapter, the various fat depots in Angus steers tend to assume a fairly fixed proportion of total fat at early stages of fattening and these proportions persist to high levels of fattening. It is true that the subcutaneous depot is the last to assume its high proportion of total fat but it is nevertheless increasing its contribution to total fat from very light weights.

There are breed differences in the partitioning and distribution of fat. Whereas distribution, particularly of subcutaneous fat, seems to be associated with shape of animals, the differences seen in the partitioning between the depots may be explainable in terms of the total amount of fat present relative to the mature fat content of the breed. We do not confirm this possibility in this chapter but pose it as a tentative explanation of some of the differences observed between breeds.

Clarification of the story of fat growth will be aided if we consider the carcass fat depots separately from the non-carcass depots and if, within the carcass, the subcutaneous and intermuscular depots are divorced from other minor depots.

In the visual appraisal of live animals subcutaneous fat assumes a role far beyond its own intrinsic importance in that it influences selection for slaughter a simple act, the consideration of which has probably influenced genetic choice and nutritional practice in the preparation of each animal. The ratio of other tissues to subcutaneous fat is therefore of vital importance. As we will show, the larger breeds, at the same weight of subcutaneous fat, have more intermuscular

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fat (at the same proportion of their final fat weight we believe they may not be different), and this therefore means that, if intermuscular fat has a major effect on eating quality, the desired level may be attained in large breeds at lower levels of subcutaneous and total carcass fat. The different fat growth patterns of the sexes may also be explainable in terms of size; and predisposition to fattening is undoubtedly inversely related to androgen levels.

As has been shown with muscle, it is necessary to have detailed anatomical and chemical studies before commercially oriented studies are undertaken if much waste of effort is to be avoided.

INTRODUCTION

The growth of fat in cattle is an extremely important part of the total growth story from several points of view. The major biological role of fat is undoubtedly as an energy store, providing a survival buffer against periodic low food availability such as in drought and in winters. Subcutaneous fat could be useful as an insulating layer against cold as shown for cattle by Young and Dietz (1971) however, most native ruminant species in Northern climates obtain their insulation primarily from a very thick coat rather than a fluctuating fat depot.

Tropical game species apparently do not have large stores of fat as Ledger (1963) reported that of 143 game carcasses dissected only 19 exceeded 5 per cent total carcass fat and only one exceeded 10 per cent. Apparently such animals do not depend on large fat stores for survival.

Domestication and selection have resulted in some breeds of cattle with a very high predisposition to fatten to the point where, of the carcass, fat may account for as much as, or more than, does muscle. This feature is particularly well developed in what have been the most popular of the British breeds, whose ability to fatten at light weights on forage diets led to their widespread use throughout the world. During the nineteenth and early part of the twentieth centuries, fat was considered a highly desirable part of a beef carcass. The success of breeders in producing animals capable of depositing large quantities of fat on their carcasses gives an indication of the degree and kind of genetic change that can be achieved in the fattening process in a relatively short time.

The demand for fat on beef has fallen under the influence of lower caloric requirements brought about by more sedentary occupations, of publicity against consumption of excessive amounts of fat by humans, and of the development of cheaper fats of vegetable origin. In beef breeding a reversal of the trend towards animals with an ability to fatten at light weights has placed the emphasis on fast growing breeds of heavy mature weights which, at normal market weights, have much less fat on their carcasses. There remains a controversy about how much fat is needed on and in beef to retain its distinct highly desired characteristics. Nevertheless in those countries where fat was most highly prized, such as the British Isles, North America and even Japan, the trend is for leaner beef. In many other countries, particularly most of the Continental European countries, fat beef was never held in particularly high regard and breeding emphasis has been, and will probably continue to be, toward efficient production of lean meat (muscle).

Early fattening breeds will find a temporary niche in crossing with large late fattening breeds as a step to less fat. The continued use of such breeds will depend on other characteristics such as adaptability to special environmental situations or maternal traits, if in fact they have special merit in these characteristics.

Fat is a major carcass tissue; it influences the beef industry in many ways. An understanding of factors influencing its growth and distribution is paramount to making logical decisions relating to production, processing and marketing of beef. Our aim in this chapter is to explain how fat grows and how we might manipulate this in feeding and breeding to produce carcasses of particular types. The growth of fat relative to other tissues has been discussed in Chapter 2 and we will now look at fat as a system in isolation.

THE NORMAL GROWTH OF FAT Partitioning of fat among the depots

Fat is undoubtedly the most variable tissue in the carcass and it varies not only in total amount but its partitioning among various depots alters markedly throughout growth.

The changes in the partitioning of fat are set out in two figures taken from a study by Johnson *et al.* (1972). Fig. 6.1 shows the actual amounts in the range of animals from foetal calves at 210 days of pregnancy right through to steers at 1,200 days. Although all depots rose with fattening, the intermuscular depot rose most, followed by the subcutaneous depot. The cattle in the study were predominantly Angus and the pattern revealed should be taken as characteristic of only that breed under the conditions of the experiment, for there is insufficient data available to enable us to derive any general pattern



Fig. 6.1 Changes in the weights of 5 fat depots relative to total side fat weight in 23 bovine carcasses aged from 210 days of gestation to 1,200 days *Source*: Johnson *et al.*, 1972

of fat growth which could be used as a model for all cattle under conditions which could be classed as normal growth.

The actual amounts of fat in the various carcass depots of the foetal calves were of course very small and dissected material must be expected to be subject to large error, however the three calves in the study ranged from 140 to 152 g of fat which was fairly evenly distributed between intermuscular and kidney fat. The most notable feature was the almost complete lack of subcutaneous fat. This pattern changed as the animals grew until the subcutaneous depot reached about 30 per cent of the total fat as the animals entered the early stages of fattening.



Fig. 6.2 Relative contribution of the 5 fat depots to total side fat weight with increase in total side fat weight *Source*: Johnson *et al.*, 1972

	Omentum fat	Mesenteric fat	Kidney fat	Pelvic fat and around genitalia	Thoracic cavity fat	Total
Weight (kg)	9.55	3.62	8.17	9.65	3.29	34.29
live weight	2.09	0.79	1.78	2.11	0.72	7.50

Table 6.1 Internal fat depots of Swedish Red and White Steers 750 days old

Source: Brännäng, 1966.

Fig. 6.2 shows the relative contribution which each depot made to the total fat of the carcass and reveals a remarkably stable situation from about the time the total side fat exceeded 16 kg. One particularly interesting point demonstrated in both figures is the lack of any substantial rise in the intramuscular fat content with advanced fattening. It may be that cattle forced to greater fatness or even fattening at greater age will produce more intramuscular fat, however the data in this work indicate that not more than about 12 per cent of the total fat in the carcass was in the intramuscular site. As these data were collected from analysis of whole muscles, it is sure that the figure shown for what is really the 'non-dissectible fat of the musculature' is slightly higher than the true intramuscular fat.

The deposition of fat in the non-carcass depots was studied by Brännäng (1966) and the pattern of relative weights can be seen in Table 6.1.

There is little data available on the relative amounts of fat found in the various internal depots in cattle of different breeds and the low value of this fat commercially does not encourage research into this area.

However, it is the sort of information which could be of assistance in explaining observed differences in dressing percentage at various levels of carcass fatness.

Distribution of fat on the commercial carcass

Fat in its amount and distribution can markedly affect the value of any carcass. It is the distribution of fat which determines if that fat is worth dollars or cents per kg, for while fat on rump steak is valuable, in the flank it is almost valueless. Also, once the level of fat rises, it is only that which is within the consumer's optimum range of fat on each cut which is valuable; that which is in excess is a liability due to its low value and the cost of labour needed to remove it.

In animals marketed at low levels of fatness there is little trimming, and therefore in such cases fat distribution is of less importance. However, in most markets excess fat will remain as the major factor affecting the yield of saleable beef from carcasses.

As long as trading methods continue which involve the sale of carcasses, or untrimmed cuts, at one point in the trade and of trimmed cuts in another, the fat distribution factor will remain a very important one.

The trend toward lighter carcass weights in beef in some places in the retail market such as in Brisbane, Australia (Parkinson, pers. comm.), is associated with a variety of influences, such as increased tenderness from the lighter and therefore presumably younger carcass, and the alleged demand for smaller joints or cuts by the housewife; but possibly the greatest factor is the higher yields obtained from this type of carcass by the retailer due to the small amount of excess fat to be trimmed. A reversal of this trend is apparent in North America, under the influence of late fattening breeds, and carcass weights are rising.

The judging of carcass competitions in some countries by assessment of yield of retail cuts is giving a lead to the influence of fat distribution and amount between individuals and groups of cattle and must serve to highlight differences between breeds.

There is little doubt that before we produce information which is going to be of direct applicability to the meat industry, that studies will need to be conducted which can be applied to monetary assessment of differences in the fat depots of cattle. This will not be done on the anatomical divisions which we have used to date, but rather in a manner more related to industrial practice, for no matter from where fat is trimmed, it is of little value. However, the difference between the fat which stays on a high-priced cut and that which is trimmed off it is indeed high. There is sufficient evidence now emerging that fat growth does follow a general plan (Johnson *et al.*, 1972, 1973a), and a continuation of anatomical and chemical studies will be needed to define clearly the growth patterns of fat just as anatomical studies have unravelled the fascinating picture of muscle growth.

However, in addition we must aim at studies which will be based on some division of fat such as follows. Fat will be classified into four categories:

- 1. fat which is sold with high-priced cuts;
- 2. fat which is sold with low-priced cuts;
- 3. fat which is removed from the carcass at slaughter;
- 4. fat which is sold with carcasses but which is of no value in the meat trade.

Once we proceed to this stage the assessment of fat comparisons of breeds, or nutritional regimes will be on a meaningful basis for the industry, but as with muscle studies the basic anatomical studies must precede the commercially oriented studies if much effort is not to be wasted.

Each of the four categories suggested above has a different economic story.

CATEGORY 1—Fat on high-priced cuts

This fat is just as valuable as the muscle it surrounds as it sells for the same price. So long as the industry does not attempt to force the consumer to a maximum acceptable amount of fat in this category, but aims to provide an optimum, then this fat will continue to be a valuable source of income. Any attempt to force higher levels on the consumer will probably result in a further reaction against the consumption of fat.



Fig. 6.3 The developmental pattern of beef steers during fattening. The numbers indicate ascending order of average relative growth rate *Source*: Luitingh, 1962

CATEGORY 2-Fat on the cheaper cuts

This fat also attracts the same price as the muscle it surrounds, but in this case it is also one of the causes for some of these cuts being cheaper. It also imparts to cuts such as brisket a great deal of the characteristic eating quality. As the level of overall fatness declines the level of this fat is likely to decline proportionately more, as it is in advanced fattening that much fat moves into these cuts which are situated mostly on the ventral part of the carcass (Luitingh, 1962) (see Fig. 6.3).

CATEGORY 3-Fat which is removed at slaughter

Fat which is removed at slaughter is not of great value but does not involve heavy expense in additional processing. Due to conditions of removal this fat can be used to make high grade tallow which is not possible with the fat trimmed in the butcher's shop.

CATEGORY 4—Fat which is trimmed in the butchering trade

Fat which is trimmed from the carcass after it enters the trade is of little commercial value and involves expense in its removal which may result in considerable elevation of the price of the carcass. So that, not only is this of little cash value, it is in fact an operating liability in most trades.

THE INFLUENCE OF BREED ON FAT GROWTH Breed differences in the partitioning of fat

By the partitioning of fat we refer to its location in the various layers of the body, whereas by distribution we refer to its location within those layers. The two layers of fat with which we are primarily concerned are the subcutaneous layer which, by definition, is laid down in the superficial fascia of the body, and the intermuscular layer which, for all practical purposes, is the remainder of the carcass fat provided that the kidney and 'channel' (pelvic) fat has been removed.

The 'improvement' of some breeds of cattle has been associated with, if not largely achieved by, the movement of a higher proportion of the total carcass fat out into the subcutaneous depot. This was inevitable as the 'improvement' was based largely on the eye assessment of cattle and this assessment has been largely dependent on adequate amounts of subcutaneous fat to mould the surface image of the beasts to the most acceptable appearance.

Ledger (1959) compared the fat partitioning between Shorthorns

reported by Callow (1948) in England and the Boran in East Africa, and suggested the simple theory that the degree of heat tolerance was associated with the ability to lay down fat in sites other than the subcutaneous site. He also made the interesting extension from this suggestion that the inability of many *Bos taurus* cattle to proceed past a store condition in hot environments was the limiting insulation of their own subcutaneous fat. In other words they proceed to thrive until their subcutaneous fat layer reaches a level where it becomes a thermal embarrassment which prevents them from grazing and so they do not continue on to acceptable levels of fat for slaughter. Some support for these general ideas was given by Pitts in discussion, following the paper of Pitts and Bullard (1968), who pointed out that he could find only one particularly significant difference between arctic and tropic zone mammals, and this was a greater percentage of the total fat in the subcutaneous depot of arctic mammals.

Callow (1961) suggested that the more heavily a species or breed is selected for traditional beef characteristics, the higher is the ratio of subcutaneous to intermuscular fat. It is interesting in 1974 that there is a swing to the European draught breeds for beef production and these cattle have not been selected for these 'traditional beef characteristics'.

Butterfield (1965a) from limited data plotted tentative patterns of fat partitioning for some breeds and it is a major gap in our present knowledge that little further evidence has been published since then. He showed that his Poll Herefords and Brahmans tended to deposit a higher proportion of their fat subcutaneously than Callow's Shorthorns and his own Angus, and this did not appear to support Callow's theory. Clearly this is an area demanding extensive investigation, for a great deal of the relative carcass value of different types of cattle depends on the manner in which they partition their fat among their fat depots. For, as shown by Preston and Willis (1970) and Harrington (1971), breed differences do exist in relative yields of high-priced and low-priced cuts and an understanding of the fattening process should help to explain these differences. Fig. 6.4 from Harrington (1971) and Cuthbertson et al. (1972) shows the variation which exists in trimmed meat relative to trimmed fat and bone and indicates a much closer relationship of trimmed meat to fat than to bone.

The publication by the Royal Smithfield Club (1966) compared Hereford, Friesian and Hereford \times Friesian steers and showed the



(a) Relationship between percentage bone and percentage fat in four goups of steers

Source: Cuthbertson et al., 1972



(b) Relationship trim fat per cent, bone per cent and meat per cent (128 assorted beef sides—all sexes) Source: Harrington, 1971

Fig. 6.4 Relationship between bone, fat and meat

differences in partitioning of fat in these cattle of different maturity types (Fig. 6.5). Ignoring the intermediate role of the crossbreds it was



Fig. 6.5 Partition of fat of Hereford------, Hereford × Friesian -------, and Friesian -------, Source: Royal Smithfield Club, 1966

clear that the Herefords partitioned a greater proportion of total fat into the subcutaneous site than did the Friesians, and a smaller proportion into the intermuscular site and also into the combined kidney, cod and channel fat sites.

There is little to be said in favour of heavy deposits of kidney fat and channel fat and it is interesting to note from the above report that, at the same liveweights, the Herefords had more subcutaneous fat, more intermuscular fat and the weights of combined kidney, channel and cod fat were not different from the Friesians. How then does the Friesian fit the reputation of dairy breeds that they have more kidney fat than beef breeds? The answer is apparent from the above publication in that cattle are selected for slaughter largely on the amount of subcutaneous fat they possess and therefore the Friesians are normally carried to greater weights than the Herefords and hence finish up with more kidney fat.

However, this whole story of kidney fat and the emphasis place on it by many, and particularly butchers attempting to downgrade the unseen carcass from the dairy animal, is most unreal and will disappear as the industry swings over to the procedure of removal of kidney fat from the carcass at an early stage of the processing. It has been a relic from the past that we have continued to market carcasses with the kidney fat intact, for this is a commodity of little value which is quite incompatible with the high value of the remainder of the carcass. To continue to sell carcasses with the kidney fat in them is akin to wrapping gold in a variable amount of lead and charging a fixed price per unit of weight of the whole.

In the classification of carcasses, the use of the minimum number of specifications as an index of composition will be facilitated if the kidney fat is removed. Kidney fat must be considered along with



Fig. 6.6 Fattening patterns of Friesian, Hereford, and Hereford × Friesian steers *Source*: Royal Smithfield Club, 1966

other internal fats, rather than with the carcasses, if a realistic evaluation of the role it plays in carcass value is to emerge. To recommend that kidney and pelvic fat should be retained in the carcass because of their value as biological criteria as in Europe is to invite continuation of the confused halo which hangs over our understanding of fat in the carcass.

A demonstration of how different breeds partition fat between the subcutaneous and intermuscular fat depots can be shown by plotting the weight of each of these depots as a percentage of their sum weight as in Fig. 6.6. This figure is compiled from data extracted from the comparative study of Friesian, Hereford and Hereford \times Friesian (Royal Smithfield Club, 1966) and is based on only the fattening phase of the study. It shows that the Friesian at all levels of fat studied has more of its fat intermuscularly than the Hereford; the Hereford has more of its fat subcutaneously than the Friesian. The crossbreds were at all stages intermediate between the two pure breeds. These data support Callow's theory.

In the last stage of fattening the Friesians actually increased the proportion of intermuscular to subcutaneous fat. However this could be due to individual variation and there is no indication of what they would do at greater levels of fatness. It would be expected that as the intermuscular fat depots filled, the proportion of fat going to the subcutaneous site would increase.

It would be unwise to suggest that we can compare the data from different experiments, and draw any firm conclusions about the fattening patterns of breeds. However, it does appear likely that the



Fig. 6.7 Fattening patterns of Shorthorn crossbred steers Source: Berg and Fukuhara, unpublished

patterns of partition into the fat depots in different breeds result from factors which are not markedly affected by minor differences in feeding and environment, provided that these are not accompanied by loss of weight. It is likely that the tendency of fat to flow into the subcutaneous site could be facilitated by the looseness of the skin and subcutaneous connective tissue sought by breeders. It may well be that differences between fattening patterns in Shorthorns and Boran discussed by Ledger (1959) and mentioned earlier could be associated with such a simple explanation.

Data from several studies, involving several breeds, are available for comparison of partitioning of fat between intermuscular and subcutaneous depots. The fattening pattern of steers sired by Shorthorn bulls from mixed cows is shown in Fig. 6.7. These animals were self-fed a high concentrate ration in Edmonton, Canada, where the temperatures for several months are mainly below 0° F and go as low as minus 40° F (Berg and Fukuhara, unpublished). The pattern for these steers is very similar to that shown for the Herefords in Fig. 6.6. Although in the more advanced stage of fattening subcutaneous fat of the Shorthorn crossbreds almost equalled intermuscular fat. This was at a higher total fat content than achieved by the Herefords.

The fattening pattern of Poll Hereford steers in the New England district of New South Wales, Australia, running on improved and natural pasture is derived from the data of Butterfield (1963a) and is shown in Fig. 6.8. It appears that these steers had advanced to the stage where more of their fat was in the subcutaneous site at much lighter weights of total fat than in other studies.



Fig. 6.8 Fattening patterns of Poll Hereford steers Source: Butterfield, 1963a

Characteristic	Weight i	ncrease	Partition of f total dissectibl weigh	fat as % of le fat at live t of
	(kg)	(%)	362 kg	466 kg
Live weight	104	29		
Carcass weight	61	32	-	
Total dissectible fat	9.7	70	100	100
Subcutaneous fat	6.2	118	38	49
Intermuscular fat	3.0	42	50	42
Kidney and channel fat	0.5	33	12	9

 Table 6.2
 Changes in fat weight and partition in 1/2 Sib-Poll Hereford steers at pasture

Source: Butterfield, 1963a.

The extremely high impetus of growth of subcutaneous fat is seen in the data set out in Table 6.2.

The picture that emerges is that during this phase of growth, when total dissectible fat increased by 70 per cent, the subcutaneous depot increased by 118 per cent while the other depots were increasing at a rate not greatly different from the rate of increase of the carcass as a whole (32 per cent). If further investigation revealed that Fig. 6.8 does indicate the true picture of that part of the fattening pattern of the Poll Hereford, then it would have important implications for carcass yields and for predictions involving subcutaneous fat measurements, as it is so different from other breeds.



Fig. 6.9 Fattening pattern of Angus steers Source: Butterfield, unpublished

The pattern of fattening of Angus steers appears to be different to that of the other breeds (Fig. 6.9) in that the proportion of the subcutaneous to intermuscular fat remained almost constant over a wider range of total fat. In the tentative patterns which Butterfield (1965a) suggested from other data this same trend was apparent in Angus steers.

It seems that the Angus reaches a high proportion of subcutaneous to intermuscular fat at relatively low weights of total fat but then has only a slightly greater impetus of fat growth in its subcutaneous site. This could have a bearing on the fact that at advanced levels of fat the Angus tends to retain a smoother appearance than the Shorthorn, and to a lesser extent the Hereford, for although reasonable amounts of subcutaneous fat tend to smooth the outlines of animals, a surplus can have the opposite effect.

Some extremely valuable information is now coming from the dissection projects of the Meat and Livestock Commission in England. Large numbers of animals are reared under comparable conditions,



Fig. 6.10 Fattening pattern of various breed groups of steers *Source*: Cuthbertson and Harrington, unpublished

and the most striking feature of the comparisons is that there is little difference between breed groups. The only outstanding difference being that the Hereford \times Friesian, as expected, had a greater proportion of its fat in the subcutaneous site than the other breed groups. There appears to be little difference in any of the other groups which could all be classified as 'unimproved' for beef conditions are yielding information which will allow valid comparisons of fattening patterns.

Fig. 6.10 shows a comparison of the fattening patterns of steers of the following breeds and crosses: Friesian, Hereford \times Friesian, Charolais \times Friesian and a group including Ayrshire and Finnish characteristics in terms of the concept of improvement in the British beef breeds. Statistically the slopes are not different, however the intercepts are highly significantly different. This indicates that between at least some of these groups of animals, at any level of carcass fat, the proportion of subcutaneous to intermuscular fat will be different, whereas the degree of change in proportions as the animals fatten will be the same irrespective of breed.

The continuation of this type of study by the MLC will produce information of great value in assessing breed merit.

Breed differences in subcutaneous fat distribution

There are differences in subcutaneous fat distribution which are well known characteristics of some breeds. For example, the excessive development of the brisket of Herefords is readily noted in carcasses and was a feature of the live assessment of the steers in the Smithfield project mentioned in the previous section. This development is all fat. The Shorthorn, when overfat, characteristically deposits surplus subcutaneous fat in lumpy formations associated with boney prominences.

Many people believe that the hump of *Bos indicus* cattle, which is of course a particularly prominent feature of the mature bull, is comprised of fat. The hump, however, is basically an enlargement of either the cervical (Brahman) or thoracic (Boran) portions of the rhomboid muscle but may have a very high proportion of intramuscular fat. The impression gained when the hump is cut in the midline in commercial carcasses is not a true representation, as the median raphe of the hump appears to contain much more fat than the bellies of the muscles either side of it. As fat has been a major factor governing selection of stud cattle of British breeds, but not in many other breeds, it would be expected that we should now have a wide variation in fattening patterns in the cattle population of the world and this is certainly the case. Those breeds which have remained under the influence of the British stud beef breeders, and the smaller dairy breeds, are mostly early maturing whereas the European draft breeds, certain small breeds like the Highlander, and the larger dairy breeds are late maturing. The characteristic of early maturity has made the British beef breeds of exceptional value for beef production over a wide spectrum of countries and particularly in harsh environments where their ability to fatten in short growing seasons at virtually any weight has made them particularly valuable.

As production methods improve the rate of growth, and the consumer set against fat increases, these same British cattle face the need to reduce their early maturity if they are to have a future as commercial cattle in the straight-bred form in competition with later maturing cattle. It may be they should not attempt to alter, but rather exploit their virtues as breeds suitable for crossing with late maturing breeds?

THE INFLUENCE OF FAT ON MUSCLE GROWTH

The effect of intramuscular fat on total muscle weight

There is considerable interest in the possible differences between cattle of various types in the amount of fat in the muscles, as this is seen in some markets as an index of eating quality, despite the failure of scientific attempts consistently to relate important eating characteristics and intramuscular fat levels. However, visible 'marbling' in muscle has a strong influence on the consumer's choice of meat in some countries (e.g., Japan, America).

There are no comparative studies available between breeds which would indicate what levels of intramuscular fat might be expected at various levels of total fatness or total weight but Fig. 6.1 (p. 145) shows the amounts obtained in the feeding experiment of Johnson *et al.* (1972). Only about 6 kg, that is, about 10 per cent of total fat was in the intramuscular site in the fattest steers and study of Fig. 6.2 (p. 146) shows that this was a fairly steady proportion attained when total side fat was only about 16 kg.

Whether 10 per cent of total fat in the intramuscular site can be

taken as a general figure to cover most cattle, under most conditions of relatively 'normal' growth, is not known, but it does seem likely that the variation will not be very great, at least between breeds, as in the above study some Friesian steers followed the same pattern as the Angus. However, there is an indication of genetic differences in marbling and this will no doubt be expressed in yield of ether extract.

Two interesting studies involving large numbers of cattle of different breeds relate the marbling as subjectively assessed, with fat thickness at similar carcass weights (Damon *et al.*, 1960; Kauffman *et al.*, 1968). The results of the two studies are plotted in Figs. 6.11 and 6.12.

The impression which is given by these two figures is that there is a close association between fatness and marbling at the same weights and that breed differences are likely to be quite small. There does not appear to be any indication that any breed will 'marble' independent of general fatness. In the Damon *et al.* data (Fig. 6.11), while fat thickness score went from 7 to 11, marbling score altered by three units and no breed fell further than about half a unit from the line of fit. In the Kauffman *et al.* data (Fig. 6.12), it appears that an increase of fat thickness from 1.5 to 2.5 cm altered marbling score by about two units, and no breed fell more than about a quarter of a unit off the line of best fit.



Fig. 6.11 Relationship between marbling score and fat thickness score: Charolais (C) N = 44; Brahman (B) N = 42; Brangus (R) N = 43; Hereford (H) N = 47; Angus (A) N = 49; Shorthorn (S) N = 50; mean slaughter weight of all breeds approximately 340 kg Source: Damon et al., 1960



Fig. 6.12 Relationship between marbling score and fat thickness: Angus (A) N = 1219; Shorthorn (S) N = 407; Hereford (H) N = 563; Red Poll (P) N = 37; others (O) N = 210; mean slaughter weight of all breeds approximately 300 kg Source: Kauffman et al., 1968

As pointed out by Preston and Willis (1970) and Carroll (1971) most scientific investigation of marbling has failed to show any relationship to eating qualities other than juiciness, except for the work done on leaner breeds by Jones (1968) which suggested a relationship to tenderness and flavour also. The chances of being able to increase marbling in breeds which do not fatten readily do not seem high, as Cundiff *et al.* (1964) reported a genetic correlation of 1 between carcass grade and backfat thickness suggesting that marbling and external fat are controlled by the same genes.

In Fig. 6.13 the data from the groups of steers of Johnson et al.



Fig. 6.13 Increase in intramuscular fat with increasing muscle plus bone weight in Angus steers Source: Johnson et al., 1972

(1972) have been plotted against the muscle plus bone weight to give an indication of the effect it would have on determination of muscle:bone ratio at different muscle plus bone weights. Certainly if any corrections to muscle:bone ratios were to be carried out to obtain fat-free muscle:bone ratios then much more information from many types of cattle and nutritional regimes would be necessary to derive suitable formulae. But the information in Figs. 6.11 and 6.12 indicate that the correction for breed would probably be small.

However, presuming a muscle:bone ratio of 4:1 at 110 kg, muscle plus bone weight, and ignoring any effect that changes of fatness may have on weight of bone, we can calculate that intramuscular fat contributes 0.27 to the muscle in the ratio of 4:1.

Similarly, with the same cattle at 40 kg muscle plus bone weight and a presumed muscle:bone ratio of 3.80:1 (calculated approximately using Berg and Butterfield's (1966) correction of 0.03 per 10 kg) the intramuscular fat contributes 0.14 to the muscle in the ratio.

The differences between the two ratios was 0.2 on a dissected muscle basis and 0.07 on a fat-free basis, which suggests that a large proportion of the changes in muscle:bone ratio associated with increased weights may be attributable to fat within the muscles.

Much more information is required of effects of fattening on both muscle and bone.

Effect of intramuscular fat on muscle-weight distribution

Studies on muscle weight are usually made on fresh whole muscles as dissected from the carcass, without consideration of the variation which might exist between the muscles in the level of intramuscular fat. Butterfield (1963a, c) noted that muscle weight distribution varied as the percentage of total dissectible fat changed, and particularly that the proportion of total muscle in the expensive parts of the carcass declined as the total dissectible fat rose above about 10 per cent of carcass weight. The most likely hypothesis to explain this phenomenon seemed to be a disproportionate partitioning of fat between the muscle groups as total fat rose.

However, Suess (1968) studied the growth coefficients of 7 muscles on fresh, fat-free and fat-and-water-free bases and found no differences due to method. This study suggested that the influence of intramuscular fat on growth patterns of muscles may not be great.

A study of the non-dissectible fat of the musculature by Johnson

et al. (1973a) showed that the differences observed in muscle weight distribution during fattening cannot be explained on the basis of fat content of the dissected muscles. This work was done on the 'standard muscle groups' and it seems likely that it can be extended to individual muscles.

THE EFFECT OF BODY WEIGHT LOSS ON FAT DEPOTS

The overall role of fat in providing its share of the energy requirements during body weight loss has been discussed in Chapter 2. We now look at changes within the fat depots, based on information from the experiment of Butterfield (1966a) using Poll Hereford steers.

In this study steers of about 19 months and averaging 362 kg liveweight lost 57 kg liveweight and 18.52 kg of dissectible fat in 64 days which was a reduction of 69.7 per cent in their dissectible fat depots. Their mean age at slaughter was 672 days.

The losses from each depot expressed as a percentage of the original weights were:

		% loss
Semi-starving steers	Subcutaneous	74.5
	Intermuscular	68.4
	Kidney fat	59.9
	Total dissectible fat	70.4

The differences between the percentage loss from these depots were not great, and data from larger numbers or under different conditions may, or may not, show a different picture. However, the ranking of greatest loss from the subcutaneous depot, followed by intermuscular, and kidney fat was the same as their ranking for normal growth at this weight and age. In other words, proportionately most fat was being taken away from the areas where most would normally have been added.

If there is any functional difference between the role of the depots, the percentage decrease probably gives the story of priorities; namely, that of the three depots the subcutaneous fat is least essential, followed by intermuscular then kidney and channel fat. However, it seems doubtful if a functional argument can be utilized substantially to explain fat changes in the same way as it can in muscle.

Percentage loss gives no idea of amounts lost from each depot. The actual amounts lost give some idea of the relative contributions from each depot to the animal energy needs.

Weight loss (kg)

Semi-starving steers	Subcutaneous	8.0
	Intermuscular	9.5
	Kidney fat	1.9
	Total dissectible fat	19.4

Thus, in this particular group of steers, about equal amounts of fat were broken down from subcutaneous and intermuscular sites and, of course, much less from around the kidneys.

The amount used from each depot must depend on the amounts available, and once a depot reaches a very low level, as did the subcutaneous depot in this case, then a much higher proportion of the needs must come from the other depots which are still not approaching depletion. For this reason this study cannot give the answers to all the questions regarding order of breakdown of fat. The question of the order of removal of fat from the various depots can be answered only by the dissection of a large series of animals throughout the entire weight loss process. Such data is unfortunately not available and we can only suggest that it seems likely that, in the first stages of weight loss, proportionately more fat would be drawn from the subcutaneous depot than from the intermuscular depot.

GROWTH OF FAT DEPOTS DURING RECOVERY AFTER BODY WEIGHT LOSS

This section is also largely based on the Poll Hereford steer study utilized in the last section. Eight steers, which had been submitted to the semi-starvation treatment outlined in the previous section, were recovered to the live weight they would have achieved at 879 days under pasture conditions. This required a recovery period on grass of 160 days and a live weight gain of 125 kg. During this recovery the total dissectible fat increased by 155.7 per cent.
The gains of each depot expressed as percentage increase of the weight of the same depot in the starved steers was as follows:

		% gain
	Subcutaneous fat	156.3
December of stars	Intermuscular fat	175.9
Recovering steers	Kidney fat	86.2
	Total dissectible fat	155.7

Again, the difference between the intermuscular and the subcutaneous depots was not great and, if real, suggests that the intermuscular fat has some priority over the subcutaneous fat in the recovery process. This is more clearly demonstrated by the actual gains (below) and the gains per kg of live weight increase in Table 6.3.

The actual amounts gained by each depot were:

		Kg increase
	(Subcutaneous	4.2
D	Intermuscular	7.8
Recovering steers	Kidney fat	1.1
	Total dissectible fat	13.1

The above figures are quite different from those for normal growth of the fat depots between the two control groups, that is, over the particular age range in the experiment, where the percentage increases were:

		% increase
Normal steers	Subcutaneous	117.9
Normal stoom	Intermuscular	42.3
Normal steers	Kidney fat	32.9
	Total dissectible fat	70.4

Nevertheless, it seems that the pattern of fattening in the recovery steers could be simply a normal pattern for animals at that level of fatness and that the partitioning of the fat between the depots is a matter of level of fatness, rather than age or muscle weight or live weight or sex or any other criterion. In other words the compositional age of the fat depots is determined by total fat and not by the weight of



Fig. 6.14 Patterns of fat partitioning during normal growth and during recovery after weight loss: growth coefficients of subcutaneous fat—normal growth 'b' = 1.17, recovery 'b' = 0.96Source: Butterfield, 1966a

other body tissues. This is supported by the data plotted in Fig. 6.14.

Over the period of gain from 672–879 days, when the recovering steers reached 430 kg live weight and normal steers could be expected to be in a fattening phase, it is enlightening to study the amounts of fat deposited in each depot relative to the live weight gain in recovering the steers and to estimate this for normal steers. This is done using the data from the total growth period of the experiment, and realizing that such data will probably slightly overestimate the total amounts laid down per day in the normal steers, as well as the amount laid down in the subcutaneous site.

Table 6.3 supports the idea that irrespective of age or weight the tendency is to replenish other fat stores before rebuilding the subcutaneous depots. This has an interesting bearing on the selection of slaughter time in cattle which have recovered from a store period. The tissue which influences selection for slaughter most is the last to recover, and it might well be that the other, economically more important, tissues are already at an optimum stage for slaughter long before the level of subcutaneous fat is acceptable. This is likely to lead to the over-fattening of such animals particularly as the skeletal

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Animals	Live	weigh	t (kg)	Fat (g) per kg of live weight gain				
	Start	End	Gain	Subcut.	Intermus.	Kidney & channel	Total	
Normal	373	430	57	60	28	5.3	94	
Recovery	305	430	125	17	31	4.5	52	

Table 6.3 Partition of fat (g) per kg of live weight gain during recovery and normal growth from 672-879 days of Poll Hereford steers, both groups terminating at same live weight (fat figures for normal growth are estimated)

growth during the store period makes the animals more angular and therefore less easily covered with the all-concealing layer of surface fat. It is likely that the erroneous belief that cattle during recovery from a store period lay down mainly fat is due to the circumstances set out above, as all other depots are likely to be overfilled with fat whilst the subcutaneous depot is being returned to a level at which cattle comply with accepted standards of visual appeal as live animals or carcasses.

THE EFFECT OF SEX ON FAT GROWTH

The study of fat growth in bulls, heifers and steers by Berg and Fukuhara (unpublished) gives a clear picture of the pattern of fattening in a group of cattle all sired by Shorthorn bulls and self-fed identical rations. The dams were mixed breeds. Although the absolute patterns of fattening for these cattle may differ from those of other breeds or under different feed conditions, the relative patterns as shown in the figures below should be applicable to a wide range of cattle and conditions.

Fig. 6.15 shows clearly that fat is the tissue which plays the largest part in altering the carcass composition between the sexes. Whereas muscle and bone follow similar paths when plotted against muscle plus bone weight, the rate of fat growth in bulls is slower than in heifers and steers throughout. Heifers and steers grow fat at a similar rate until the heifers enter a rapid fattening phase at about 60 kg muscle plus bone weight. The impetus of fat deposition in steers increased at about 75 kg and the bulls at 85 kg of muscle plus bone weight.

The different rates of fattening of the sexes determine the range of



Fig. 6.15 Growth patterns of muscle fat and bone of the sexes relative to muscle plus bone weight *Source*: Berg and Fukuhara, unpublished

variation of carcass weights over which they may be sold with optimum or near optimum fat cover. This can be extremely important in obtaining the maximum yield of beef per animal, for, whereas heifers may have to be slaughtered over a small weight range at light carcass weights to yield optimum fat cover, bulls can be slaughtered over a wider weight range and carried to heavier carcass weights. In other words, the faster the rate of fattening the more critical is the choice of slaughter weight. The lighter the animal fattens the lighter is the carcass. The impression gained from feeding bulls of a late maturing hybrid strain is that optimum fatness for Canadian grading can be obtained over a range of about 200 lb liveweight. This range would surely be much less for heifers, particularly those from early maturing breeds.

Comparison of the patterns displayed in the Figs. 6.16, 6.17 and



Fig. 6.16 Relative growth patterns of dissectible fat depots in fore- and hindquarters of the sexes *Source*: Berg and Fukuhara, unpublished

6.18 provides an interesting illustration of the relative fat partitioning in the fore- and hindquarter. In Fig. 6.16 it is clear that in all three sexes the hindquarter contains more of the total fat but that the patterns of fattening for both hind- and forequarter are similar within each sex. Fig. 6.17 shows that this picture of fattening as shown by the total fat is shared by the subcutaneous fat, however in Fig. 6.18 it is clear that in all sexes it is the forequarter which receives the greatest amount of intermuscular fat, and that the intermuscular fattening of the hindquarters is not greatly different between the sexes.

The implications are extremely interesting from a meat quality point of view as the three sexes appear to be very similar in the way the intermuscular fat of the hindquarter is deposited.

As the steers and heifers have much more intermuscular fat in the forequarter at the same level of intermuscular fat in the hindquarter, it should be possible to produce bulls with optimum intermuscular fatness of the expensive hindquarter without the excessive deposition of the cheaper forequarter fat which might be associated with heifers





and steers at the same carcass weight. It should also be possible to produce bulls with the optimum of intermuscular fat in the expensive hindquarter at a much lower level of subcutaneous fat than in the heifers or steers.

The above results confirm the usual impressions that heifers fatten at lighter weights than steers, which fatten at lighter weights than bulls. The implication of this in the meat industry is obviously that, if a uniform level of fatness is sought in slaughter stock, and provided the cattle have entered the phase of high impetus fat growth, then heifers should be slaughtered lighter than steers which should be slaughtered lighter than bulls.

However, as can be seen from Figs. 6.15 to 6.18, the steers and heifers follow similar fat growth impetus up to the commencement of the fattening phase and, therefore, if breeds are used in which the fattening phase is delayed until after the desired weight of slaughter is reached, there would be no need to differentiate between heifers and steers on the basis of fat content. In the particular cattle used by Berg and





Source: Berg and Fukuhara, unpublished

Fukuhara (unpublished) (i.e., Shorthorn crossbreds), and under their feed conditions, such a situation would apply until the cattle reached a carcass weight of about 174 kg (about 380 lb). In much later maturing types of cattle, such as Friesian and the European draught breeds, the critical carcass weight at which the body composition of steers and heifers diverge is expected to be much higher.

Fig. 6.18 shows that, as fattening advances, impetus of intermuscular fat growth is greater in the forequarter than in the hind in the three sexes. Most of the increased impetus of intermuscular fat as a whole obviously comes from increase in the forequarter, so that as the fattening process advances the distribution of fat from a commercial standpoint becomes progressively less desirable; and this shift of fat weight occurs earliest in the heifer followed by the steer and bull. This again provides evidence for the slaughtering of heifers at the lightest weights followed by steers and then bulls.

Brännäng (1966) studied the deposition of thoracic and abdominal cavity fat as well as carcass fat, in bulls which averaged 493 kg live-

Internal fat	Omentum fat	Mesenteric fat	Kidney fat	Fat from pelvic region & genitalia	Fat from thoracic cavity	Total
Weight (kg) in						
Bulls	6.84	3.17	5.82	6.70	2.65	25.19
Steers	9.55	3.62	8.17	9.65	3.29	34.29
% of live weight						
Bulls	1.38	0.65	1.18	1.35	0.53	5.09
Steers	2.09	0.79	1.78	2.11	0.72	7.50
				Extra-pl	eural and	
Carcass fat depots	Subcutaneous fat		ntermusc fat	ular extra-po f	Total	
Weight (kg) in						
Bulls	,	2.90	8.70	1.	.35	13.95
Steers	(6.67	10.93	1.	.77	19.37
% of live weight						
Bulls	(0.79	1.76	0.	27	2.82
Steers		1.47	2.40	0.	39	4.26

Table 6.4 Comparison of fat deposition in monozygous twin bulls and steers

Source: Brännäng, 1966.

Depot	% increase in amount of fat due to castration	Depot	% increase in amount of fat due to castration
Non-carcass	36	Carcass	39
Omental	40	Subcutaneous	71
Kidney	40	Intermuscular	26
Pelvis and genitalia	44		
Thoracic	24		
Mesenteric	14		

 Table 6.5
 Fat distribution changes between depots due to castration

Source: Brännäng, 1966.

weight and steers of 455 kg. The means of fat weights and percentage of liveweight in the internal depots are given in Table 6.4.

There is clearly an increase in deposition of fat in all fat depots as a result of castration.

Brännäng presented the following data (Table 6.5) from which he concluded:

There is thus a gradient associated with the increase of fat in the steers which starts at the centre of the body and extends outwards, i.e., the nearer the centre (internal organs) the fat deposition [sic] the less it is influenced by castration, in other words, the early deposited fat is less affected by castration than later deposited fat.

However, we find it difficult to see any single gradient in this data as the intermuscular fat is obviously much less affected than several of the internal depots. Nevertheless from a carcass viewpoint the important aspects are:

- 1. On a percentage basis total carcass fat and total internal fat were affected in a very similar degree by castration, although the actual weights showed that the steers gained 9.1 lb of internal fat and only 5.4 lb of carcass fat. Castration therefore would tend to depress dressing percentage due to its effect on fat.
- 2. The subcutaneous depot is affected much more than the intermuscular depot, which is of importance from several aspects:
 - (a) if the proportion of fat in meat influences its eating quality it should be possible to reach the optimum level in bulls with less external fat cover;
 - (b) measures of subcutaneous fat in bulls and steers will bear different relationships to total fat. This factor is of importance in estimating body composition using subcutaneous fat thickness as an index.

It seems realistic to regard the phenomenon of fat deposition as being dependent to some extent on local pressures. Up to a certain level of fatness it seems easier for fat to flow into crevices between muscles than to lift the skin away from the muscles by occupying the superficial fascia. Eventually a stage is reached where the former low-pressure sites become of higher pressure than the subcutaneous site, and then a continuous balancing effect keeps the two sites filling at once with the subcutaneous site eventually receiving the bulk of the fat as the pressures in the intermuscular site reach a maximum. That the intermuscular site can be pushed to a functionally improper level is evidenced by the misalignment of hindlimb bones in cattle, particularly young bulls, which have been gorged for show purposes.

7 The growth of muscle of cattle relative to that of other species

'The beef calf is "born wrong" from a beef standpoint, and no known method of feeding and management can correct its deficiency.' (Vaughan, 1939)

IN BRIEF The structure of cattle, which has evolved, is the picture which the cattle breeders have been trying to retouch for many years. They have certainly succeeded in altering the external appearance, they have succeeded in altering the fattening patterns, but they have achieved little else and in particular they have achieved nothing in attempts to alter the muscle weight distribution. What then are the strong factors which defy the efforts of the animal breeders?

Study of some other species of animals gives us an opportunity to try to explain why cattle musculature is built in the way that it is and why it defies our efforts to change it.

It appears that the smaller the species the more likely it is that an increased proportion of its muscle weight will be concentrated around its spinal column. The more agile, the greater is the development of the muscles in the distal parts of the limbs. The more mobile, the greater the proportion in the whole of the limbs. The domestication of animals appears to bring about an increase in the relative weight of the muscles of the abdominal wall to cope with the more continuously fully loaded digestive tract. The more aggressive animals have relatively larger muscles in the neck region, in line with their method of fighting.

The *Bos taurus* and *Bos indicus* domestic cattle by their size, their relative immobility, their domestication and their placidity seem destined to retain their present muscle weight distribution no matter how much man would like to change it.

INTRODUCTION

Animals of different species usually vary in their external appearance more than members of the same species. We have seen that various cattle of widely different external appearance have very similar muscle weight distribution, and it would therefore seem that the major reasons why cattle have their typical, and remarkably uniform, distribution of muscle weight are not to be found in studies of external appearance. However, we would like to know why cattle have their present relative muscle growth patterns, and consequent muscle weight distribution, so that we may search in the most potentially fruitful areas to bring about change. That is, of course, if change is possible.

By studying other animals it is possible that we may be able to

gain information which will lead us to a better understanding of the muscle growth patterns of cattle.

The information in this chapter will, in many areas, be drawn from statistically inadequate samples, in fact it is rarely in this type of work that we can claim to have adequately sampled a breed or population. In order that the reader may be able to assess the reliability of the data, and any conclusions made from them, the number of animals will be indicated where appropriate. Nevertheless for some species, notably the pig, sheep and elephant seal, we do have large amounts of information available from various studies, although for the sake of clarity we may use only selected representative individuals or small groups for our purpose here.

Depending on the information available from other species the most suitable cattle data are used for comparison, for example, data from a mature boar will be compared with those of a mature bull. The data are eventually brought together in the form of indices directly comparable with cattle in the hope that similarities and differences of various species for certain characteristics may cast some light on the muscle weight distribution of cattle.

The first species to be considered is the pig.

MUSCLE GROWTH OF PIGS RELATIVE TO CATTLE

Table 7.1 is taken from the work of Richmond and Berg (1971) and shows their analysis of the muscle weight distribution of 109 pigs of two sexes, three breeds, and at four weights.

There are several interesting aspects of these comparisons which indicate that the concept of uniformity of muscle weight distribution within a species, irrespective of breed, is equally true in pigs as it is in cattle. The differences between breeds in Table 7.1 are confined to only one muscle group and are then so small as to be of no economic importance, as demonstrated in the similar yields of 'expensive' muscle weights.

The weight range of slaughter in this work covered a period when differential muscle growth was almost completely absent when considered on the basis of muscle groups. It can be presumed that this also applied to the vast majority of individual muscles. The only exception to this uniform relative growth rate is shown by the intrinsic muscles of the thorax and neck, which have grown a little faster than total muscle over the range of weights. This aligns with the findings of very late development in steers and bulls, however the barrows are not significantly different from the gilts, as may have been expected

Musels snown		Live weight (kg)				Breeds**		Sex		
Muscle group	23*	68	91	114	D	н	Y	В	G	
1. Proximal pelvic limb	26.56	28.40	28.25	28.67	28.39	28.42	28.50	28.67	28.21	
2. Distal pelvic limb	3.99	3.96	3.84	3.87	3.86	3.84	3.97	3.84	3.95	
3. Spinal	16.83	17.01	17.42	17.44	17.69 ^ª	17.17 ^{ab}	17.01 [*]	17.54 ^ª	17.05	
4. Abdominal	12.41	11.32	10.98	11.16	11.16	11.21	11.10	11.22	11.09	
5. Proximal thoracic limb	12.35	12.29	12.05	11.79	11.87	11.94	12.32	11.90	12.18	
6. Distal thoracic limb	2.15	1.94	1.89	1.85	1.88	1.89	1.91	1.84"	1.95 ^b	
7. Thorax to thoracic limb	7.35	7.56	7.64	7.38	7.42	7.57	7.58	7.48	7.57	
8. Neck to thoracic limb	4.39	4.90	4.84	4.97	4.88	4.91	4.92	4.77	5.03	
9. Neck and thorax	9.28	9.39°	10.02	9.76 ^{ab}	9.66	9.81	9.69	9.66	9.78	
10. Scrap	4.69	3.21	3.06	3.08	3.15	3.20	3.01	3.07	3.17	
Expensive groups A	30.61	32.36	32.09	32.54	32.25	32.27	32.48	32.50	32.16	
В	47.46	49.38	49.51	49.98	49.95	49.44	49.48	50.04 ^a	49.20 ^b	
С	59.81	61.67	61.56	61.78	61.82	61.38	61.80	61.94	61.39	

Table 7.1	Standard muscle groups' as percentage of weight of total side muscle in 109 barrows and gilt	ts of
three breed	s and slaughtered at four live weights	

*23 kg group not tested statistically against other weight groups

**D = Duroc × Yorkshire; H = Hampshire × Yorkshire; Y = Yorkshire

A (Group 1 + Group 2); B (Group 1 + Group 2 + Group 3); C (Group 1 + Group 2 + Group 3 + Group 5) $a^{b^{c}}$ Means within the same classification followed by different letters differ significantly at P < 0.05

Source: Richmond and Berg, 1971.

if the barrows were weakly following the path to crest development which may be exhibited by mature boars, similarly to bulls.

The muscle weight distribution of the heaviest barrows is compared with that of mature steers in Table 7.2 and the indices of differences between pigs and cattle are illustrated in Fig. 7.1.

The two studies used in Table 7.2 are ideal for comparison as they were carried out in the same laboratory with the same core staff engaged in dissection.

The major difference between the pig and the ox is that the pig has a much greater proportion of his total muscle weight surrounding the spinal column. It is tempting to suggest that this is the result of concentration of effort by breeders to attain the maximum amount of muscle in that part of the body which the consumer of pig meat seeks. Such a suggestion is soon moderated by the examination of the data for each of the other smaller species, the wool-type sheep and deer, which also show a rise in this group relative to the larger species.

The muscles in the two groups located distally in the limbs of the pigs are relatively small and this seems to align with the reduced agility of pigs compared with the other species.

The muscles connecting the thorax to the thoracic limb are also

	Weight of m	uscle group	as % of total muscl	e weight
Muscle group	Steers ¹	Barrows ²	Barrows relative to steers	Index*
1. Proximal pelvic limb	29.6	28.7	- 0.9	97
2. Distal pelvic limb	4.3	3.9	- 0.4	91
3. Around spinal column	n 12.3	17.4	+ 4.9	141
4. Abdominal wall	10.9	11.2	+0.3	103
5. Proximal thoracic lim	b 12.6	11.8	- 0.8	94
6. Distal thoracic limb	2.4	1.9	-0.5	79
7. Thorax to thoracic lin	nb 10.6	7.4	- 3.2	70
8. Neck to thoracic limb	5.4	5.0	- 0.4	93
9. Neck and thorax	1.8	3.1	+ 1.2	97

Table 7.2	The muscle	weight	distribution	of steers	and	barrows

*Index = pig value relative to cattle = 100

¹Steers mean total side muscle weight 69.3 kg N = 85

Source: Berg and Mukhoty, 1970.

²Barrows at total side muscle weight 17.3 kg N = 12Source: Richmond and Berg, 1971.



Fig. 7.1 Muscle weight distribution of the pig relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in same group in cattle = 100

reduced in the pig and, indeed, it will be seen that all the other species (except the elephant seal) are less developed here than the ox.

MUSCLE GROWTH OF SHEEP RELATIVE TO CATTLE

Our data for this section comes from two large studies. The first carried out in New Zealand by Fourie (1965) and the second in Australia by Lohse (1971). Fourie worked with Southdowns, Romney Marsh and crosses between these breeds, while Lohse worked with a Peppin strain of Merinos.

Fourie found that breed had no effect on the relationship of the weight of the largest individual muscles to total muscle weight, although he did report that certain muscles of the Southdown appeared to achieve relative changes at lower ages than the Romney. This would be compatible with the maturity status of the two breeds, and is similar to the effect which is evident in the cattle data of Berg and Mukhoty (1970) where Jersey bulls achieved mature muscle development at lighter weights than bulls of larger breeds.

Table 7.3 is based on data from Lohse's study of the Peppin Merino and his rams are compared with bulls from the study of Berg and Mukhoty.

The sheep, as a small domestic ruminant, is probably expected to be more like the ox than any other animal and, indeed, its muscle weight distribution features only three major departures from that of the ox. The muscles surrounding the spinal column are a much higher proportion of total muscle than in the ox and are comparable with the

		Weight of m	uscle group a	as $\%$ of total musc	ele weight
	Muscle group	Bulls ¹	Rams ²	Rams relative to bulls	Index*
1.	Proximal pelvic limb	28.4	26.6	- 1.8	94
2.	Distal pelvic limb	4.3	4.7	+ 0.4	109
3.	Around spinal column	12.5	17.4	+ 4.9	139
4.	Abdominal wall	9.7	9.4	- 0.3	97
5.	Proximal thoracic limb	12.5	11.2	- 1.3	90
6.	Distal thoracic limb	2.3	3.0	+ 0.7	130
7.	Thorax to thoracic limit	o 10.5	7.6	- 2.9	72
8.	Neck to thoracic limb	5.5	6.0	+ 0.5	109
9.	Neck and thorax	12.5	11.2	- 1.3	90

Table 7.3 The muscle weight distribution of Merino rams and Bos taurus bulls

*Index = sheep value relative to cattle = 100

¹ Bulls, mean total side muscle weights 77.6 kg N = 63Source: Berg and Mukhoty, 1970. ² Rams mean total side muscle weights 4.3 kg N = 2

Rams mean total side muscle weights 4.3 kg N = 2Source: Lohse, 1971.



Fig. 7.2 Muscle weight distribution of the sheep relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100

pig. In keeping with most of the other species, except the pig, the distal muscles of the thoracic limb are better developed. Again the muscles connecting the thorax to the thoracic limb are less well developed.

The muscle weight distribution of the sheep relative to cattle is illustrated in Fig. 7.2.

MUSCLE GROWTH OF WATER BUFFALO

(Bubalus bubalis) RELATIVE TO CATTLE

The data available on this species is from the dissection of two bulls. The muscle weight distribution of these bulls compared with *Bos taurus* cattle bulls of similar weight is set out in Table 7.4.

The data from each buffalo is compared with the mean figures for *Bos taurus* bulls of comparable weight.

There is some inconsistency between the results for the small and large buffalo bulls which makes interpretation difficult. However, some consistent differences from the ox emerge. The buffalo has a greatly reduced proportion of total muscle surrounding the spinal column. This is associated with lumbar vertebrae which are different from cattle. Their transverse processes curve ventrally (Butterfield, 1964) and the dorsal spines are relatively short.

The hindleg groups appear to be very similar to the ox, however



Fig. 7.3 Muscle weight distribution of the water buffalo relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100. Buffalo data are mean of 2 bulls in Table 7.4

		Bos taurus ¹	Big buffalo ²	Buffalo relative to Bos taurus	Index*	Bos taurus ³	Small buffalo⁴	Buffalo relative to Bos taurus	Index*
1.	Proximal pelvic limb	28.4	30.0	+1.6	106	34.6	34.5	-0.1	100
2.	Distal pelvic limb	4.3	4.6	+0.3	107	5.5	5.6	+0.1	102
3.	Around spinal column	12.5	9.4	-3.1	75	12.7	10.6	-2.1	83
4.	Abdominal wall	9.7	8.6	-1.1	89	8.9	6.2	-2.7	70
5.	Proximal thoracic limb	12.5	12.6	+0.1	101	10.3	13.6	+3.3	132
6.	Distal thoracic limb	2.3	2.7	+0.4	117	3.0	2.9	0.1	97
7.	Thorax to thoracic limb	10.5	9.6	-0.9	91	9.2	9.3	+0.1	101
8.	Neck to thoracic limb	5.5	8.3	+2.8	151	6.9	6.2	~0.7	90
9.	Neck and thorax	12.5	13.5	+1.0	108	8.7	10.8	+2.1	124

Table 7.4 The muscle weight distribution of Bos taurus bulls and buffalo bulls

* Index = buffalo value relative to cattle = 100

- ¹ Bulls mean muscle weight 77.6 kg N = 63Source : Berg and Mukhoty, 1970.
- ² Buffalo bull muscle weight 80.2 kg N = 1

³ Bulls of mean muscle weight 34.2 kg Brahman \times Shorthorn and Brahman \times Friesian N = 2

⁴ Buffalo bull muscle weight 34.6 kg N = 1Source: Butterfield, unpublished.

the picture is less clear for the forelimb. The indices for the two groups suggest a relative increase in this region which is not as large as may have been anticipated in the larger bull based on external appearance. Cockrill (1967) ascribed the ability of these animals to move easily in mud to the exceptionally flexible fetlock and pastern joints. If this is indeed so, it might have been expected that the digital flexors and extensors found in the distal muscles of each limb would be relatively much larger than in cattle. Our figures do not indicate any large difference, although the buffalo is slightly heavier in these muscles. Our specimens came from a life in relatively dry yards and it is possible that a lifetime in the paddy fields might provide a different picture.

This is the one species in which the muscles attaching the thorax to the thoracic limb are of similar relative weight to the ox.

MUSCLE GROWTH OF BANTENG (Bos sondiacus) **RELATIVE TO CATTLE**

The only data available is from a single banteng steer. The muscle weight distribution of this steer is compared with Bos taurus steers in Table 7.5.

	Weight of mu	iscle group	as % of total muse	ele weight
Muscle group	Bos taurus steers ¹	Banteng steer ²	Banteng relative to Bos taurus	Index*
1. Proximal pelvic limb	29.6	36.4	+ 6.8	123
2. Distal pelvic limb	4.3	6.1	+ 1.8	142
3. Around spinal column	12.3	12.7	+0.4	103
4. Abdominal wall	10.9	8.3	- 2.6	76
5. Proximal thoracic limb.	12.6	11.4	-1.2	90
6. Distal thoracic limb	2.4	3.2	+0.8	133
7. Thorax to thoracic limb	10.6	7.5	- 3.1	71
8. Neck to thoracic limb	5.4	5.7	+0.3	106
9. Neck and thorax	10.1	7.4	- 2.7	73

Table 7.5	The	muscle	weight	distribution	of	Bos	taurus	and	banteng	steers
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*Index = banteng values relative to Bos taurus = 100

¹Steers mean side muscle weight 69.3 kg N = 85

Source: Bergard Mukhoty, 1970.

²Banteng steer side muscle weight 26.1 kg N = 1

Source: Butterfield, unpublished.

This animal has a much higher proportion of its muscle weight in the hindlimb and around the spinal column, and less muscle weight in the forequarter and abdominal wall.

The marked increase in development of the distal muscles of all limbs is probably an indication of the agility of the animal; while the decrease in the weight of muscles in the abdominal wall is more typical of non-domesticated species studied.

These cattle are somewhat similar in external appearance to deer and, in fact, resemble them perhaps more than they do other cattle, so that it is not surprising that the general picture of its muscle weight distribution is more like the deer than the ox, with the notable exception of the muscles surrounding the spinal column, in which the banteng resemble *Bos taurus*. It may be that species size is a major factor in the development of this group of muscles and data from the larger deer species could give a lead to this question. The lighter intrinsic muscles of the neck and thorax are in line with the external appearance of these animals.

The muscle weight distribution of the banteng relative to Bos taurus is shown in Fig. 7.4.



Fig. 7.4 Muscle weight distribution of the banteng relative to *Bos taurus* cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100

MUSCLE GROWTH OF THE MOOSE (Alces alces) RELATIVE TO CATTLE

The data are from three bull moose, whose muscle weight distribution is compared with appropriate *Bos taurus* bulls in Table 7.6 Two of the moose were mature bulls and one immature.

The index figures for the moose of two sizes dissected emerge as quite similar. It is perhaps a surprise, and certainly a sobering thought, to those who believe it is simple to assess relative muscle development in the live animal, to find that the moose is relatively better developed in the hindquarter muscles than the ox.

This is a good illustration of the influence of length of bones in altering the appearance of an animal relative to muscle development. It is similarly difficult to assess the relative muscle development between a short-legged animal of a British beef breed and a longer-legged Brahman or Chianina.

The most outstanding feature of the moose is the massive development of the muscles of the distal part of the limbs and, in fact, all four intrinsic groups of the limbs are well developed. This is no doubt



Fig. 7.5 Muscle weight distribution of the moose relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100. Moose data are mean of 3 bulls

		Weight of muscle group as % of total muscle weight									
	Muscle group	Bos taurus bull ¹	Big moose bulls ²	Moose relative to Bos taurus	Index*	<i>B. taurus</i> bulls ³	Small moose bulls ⁴	Moose relative to Bos taurus	Index*		
1.	Proximal pelvic limb	26.5	29.7	+3.2	112	28.4	34.7	+6.3	122		
2.	Distal pelvic limb	3.7	5.9	+2.2	159	4.3	6.5	+2.2	151		
3.	Around spinal column	11.5	11.5	+0.0	100	12.4	11.3	-1.1	91		
4.	Abdominal wall	9.3	5.9	-3.4	63	9.7	5.0	-4.7	52		
5.	Proximal thoracic limb	13.1	17.4	+4.3	133	12.5	16.6	+4.1	133		
6.	Distal thoracic limb	2.4	3.6	+1.2	150	2.3	3.8	+1.5	165		
7.	Thorax to thoracic limb	10.4	9.0	-1.4	87	10.5	7.9	-2.6	75		
8.	Neck to thoracic limb	7.3	6.2	-1.1	85	5.5	5.1	-0.4	93		
9.	Neck and thorax	14.1	9.1	-5.0	65	12.5	7.7	-4.8	62		

Table 7.6 The muscle-weight distribution of Bos taurus and moose bulls

*Index = moose value relative to cattle = 100

¹ Angus × Charolais bull total side muscle weight 193.9 kg N = 1

- ² Moose bulls mean total side muscle weight 84.1 kg N = 2Source: Berg, unpublished.
- ³ Bos taurus bulls total side muscle weight 77.6 kg N = 63Source: Berg and Mukhoty, 1970.

⁴ Moose bull total side muscle weight 52.1 kg N = 1

associated with the special wading habit of the species, which demands individual action from the limbs rather than a co-ordinated effort involving the whole musculature.

The three forequarter groups associated with the trunk and attachment of the limb are smaller than in the ox and in fact have the smallest index figures for any species studied for the intrinsic muscles of the thorax and neck.

In common with the other wild species the abdominal wall is very light.

The muscle weight distribution of the moose relative to *Bos taurus* is shown in Fig. 7.5.

MUSCLE GROWTH OF WHITE-TAILED DEER

(Odocoileus virginianus) RELATIVE TO CATTLE

The data from three female deer and one mature male are compared with that of appropriate heifers and bulls, in Table 7.7.

Both female and male deer show a greater proportion of their muscle weight in the hindlimbs and around the spinal column than cattle. They also show a decrease in the abdominal wall, the proximal



Fig. 7.6 Muscle weight distribution of the white-tailed deer relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100. Deer data are mean of 3 females and 1 male deer

		Weight of muscle group as % of total muscle weight								
	Muscle group	Heifers ¹	Female deer ²	Deer relative to heifers	Index*	Mature bull ³	Mature male deer ⁴	Deer relative to bull	Index*	
1.	Proximal pelvic limb	31.5	35.7	+4.7	113	26.5	28.7	+2.2	108	
2.	Distal pelvic limb	4.3	5.8	+1.5	135	3.7	4.8	+1.1	129	
3.	Around spinal column	12.1	14.7	+2.6	121	11.5	14.1	+2.6	123	
4.	Abdominal wall	11.5	6.8	-4.7	59	9.3	4.8	-4.5	52	
5.	Proximal thoracic limb	12.4	11.4	-1.0	92	13.1	11.3	-1.8	86	
6.	Distal thoracic limb	2.3	3.1	+0.8	135	2.5	2.5	-0.1	96	
7.	Thorax to thoracic limb	10.3	7.8	-2.5	76	10.4	7.4	-3.0	71	
8.	Neck to thoracic limb	5.2	3.3	-1.9	63	7.3	7.4	+0.1	101	
9.	Neck and thorax	9.0	8.9	-0.1	99	14.1	15.6	+1.5	111	

Table 7.7 The muscle-weight distribution of Bos taurus and deer (O. virginianus)

* Index = Deer value relative to cattle = 100

¹ Heifers mean total side muscle weight 51.0 kg N = 22Source: Berg and Mukhoty, 1970.

² Female deer mean total side muscle weight 9.9 kg N = 3

³ Angus × Charolais bull total side muscle weight 193.9 kg N = 1

⁴ Mature male deer total side muscle weight 28.3 kg N = 1Source: Berg, unpublished.

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part of the thoracic limb and the muscles connecting the thorax to the thoracic limb. However, the mature male deer shows a slightly greater response to the male hormone in his development of forequarter groups than does the bull. Muscle weight distribution of the deer relative to *Bos taurus* is shown in Fig. 7.6.

MUSCLE GROWTH OF THE BISON (Bison bison) RELATIVE TO CATTLE

The data from a single male bison is compared with appropriate *Bos taurus* bulls in Table 7.8.

Surprisingly, and particularly so to those who might regard the bison to be poorly developed in the hindquarter, this bull showed less variation from cattle than any species with which comparison was made. Apart from the lighter thorax to thoracic limb muscles, consistent to all except the buffalo, the only major change was a reduction in abdominal wall and a very marked increase in the muscles connecting the neck to the thoracic limb. It was interesting that this increase in forequarter muscles was not associated with an increase in the intrinsic muscles of the neck and thorax, because in most other species where sex-induced differences are seen in the neck, they are most apparent

		Weight of muscle group as $\%$ of total muscle weight						
	Muscle group	Bos taurus bulls ¹	Bison bull ²	Bison relative to Bos taurus	Index*			
1.	Proximal pelvic limb	28.4	30.7	+ 2.3	108			
2.	Distal pelvic limb	4.3	4.2	- 0.1	98			
3.	Around spinal column	12.4	12.7	+ 0.3	102			
4.	Abdominal wall	9.7	6.9	-2.8	71			
5.	Proximal thoracic limb	12.5	13.0	+ 0.5	104			
6.	Distal thoracic limb	2.3	2.3	+ 0.0	100			
7.	Thorax to thoracic limb	10.5	8.8	- 1.7	84			
8.	Neck to thoracic limb	5.5	8.7	+ 3.2	158			
9.	Neck and thorax	12.5	11.4	- 1.1	91			

1 able 7.0 The muscle-weight distribution of <i>Bos laurus</i> and dison	able 7.8	The muscle-weight distri	ibution of <i>Bos</i>	taurus and	bison	bul
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* Index = bison value relative to cattle = 100

¹ Bull mean side muscle weight 77.6 kg N = 63Source : Berg and Mukhoty, 1970.

² Bison bull side muscle weight 70.9 kg N = 1Source: Berg, unpublished.



Fig. 7.7 Muscle weight distribution of the bison relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100

in this intrinsic group. However, the hump of *Bos indicus* bulls is developed in the rhomboid muscle in either its cervical part (Brahman) or thoracic part (Boran). The rhomboid muscle is associated with the attachment of the forelimb to the neck and thorax, and hence this enlargement in *Bos indicus* cattle is in the same group as the enlargement in bison. It therefore appears that *Bos indicus* is more like the bison than it is like *Bos taurus* in this characteristic, a fact which would be gleefully proclaimed by the detractors of the Brahman.

The bison shows remarkably little change from the *Bos taurus* bull and the only major change is in the muscles connecting the neck to the thoracic limb.

The muscle-weight distribution of the bison relative to *Bos taurus* is shown in Fig. 7.7.

MUSCLE GROWTH OF ELEPHANT SEAL

(Mirounga leonina) RELATIVE TO CATTLE

A very extensive study of growth and development of the elephant seal by Bryden (1969) included a study of muscle weight distribution which produced a great deal of substantial evidence on the effect of function on relative muscle growth. For the purpose of this section the

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		Weight of n	nuscle group	as% of total mus	scle weight
	Muscle group	Mature bull ¹	Mature Elephant seal bull ²	Elephant seal relative to Bos taurus	Index*
1.	Proximal pelvic limb	26.5)			
	•	30.2	5.9	- 24.3	20
2.	Distal pelvic limb	3.7			
3.	Around spinal column	11.5	21.8	+10.3	190
4.	Abdominal wall	9.3	26.0	+ 16.7	280
5.	Proximal thoracic limb	13.1)			
		15.5	4.7	- 10.8	30
6.	Distal thoracic limb	2.4			
7.	Thorax to thoracic limb	10.4	12.5	+ 2.1	120
8.	Neck to thoracic limb	7.3	3.9	- 3.4	53
9.	Neck and thorax	14.1	22.1	+ 8.0	157
	Head		3.0		
	Scrap	1.7	0.2	—	

Table 7.9	The muscle-weight	distribution	of a	Bos	taurus	bull	and
elephant se	al bull						

*Index = elephant seal value relative to cattle = 100

¹ Angus × Charolais bull total side muscle weight 193.9 kg N = 1

Source: Berg, unpublished. m

² Elephant seal bull total side muscle weight 673.3 kg N = 1Source: Bryden, 1969i

muscle weight distribution of mature male seals is compared with that of a mature *Bos taurus* bull. Due to the extreme differences of shape the standard muscle groups were modified by Bryden and an attempt is made in Table 7.8 to align the data as well as possible. In order to do this certain groups are combined.

The elephant seal shows a major change in muscle weight distribution as expected for an animal which has entirely different methods of locomotion. Most of the muscle weight is concentrated in the trunk and the limbs contain only a small portion.

The muscle weight distribution of the elephant seal relative to *Bos taurus* is shown in Fig. 7.8.

In line with the reduced function of legs in this species there is a marked shift of muscle weight to the muscles of the trunk. Of particular



Fig. 7.8 Muscle weight distribution of the elephant seal relative to cattle. Index figures are percentage of total muscle in each group relative to the percentage in the same group in cattle = 100Source: M. M. Bryden, pers. comm

interest is the heavy abdominal wall which plays a large part in locomotion (Bryden, 1969).

No other very sensible comparisons seem possible.

GENERAL CONSIDERATIONS

In Table 7.10 is set out the relative muscle weight distribution of the various species studied. The table has been prepared by bringing together the index figures from the preceding tables. Where more than one comparison has been made from a type of animal (e.g., male and female deer) these are combined and the mean figure used in Table 7.10.

THE MUSCLE GROUPS

Many sobering thoughts arise from scrutiny of Table 7.10. No cattle breeder would concede that the moose has acceptable proportions and yet it appears that, from a meat point of view, his muscle weight distribution in more desirable than cattle. It may be that the bones in the moose are so long that the muscles are stretched out so thin that economically important alterations in shape of cuts of meat would result. However, this is likely to be of minimal importance in an animal so large as the moose, and the concentration of thought on the importance of shape in cuts attributable to length of bones

		-							
Muscle groups	Bos taurus	Pig	Sheep	Water buffalo	Banteng	Moose	Deer	Bison	Elephant seal
1. Proximal pelvic limb	100	97	94	103	123	117	111	108)	20
2. Distal pelvic limb	100	91	109	105	142	155	132	98∫	20
3. Around spinal column	100	141	139	79	103	96	122	102	190
4. Abdominal wall	100	103	97	79	76	58	56	71	280
5. Proximal thoracic limb	100	94	90	117	90	133	89	104)	20
6. Distal thoracic limb	100	79	130	107	133	158	115	100∫	30
7. Thorax to thoracic limb	100	70	72	96	71	81	74	84	120
8. Neck to thoracic limb	100	93	109	120	106	89	82	158	53
9. Neck and thorax	100	97	90	116	73	64	105	91	157

Table 7.10 Muscle-weight distribution of several species expressed relative to *Bos taurus*. Weight of standard muscle groups as per cent of total muscle of each species compared with similar value from appropriate *Bos taurus* animals = 100

should be more a feature of smaller species—if, in fact, it is of any great importance even there. The work of Kirton and Pickering (1967) in New Zealand on lamb leads us to believe that its importance even in small meat animals has been over-rated.

The muscles around the spinal column

The 'improved' breeds of pigs and 'unimproved' (for meat) Peppin Merino sheep have similar relative weight in the muscles surrounding their spinal columns. The other relatively small animal, the deer, is also better developed in the muscles around the spinal column than the larger animals. It would appear that all of the larger species (except the water buffalo) can be grouped together. The buffalo has lighter muscles around its spinal column than the other large species. There is obviously some reason why the smaller species need heavier muscles in this group than the larger ones. From unpublished data kindly supplied by Ledger, we are able to extract relevant information. Ledger divided the musculature of a series of game animals into four groups of which 'loin' was one group. The percentage which this group represented of total muscle weight is shown in Fig. 7.9. There appear to be two separate populations in that the Thompson's gazelle, gerenuk, impala, Grant's gazelle, warthog and topi clearly show a reduction in the proportion of the musculature in this group as the species' size increases. A similar pattern is set by the Uganda kob, oryx, waterbuck, wildebeest and eland. There may be something about these two groupings which makes them different.



Fig. 7.9 Muscles of 'loin' in various game species as a percentage of total muscle weight

Sources: Ledger, 1963, 1968 and pers. comm

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The ranking of indices of this muscle group clearly demonstrates the difference between the small and large species: buffalo (79), moose (96), ox (100), bison (102), banteng (103), deer (122), sheep (139) and pig (141). We might therefore call this a 'size index' to muscle weight distribution.

The intrinsic muscles of the limbs

The most agile animals have the largest relative development in the distal muscles of the limbs, and the least agile (the pig) has the poorest development here. Combining the index figures for the two groups of muscles in the distal parts of the limbs an 'agility index' for each species would give a ranking as follows: pig (85), bison (99), ox (100), buffalo (105), sheep (119), deer (123), moose (156), banteng (158).

To illustrate further the relative power of locomotion of the various species, an index can be drawn up on the basis of the combined intrinsic muscle groups of the limbs (groups 1, 2, 5 and 6) which gives the following ranking for a 'locomotion index': elephant seal (12), pig (90), ox (100), bison (102), sheep (106), buffalo (108), deer (112), banteng (122) and moose (140).

So in the major muscle groups from a meat aspect the ox has little going for it, as it is too big to obtain the maximum muscle development around the spinal column and insufficiently mobile to obtain the maximum muscle in its legs.

The muscles of the abdominal wall

The development of the muscles of the belly wall appears to tell an interesting story. These muscles are certainly not the most sought after in the meat trade, but they are most essential to the animal in supporting the abdominal viscera. The values in Table 7.10 indicate that the more highly improved meat species have heavier abdominal wall muscles than their wild counterparts. This produces the most interesting possibility that modern animal breeding has increased the proportion of this late developing musculature. Hammond's concepts in which he attributed late development to the loin, were in fact based largely on the late development of the abdominal wall and if it were possible to alter muscle weight distribution by breeding, then this is the muscle group most likely to be affected.

However, it is doubtful if there is any reason to believe that the difference between pigs and cattle on one hand, and the wild species on the other, has anything to do with selection for meat, as the Merino sheep has certainly not been selected for meat characteristics and yet they are very similar to the pigs and cattle.

Any data on this group of muscles must be treated with considerable caution unless the full nutritional history is known, for, as has been shown earlier in Chapter 2, this group of muscles is subject to considerable variation from the nature of the diet. Both the buffalo bulls in this study had been reared in captivity and fed on a diet with a high level of concentrates. It is therefore possible that the figures for this species may not be truly representative of buffalo in the field.

On the data available it appears that an 'abdominal wall index' gives the following ranking: deer (55), moose (57), bison (71), banteng (76), buffalo (79), sheep (97), ox (100), pig (103) and elephant seal (290).

The effect of utilizing these muscles for locomotion is clearly seen in the elephant seal.

The muscles connecting the thorax to the thoracic limb

A most interesting comparison is provided by the various figures for the muscles which attach the thoracic limb to the thorax. For here two species fall out as quite different from the others. These are the ox and the buffalo, which are relatively heavier in this group than any other species studied, except the elephant seal. This group of muscles is largely concerned with the support of weight of the cranial end of the animal and it is tempting to think that the additional fat laid down in the cranial end of modern beef cattle needs additional muscular support. However, this cannot be the case with the buffalo, and surely also the weight of the additional musculature in species like the bison would also produce a similar effect. No simple explanation comes to mind for the 'weight support index' and the animals are ranked: pig (70), banteng (71), sheep (72), deer (73), moose (81), bison (84), buffalo (96), ox (100) and elephant seal (120).

Certainly the animals which are (or appear to be) lightest at the cranial end have the lightest muscles in this group, but the surprising thing is that the animals which appear to be proportionally heavier in the forequarter than cattle do not have a relatively heavier muscle group than cattle.

The muscles of the neck and cranial trunk

The development of the neck region of the various species is influenced by the musculature of two groups: the muscles connecting the neck to the thoracic limb and those which are intrinsic to the neck or the neck and thorax. It has been shown in Chapter 5 that the major changes associated with sexual maturity of *Bos taurus* bulls occur in the intrinsic muscles of the neck, however, as we see from Table 7.10, the main differences of muscle development associated with the observed external appearance of certain species occur in the muscles connecting the neck to the thoracic limb. As can be seen, the two species which are noted for their heavy appearance in the forequarter (the bison and the buffalo) have a high index figure for the neck-to-limb group. The difference between the two buffalo bulls (Table 7.4) indicates that sexual maturity may have an influence on this group of muscles in the buffalo which is not apparent in *Bos taurus* bulls.

The 'neck index' ranking is as follows: elephant seal (53), deer (82), moose (89), pig (93), ox (100), banteng (106), sheep (109), buffalo (120) and bison (158).

Only small differences occur in the intrinsic muscles of the neck and thorax, except for the moose and banteng, both of which are relatively much lighter than the other animals, and the small buffalo, which is relatively heavier. The ranking of this 'cranial trunk index' is: moose (64), banteng (73), sheep (90), bison (91), pig (97), ox (100), deer (105) buffalo (116).

It seems difficult to understand why the deer should rank so high in this group as it appears to have a very light neck.

No doubt the answers to the relative weights in this group are to be found in studies of relative skeletal development. Unfortunately no such studies have been completed.

Fantasy

Having reached this stage of comparison with other species it is interesting to now look over the data and try to decide why the ox has the type of muscle weight distribution which has been shown to be so characteristic of the species.

Does it have its low weight of muscles surrounding the spinal column relative to pig and sheep and small deer because of its size? Most of the animals considered which are of approximately the same size as cattle, have about the same proportion of their musculature in that region. This may be pure chance, and the fact that the buffalo has a much lower proportion indicates that there is probably no functional reason why an animal of about cattle size must have about 12 per cent of its total muscle weight around its spinal column. If size is a major factor in determining the weight of muscle around the spinal column then we might expect that there would be some range within the cattle species, between the large and small breeds, for example, the tiny Galloway might be expected to be higher than the huge Chianina. In comparisons of breeds so far completed, no evidence is forthcoming of any breed differences which could be attributed to size. No data are available from breeds of quite such diverse size as the ones mentioned above, but Berg and Mukhoty's data in Table 5.7 show no differences between the small Jersey and the large Friesian.

It seems very doubtful if there is any difference to be found in our cattle population and if the price of increase in the proportion of this group was to be a general reduction in body size then it is not likely that it would be pursued.

The development of muscles in the limbs is clearly associated with locomotion, and it also seems logical that the more agile animals should be better developed in the muscles of finer movement, notably the flexors and extensors of the digits and of the carpus and tarsus.

Those animals which are called upon to make powerful movements in locomotion can be expected to be well developed in the muscles previously referred to as the luxury muscles (Chapter 4), the highaverage impetus muscles found in the proximal part of the pelvic limb and, to a lesser extent, the muscles of the proximal part of the thoracic limb. These muscles are particularly well developed in the moose, an animal which, by habitually walking in swampy ground, is required to have powerful individual limb action.

Where then do we look for the cattle which might be better developed in these muscles? Obviously the draft breeds are our most likely source.

The general run of cattle are not very agile, they are not particularly powerful, and this is why they have a proportionate distribution of muscle weight which does not concentrate as much of the total muscle resources in those regions concerned with these activities.

There is unlikely to be any great enthusiasm relatively to increase other parts of the musculature. However, a reduction in any other group could proportionately increase the sought after groups of the legs and loin. It is therefore of interest to note that the ox, along with the other domestic species, the pig and the sheep, has a large weight of muscle in its abdominal wall. Did this come about by the selection for early maturity, in the way Hammond suggested would happen, when he attributed the growth pattern of these muscles to the loin? It would seem not to be so, as the unimproved (for meat) Peppin Merino has a similar proportion to the ox and the pig. The simple answer appears to be that domestication allows the luxury of a full belly on most occasions and the response to this is a direct increase of abdominal wall muscle.

No doubt the feeding of non-bulky diets could have the desired effect of reducing abdominal wall muscle weight, but this could well be a step in the wrong direction, for the future of beef production in many countries is dependent on the ability of the cattle to graze low quality pastures.

There seems to be no logical explanation of why *Bos taurus*, *Bos indicus* and the buffalo have heavier muscles supporting the weight of the rib cage on the thoracic limbs than the other species.

The fighting characteristics of the mature male are undoubtedly tied up with the development of the muscles in the neck region, whether they are intrinsic or concerned with the attachment of the forelimb. The position of the ox in the rankings for these groups indicates an intermediate state for the ox between what might be regarded as more aggressive species, such as buffalo and bison, and less aggressive species, such as deer and pig.

What hope, then, of finding cattle within the population which might have more desirable muscle weight distribution? The most obvious populations are: the draft cattle of the world for those with better proportions of musculature in the limbs; the smaller breeds of cattle for those with a higher proportion of muscle weight around the spinal column; and cattle which have not been subject to domestication for those with lighter abdominal walls—although this characteristic would scarcely be worth chasing, as the effects of domestication would probably soon produce modification to the same state as the present domestic breeds.

It may be that there are species of cattle, which are more or less aggressive, which could be found to have more or less of their total muscle weight in the neck region.

8 Methods of measuring and predicting carcass composition

IN BRIEF Beef cattle are raised for the edible product they produce. The amount and quality of the edible portion of a beef carcass is influenced by its composition. Accurate estimation or prediction of the edible portion of a beef carcass could be very useful to many segments of the beef industry. Accurate carcass assessment could facilitate trade between packer, wholesaler and retailer. The information on carcass assessment fed back to the producer could aid in his decisions on selection of breeding stock. Accurate live animal assessment could facilitate trade between and could be of great help to the producer in his breeding program.

Carcass composition estimation is concerned with predicting the amount of edible product. Edible product yield is influenced by the proportion of muscle, fat and bone and thus by those factors which influence growth of these tissues discussed in previous chapters of this book. The amount of edible product obtained from a carcass is also influenced by the butcher's skill and by consumer preferences in the trade area or country. Differences occur in how much fat and bone is acceptable along with muscle tissue in edible product. Muscle is the most important tissue of the beef carcass. Fat is the packaging in which beef is delivered. For general application the world over, total muscle is the most logical quantitative end point as a measure of desirable carcass composition. It is related to edible portion under any type of demand. Any particular market can specify how much fat it desires and will accept along with the muscle. We have seen that muscle distribution is quite constant within sex and slaughter weight groups and is little influenced by breed. Therefore it seems of little value to attempt to estimate muscle distribution and such misleading concepts as proportions of high-priced cuts. Thus per cent total muscle should be the end point against which other estimates are compared. Alternately per cent total fat, which goes up as per cent muscle goes down can be a useful end point.

Estimation of carcass composition can be attempted from examination and measurements which can be made on the carcass or on the live animal. Techniques used should in general be inexpensive, rapid and relatively simple to carry out, non-destructive and should leave no harmful residues. Greater cost and effort may be acceptable where greater use is made of the information such as for breeding selection decisions.

Attempts to estimate carcass composition from measurements made on the carcass have been numerous. The most useful and accurate measure of fatness has been the depth of back fat measured on the exposed rib cut of the quartered side. Area of the longissimus dorsi muscle at the same location shows a small positive relationship to total muscle. Carcass weight within a group of animals of a particular $L_{h-1}d$ and sex, fed the same way, is reasonably predictive of composition. However its usefulness breaks down when attempting to predict
composition in animals of different breeds and nutritional history. Measurements of length, width, depth and various combinations and ratios of these linear measurements have been of little use in predicting composition. Visual judgement of conformation has been no more useful than the various linear measurements. Conformation as judged has been more influenced by fat than by muscle. Some attempts to separate fatness and conformation based on muscling show some promise. Measuring the specific gravity of a side by weighing in water appears to be the most accurate method of measuring carcass composition. It could be easily worked into the routine of a packing plant and is a relatively simple, non-destructive method. However its use has not caught on in the industry.

Predicting carcass composition of live animals is a further step removed and more difficult than predictions made from the carcass. Live judging or visual appraisal has been a rather ineffective method. With recent improvement in knowledge of the factors which influence composition, judges can broadly classify animals into groupings based on the relative fatness. Many attempts have been made to correlate length, width, depth, height, circumference and various ratios of these to composition with little success. Routine live animal measurements are of little value for predicting carcass composition. From this we can infer that changing shape or dimensions will not likely alter composition. The most promising techniques for live animal assessment are ultrasonic scanning and potassium 40 counting. Ultrasonic scanning is low cost, non-destructive, non-harmful and portable. Potassium 40 requires expensive equipment but is also non-destructive, non-harmful and reasonably accurate. There is a current danger of being overimpressed with gadgetry and the computer. Some techniques being used are not accurately predicting composition and interpretations are quite misleading. More research is required to improve the accuracy and applicability of these and other live animal evaluation methods.

INTRODUCTION

By now the reader will appreciate some of the complexities of growth, development and body composition. Live weight growth comprises many components, some of little or no economic value—gut fill, head, feet, hide and viscera—parts which are separated from the dressed carcass at slaughter. Even the commercially dressed carcass contains parts of little economic value such as bone and fat trim. Different parts of the commercial carcass command different prices and these can vary from time to time and place to place. We have seen that even the major tissues (muscle and fat) are not homogeneous in their makeup over the body and that their composition varies with age and other factors.

These complexities must not divert us for there is a great need to be able to measure or estimate body and carcass composition in terms of chemical or physical components. Nutritionists wish to know composition in order properly to assess the value of particular feeds or nutrients; physiologists wish to know composition to assist in understanding body functions; breeders wish an estimate of composition in order to bring about desired changes by planned matings; and the trade needs a reliable method for classifying the range of products in commerce.

Trends in the past have indicated that methods used were not good enough; assumed predictors often led producers down the garden path. Attempts to increase the proportion of high-priced cuts by selection for thickness and smoothness over back and loin resulted in a shift of a greater proportion of fat to the surface of the animal with no effect on muscle distribution. Conformation, emphasizing thickness, resulted in a greater increase in fat than in muscle (Hammond, 1932). There has been considerable effort expended in trying to relate visual features to desired carcass quality with little understanding of what makes up a desirable carcass. Thus we find that since 'short and thick' were proven to be poor criteria, 'long and narrow' are now in vogue. Neither approach is likely to affect carcass composition in a desired direction.

Animals of very different types have been shown to be quite similar in carcass composition (e.g., Harrington, 1972). Thus changing the visual type or conformation may not yield the desired result in terms of composition. More direct measures are needed. Breeders who were once overimpressed with short, broad heads and wide muzzles, are now looking for longer, narrower heads as indicators of better performance. Performance should be measured directly, not guessed at by some presumed association.

Considerable research involving many diverse techniques has been and is being done in attempts to develop reliable measures of carcass composition. Methods being tried are direct or indirect, destructive or non-destructive, costly or cheap, time consuming or fast, sophisticated or simple, but all have essentially the same goals those of estimating with reasonable accuracy the composition of the body or of the carcass or of the tissues of the carcass and their distribution. Equipment ranges from a small metal ruler for measuring backfat in swine to a large whole body scintillation counter for measuring naturally occurring radioactive potassium (*⁶K) to estimate muscle mass in cattle. Techniques include measurement of body or carcass density or specific gravity, chemical and radioisotope dilution techniques, probes, X-rays, ultrasonics, photogrametry and measure ments on carcass parts related to the whole. Other possible techniques include ultrasonic hollography (a rather impressive name for attempts to make three dimensional measurements of the different parts of an animal) and thermography, whereby an infra red sensing device takes advantage of differences in temperature of fat and muscle to record subcutaneous fat contours on an animal. Of course there will always be those who prefer to guess, and among them will be some of our most prominent breeders and eminent professors.

In this day of scientific achievement it should be technically possible to characterize the composition of the body and the carcass in any required detail. Whether we are prepared to allocate sufficient resources to develop such techniques and whether having developed them, it will be economically possible to use them are separate considerations. The choice will be in attempting to get the best of both worlds—technical accuracy and economic feasibility.

END POINT FOR PREDICTION OF COMPOSITION

What one is looking for in body or carcass composition depends on the particular interest of the person involved. Researchers in nutrition are interested in whole body chemical components as a total measure of feed use. The manager of a slaughter plant is interested in the yield in terms of carcass to live weight; a meat retailer is interested in the percentage of saleable meat and the proportion of high-priced cuts. Can one or more end point satisfy a wide section of the meat industry? The advantages and disadvantages of a number of end points will be discussed.

Edible portion

Beef is produced for its edible portion. No matter what end point is chosen this must be kept in mind. Logically, many argue that the only final appraisal of carcass merit must be the amount of edible product. Our concern is not with this concept which is basically sound, but with the application of this concept in such a way that directed improvement in the product can result and be measured over time and from country to country.

The first problem is one of definition, and edible portion has been defined in many ways. It may be the portion the butcher is able to sell to the consumer which will vary with the butcher's skill, local trade and the country or area concerned. Most of the variation in the product offered the consumer is in the amount of fat and bone which is included with the muscle. Differences in cutting or standardization of cutting result in variability in the product offered throughout the world, but undoubtedly the differences in fatness sought will alone spell confusion if edible portion is to be used as a goal in improvement of cattle. For example, in a market which requires three-quarters of an inch of fat a carcass may have a very high yield of edible beef, yet that same carcass would have a very low yield in a market requiring only a quarter of an inch of fat.

The changes which will inevitably take place in the desires of various consumer groups will bring change in the definition of edible meat in any one area and this further adds to the undesirability of this criterion of measurement.

The question is whether or not an industry can progress and improve its product if it is aiming at a target which is not only moving, but is also ill-defined. Such is the target set by 'edible product'. No wonder the aim has been so poor.

Harrington (1971) put the problem of 'saleable meat' quite well when he said:

If one type of animal is generally used in one type of trade, and a second in another it might be quite unfair to compare them by a standard cutting test which reduces cuts as far as possible to a constant level of fatness; conversely, it would be unfair to compare two types by cutting tests appropriate to different trades without suitable qualification. This must be borne in mind when considering the use of cutting tests to demonstrate breed differences in yields of saleable meat; certainly these are needed, provided they are truly comparative, but they can only be evaluated fully if supported by complete separation data to reveal what 'saleable meat' is considered to be.

Despite the statement by Preston and Willis (1970) that 'The supermarket does not advertise longissimus dorsi or biceps femoris, nor is it ever likely to', there is a marked trend towards evaluation of meat animals according to their muscle content. We propose muscle mass as the logical target for the beef industry. Muscle constitutes by far the most important part of edible beef. Fat is increasingly regarded as the packaging in which muscle is delivered. Some people require large amounts, some small; few buy it for its own intrinsic value but rather for the characteristics which it imparts to the muscle it surrounds. Muscle is predictive of the edible product no matter what particular consumers' desire or what proportions of fat or bone are acceptable in the consumer's product. It provides a reliable standard for comparison from one geographic region to another and over time. We have seen that distribution of muscle weight over the body is fairly constant within sex and weight. Perhaps breeders and geneticists will find ways to change muscle weight distribution, but no progress has been made towards this end by the use of end points of the past such as conformation, proportion of high-priced cuts, etc. It would seem logical that concentrating on the total muscle mass will coincidentally not result in unwanted changes in muscle weight distribution or in proportion of high-priced cuts within normal cattle.

Use of proportion of high-priced cuts has led to, and still does lead to, erroneous conclusions. For example, the concepts of the Hammond school of late maturity of the loin, and of the loin as a growth centre, arose primarily because fat was heavily laid down in this cut, which included the abdominal wall, at late stages of fattening. More recent authors still confuse total muscle and muscle weight distribution effects. Whereas Harrington (1972) found Charolais × Friesian crossbreds had identical percentage of high-priced cuts to Friesians (see Chapter 1, p. 1), Preston and Willis (1970) in their essentially excellent book on beef production, after expounding the arguments relating to the fixity of muscle weight distribution, fell into the trap of interpreting their own results as indicating that some breeds (e.g., Charolais) have a higher proportion of high-priced cuts than others as a direct result of superior muscle weight distribution (p. 404). This claim has been discussed in Chapter 5 (p. 135). This example illustrates the dangers of extrapolating data obtained from edible meat assessments to its major component-muscle-and again highlights the concept that to use edible meat as a goal in genetic improvement will continue the confusion of the past.

It would be unfortunate if any end point chosen for beef production should lead to a drop in desirability of the product. In advocating total muscle as the logical quantitative end point we do not pretend that it constitutes all of the edible parts of the carcass; in fact, acceptability still is enhanced by associated intramuscular and surface fat. We merely hold that although emphasizing total muscle any market or consumer group can specify how much fat they desire or will accept along with the muscle.

Whole body chemical analysis

Early workers beginning with Lawes and Gilbert in the nineteenth century followed by Haecker (1920), Moulton *et al.* (1922) and others analysed the total empty body of cattle by summing separate analyses

for different parts and tissues. At present, chemical analyses are pretty well restricted to the commercial carcass and possibly some of the other parts and organs (Morris and Moir, 1963).

Whole body analysis has the advantage that a precise inventory of food nutrients could be ascertained in the body. Its disadvantages were, and are, a high cost (particularly for cattle); it is very tedious and time consuming; it is difficult to get representative samples and it does not differentiate between the tissues or between edible and more valuable parts v. non-edible and less valuable parts. It has been shown in Chapter 3 that about a quarter to a third of the major components water, protein and fat—occur in the non-carcass parts. The fraction of each chemical component which is found in the most desirable tissue, the muscle, varies with the age and weight of the animal as well as other factors. Thus a knowledge of whole body chemical composition still leaves one in a quandry in attempting to relate to the edible tissues of the carcass. Chemical analysis of the whole body or of the carcass will continue to be valuable in research for specific purposes, but is not likely to be a useful end point for beef production.

Physical separation of the tissues of the carcass

Various tissue separation techniques are now used to find values for the amount of muscle, bone and fat in a carcass. Early studies were based on commercial cutting methods with the subsequent separation of the 'flesh' (muscle and fat) and bone (Haecker, 1920). More recently Luitingh (1962) dissected cuts from steers of three ages, either fattened or unfattened, and reached conclusions regarding the effect of fattening on carcass proportions which were at some variance with the previously held opinions. This work by Luitingh highlighted the fact that different interpretations of body proportions were able to be reached by the selection of different lines of separation of 'cuts', and by the more detailed separation of the 'flesh' component into muscle and fat.

The introduction by Walker (1961) of a total dissection technique based on the complete carcass as the unit of dissection established a much more logical approach to the determination of carcass composition. Arbitrary divisions which have no basis in biology are not made and the muscle, bone and fat systems can be studied as near-complete functional systems.

The work prior to the introduction of Walker's dissection technique was influenced by a commendable desire to align results with commercial utilization of carcasses.

It is now clear that, although refined techniques using cuts such as outlined by Carroll (1972) or Cuthbertson *et al.* (1972) are extremely valuable in assessing the results of applied research, the initial use of cuts should have succeeded, not preceded, the detailed anatomical dissection in the evolution of physical separation methods.

The total dissection technique has yielded a great deal of information on the musculature from the weights of individual muscles and bones of serially slaughtered animals, and the factors affecting variations in muscle-weight distribution are now well understood. A certain amount of information on fat distribution has also been obtained although, as this system extends proportionately more than the musculature into the non-carcass regions of the body, its complete understanding must await more extensive studies involving the many specific areas of fat deposition throughout the whole body. Such a study has already been undertaken in sheep (Warren, 1974) and should not be long delayed in cattle. In the meantime valuable information on carcass fat distribution and partitioning is coming forth from anatomical dissection studies (Johnson *et al.*, 1972, 1973a; Berg and Fukuhara, unpublished) and from the modified technique of the Meat and Livestock Commission (Cuthbertson *et al.*, 1972).

The disadvantages of the total dissection technique are that it is time consuming, needs skilled labour and is costly. Also the variation in the chemical composition of each tissue means that the results cannot be extrapolated to indicate changes of chemical composition. However, physical dissection followed by chemical analysis of the various dissected tissues produces a maximum of valuable information, with a high level of both commercial and scientific applicability.

This cannot be a routine process for commercial or other moderate and large scale projects but should be an end point against which other less precise and indirect methods of predicting carcass composition are tested.

Combined end points

Physical dissection, muscle by muscle, has resulted in establishing certain criteria whereby logical end points for carcass analyses can be established. First, there is little point in attempting to estimate the proportions of muscle in certain regions of the body. Muscle distribution follows rather fixed patterns according to the sex and stage of development of the animal. Breeds influence muscle weight distribution only in that their rate of maturation differs and one breed may reach a more 'mature' distribution than another at a given slaughter weight (see Chapter 5). Therefore a method is needed which can measure or predict the total muscle mass with little need (on a routine basis) to be concerned about muscle weight distribution.

Fat tissue provides a somewhat different problem. Fat is the most variable and also the most malleable tissue of the body. Selection has changed the proportions of fat in the different depots (e.g., subcutaneous, intermuscular and kidney). However, the distribution within the depots seems to follow the path of least resistance and is related to the total amount of fat present. In many markets kidney fat is being removed at slaughter; in most meat outlets it is considered waste and therefore it is best removed at the slaughter house where it can be channelled towards the production of top quality tallow. There seems little need to predict amount of kidney fat as it could easily be measured, and also there is little reason to separate it from other internal fats. It may be that techniques will have to be developed which will predict subcutaneous fat and intermuscular fat independently. In the meantime total dissectible fat will probably be the recognized end point for appraising fatness of a carcass.

A rather streamlined technique which combines physical and chemical analyses is evolving in certain laboratories (Lohman *et al.*, 1966; Frahm *et al.*, 1971). This involves a separation of the soft tissues from the bones and a rough (or detailed) separation of the muscle and fat tissues. The fat content of the muscle mass is then determined chemically leaving the fat-free muscle mass. If chemical fat is also determined in the fat tissue most of the useful and relevant information will be obtained.

Thus per cent total dissectible muscle should be the end point against which other predictive techniques are compared. Alternatively per cent total fat, which goes up as muscle goes down, can be estimated. Research workers should be encouraged to analyse chemically the physically separated tissues for maximizing return in information from their projects.

Misguided predictions

We are moved to say something about the mass of predictions which currently fill, and in the recent past have filled, animal science journals. A live judging score correlated with a visual score on the carcass is meaningless without a more precise and realistic end point. Likewise correlating various live measurements and proportions to similar

measurements and proportions on the carcass are quite meaningless. Falling in this class are live probes and carcass backfat measures, ultrasonic loin-eye measurement on the live animal with loin-eye area on the carcass, estimation of wholesale cuts by measurements on the live animal and a host of others. If a live backfat measure is to be of any use it must predict carcass composition not another backfat measure. How useful is a 0.6 correlation of ultrasonic loin-eye measurement to carcass loin-eye area when the latter has only 0.2 correlation with per cent carcass muscle?

Furthermore, many researchers have relied heavily on the correlation coefficient as a measure of accuracy or usefulness of certain measurement techniques. To quote Norton (1968) in this context, 'the correlation coefficient is a comparatively meaningless and useless statistic'. The size of a correlation coefficient is most influenced by the range in the data of the trait being predicted. For example, prediction equations for 'retail yield' may be calculated from data including ranges of animals from calves to old cows and from near zero per cent separable fat to upwards of 40 per cent. Many extremely high correlation coefficients result from analyses of such data, but how useful are they? What is needed in most cases is an estimate of how well the prediction will work within a narrower range or within a specific class of animals, for example steers or heifers at acceptable slaughter weight.

If the correlation coefficient is 'comparatively meaningless and useless', what are the alternatives? The value of any prediction can best be ascertained by examining the residual variation obtained by the difference between predicted and actual values of the characteristics being predicted. The statistic that measures the residual variation is the standard error of estimate, sometimes called the residual standard deviation. If the standard error (which is really the standard deviation remaining after prediction) is listed as a percentage of the mean of the predicted variable, we have the residual coefficient of variation which gives a common ground for comparing the accuracy of prediction equations for different traits or end points.

Unless the standard error and/or the residual coefficient of variation are given along with prediction equations, the best use for such equations along with the correlation coefficients and the data from which they were calculated might be to feed them back to the cattle from which they came. In this way pollution of the animal breeding literature by tables of useless correlation coefficients might be reduced.

CARCASS PREDICTIONS

Techniques for predicting carcass composition will be most useful if they are not costly, if they are simple to carry out and if they are nondestructive of the carcass. Needless to say, reasonable accuracy is hoped for in predicting the total or percentage of any tissue in the carcass. Information on carcass composition may be desired as end points for nutritional or physiological experiments, as estimates of the breeding merit of sires or as the basis for classifying carcasses during marketing.

Many methods of evaluating carcass composition are possible varying in the amount of time and effort required and in their complexity. The simplest methods involve measurements which can be made directly on the carcass while the most complex may involve physical dissection or tissue separation and chemical analyses to varying degrees.

In balancing expense against accuracy, a system for general application in carcass classification needs to be inexpensive, but at the same time it must be soundly based in scientifically established knowledge of the factors influencing carcass composition. The maximum acceptable level of cost of classification of carcasses must be determined in light of the returns it could bring to all sections of the cattle and beef industry—not just to the butchering industry.

Carcass measurements

Measurements which can be taken on a carcass and which have been tested for their usefulness in predicting carcass composition include weight of carcass, backfat thickness, area of the longissimus dorsi muscle (rib-eye area) weight of kidney fat, carcass length, carcass width and carcass depth (e.g., Epley *et al.*, 1970; Busch *et al.*, 1969).

It has been shown (Chapter 2) that as animals grow their carcass composition changes. In animals fed for slaughter, the proportion of fat increases at the expense primarily of muscle tissue. Under such circumstances it is not surprising that weight has a high relationship to composition. This apparent dependence of composition on weight had led some researchers to state that body composition is almost entirely controlled by weight (Reid *et al.*, 1968). However, there are important exceptions to this weight dependency on composition at given weights as we have pointed out. Sexes differ in composition at given weights as do breeds and animals fed on widely differing planes of nutrition. Thus, weight as a predictor of carcass composition could

be useful within sex, breed group, ration, etc., but might have only limited usefulness generally. It would be most desirable to have predictors which could be used for various breeds and crosses and for those of varying nutritional histories if not across sexes.

Backfat thickness measured over the longissimus dorsi muscle has proven to be a useful predictor of total or percentage fat and indirectly of muscle in a carcass. For practical purposes, perhaps, breed and sex differences in the relationship of backfat to total carcass fat can be ignored, but more research is needed in this area. We have shown that the ratio of subcutaneous to intermuscular fat differs among breeds (Chapter 6) and this indicates that a certain depth of backfat would indicate different amounts of total fat for different breeds.

Area of the rib-eye muscle measured at the various sites at which carcasses are quartered has been used as an estimate of carcass muscling. It unfortunately accounts for only a small amount of variation in total or per cent muscle. However, as it does account for some of the variation in carcass muscling, and because it is relatively easy to obtain and because better simple and direct measures of muscling have not been devised, it continues to be advocated with other simple measures for estimating carcass composition. There are those who advocate the measurement of the rib-eye on its own merit as being part of an important high-priced cut (Neimann-Sørensen, 1972). The validity of this approach can certainly be questioned because of the relative constancy of muscle weight proportions which we have been shown to exist among various breeds and types of cattle (Chapter 4).

Kidney fat weight or per cent has occasionally been shown to be related to carcass fatness and therefore to per cent fat. This is true in those instances where kidney fat is left on the dressed carcass and thus becomes a part of excess fat trim. It is interesting that the regression of kidney fat in the USDA yield formula of Murphy *et al.* (1960) is only slightly greater than 1.0 thus accounting basically only for its own removal. With a general and logical trend to removal of kidney fat during slaughter, it is unlikely that the contribution of kidney fat to the prediction of carcass composition will warrant its continued recording.

Various linear measurements on the carcass including length, width and depth have been advocated as useful predictors of carcass composition (Yeates, 1952, 1959; Kneebone *et al.*, 1950). Length seems to have no predictive value, while width measurements designed to estimate plumpness and muscling usually are influenced more by fat than by muscle (Butterfield, 1965b). Depth measurements seem to have no predictive value. Ratios of length, depth and width measurements, although they may describe shape, have little predictive value for composition (Busch et al., 1969; Fredeen et al., 1971).

Subjective estimates of carcass composition are the basis for much of the grading of carcasses and of trading in carcasses in many countries. Subjective estimates are difficult to quantify and they have not stood up to objective assessment (Busch et al., 1969). Conformation has in the past been the main basis for subjective assessment of carcasses. It has been shown to be more influenced by fat than by muscle (Luitingh, 1962). Recent attempts to estimate fatness subjectively, followed by subjective estimates of muscling within fat classes, may prove more predictive (Harrington, pers. comm.). A knowledge of effects of fat and muscle on the anatomy of shape gained from total anatomical dissection studies will no doubt make such a procedure more promising. Subjective evaluations, if they are to be applied routinely, are further limited by human error. Some individuals can perhaps develop excellent aptitude for judgement but differences between individuals (graders) will be a continuing problem. And although we have demonstrated that there is considerable difficulty in describing the complex structure of the cattle carcass by a few simple measurements it is surely within the ingenuity of man to produce systems of measurement which will quantify the proportions of muscle, bone and fat within the carcass.

Part to whole predictions

Hopper (1944) suggested the rib cut as a predictor of the whole. This was subsequently developed into a prediction formula for carcass composition by Hankins and Howe (1946). This technique, based on physical separation of the 9-10-11th rib cut into muscle, fat and bone, has had widespread use for prediction purposes in cattle experiments. The rib cut was chosen for its easy accessibility but it has certain possible shortcomings from other considerations. The relation of muscle to fat in the rib cut could be expected to relate approximately to muscle and fat in the carcass, although there is considerable room for error, particularly between operators and between levels of fatness in the cutting procedures. However, the amount of bone in a rib cut is subject to several errors such as the division of the backbone, difficulty in following precisely the same anatomical boundaries in separating the cut from the carcass, and the effect of removing the lower part of the rib without benefit of good anatomical criteria.

Larger cuts have been used as predictors of saleable meat such as the trimmed round and the pistol cut of certain European countries (Neimann-Sørensen, 1972). The round and the pistol cut contain a large part of the high-priced muscle and are relatively easy to trim of excess fat, making them reasonably reliable as predictors of saleable portion. A considerable amount of research has been done where total retail style cutting (variously defined) has been the end point for carcass evaluation (Busch *et al.*, 1969; Epley *et al.*, 1970; Fredeen *et al.*, 1971). We find many modifications of these procedures from bone-in retail cuts trimmed to certain fat tolerance to defatted, boneless muscle. The problems of interpreting and using the results of these techniques has been discussed earlier (p. 204).

Allen *et al.* (1969) studied the relationship of physically separable muscle, fat and bone of one side of the carcass of eighty steers with retail cuts on the other side. They found 71 per cent or less of the variation in total muscle and fat weight was accounted for by per cent retail cuts and fat trim. They concluded that retail cuts do not predict separable components as well as separable components of some selected parts. This research bears out the contention that retail cutability may be subject to too many errors to make it a reliable end point for carcass composition evaluation.

Butterfield (1962, 1965b) suggested the shin as a possible predictor of carcass composition. He developed equations using the weights of the radius and ulna and the weight of associated muscles. The shin is a cheap region of the carcass, its removal does not lower the value of the remainder of the carcass and its dissection can be precisely defined anatomically. However, the precision of prediction from use of the shin is not as high as desired for some purposes as the muscles of the shin probably make up too small a proportion of the whole. With much anatomical data available and a climate of thought which accepts greater sacrifice of the carcass as a good investment, it is expected that more accurate prediction equations will be forthcoming using larger muscles with the more reliable measurements.

Specific gravity

The use of specific gravity or density in the prediction of carcass composition was discussed by Pearson *et al.* (1968) and results from its use were presented by Garrett (1968). The method is based on the Archimedean principle that a body immersed in water displaces a volume equal to its own. Thus by weighing in air and weighing in

water carcass density can be determined. For practical purposes the carcass can be considered a two-component system, fat and fat-free. Although this assumption is not precisely true (see Chapter 3) it is near enough to produce reasonable estimates of fat and fat-free components in carcasses from animals over the range of normal slaughter weights. Fat has a density of about 0.90 and muscle about 1.10. A 0.002 change in density is about equal to a 1 per cent change in carcass fatness.

Specific gravity is simple and easily determined. There is no loss of value to the carcass and the measurements can be made for small groups of cattle routinely in a slaughter plant with simple equipment and little interruption of routine.

According to Garrett (1968), the standard errors of estimate are too high to be very precise in predicting the composition of individual carcasses but in experiments where replication is possible, the use of specific gravity can demonstrate differences between groups in body composition. This approach would also apply to carcass composition estimates of sire progeny groups where a number of carcasses could be measured. One possible advantage of specific gravity is that results do not seem to be influenced by weight of the carcass (Garrett, 1968). If it proves to be independent of sex and breed type as well it could have quite general application to any kind of carcass. Further research is necessary to check these possibilities.

Combined carcass predictions

Multiple regression techniques allow the possible use of several predictors in one equation. This is the basis for the USDA Yield-grade formula (Murphy *et al.*, 1960), where the edible portion of the primal cuts is estimated from a linear combination of backfat thickness, rib-eye area, carcass weight and kidney fat percentage. It would be most desirable if prediction equations could be used for all breed types and perhaps for all sexes (bulls, steers and heifers) over a wide age and weight range. Carcass weight does not satisfy this requirement because the regressions relating fat trim to carcass weight will differ for different breeds and sexes. For example, the late maturing breeds will have lower levels of fat at equal carcass weights than early maturing breeds. Similarly heifers are generally fatter than steers and bulls at the same carcass weights. Therefore prediction equations would have to be designed for specific breed groups and separately for each sex, which would make their general application less practical. Linear

measurements highly correlated to weight might be subject to the same shortcomings as weight with respect to general application and therefore their inclusion should be viewed with caution.

Specific gravity shows the most promise as far as being independent of breed or sex in predicting carcass fat. Perhaps specific gravity of a cut may prove to be sufficiently predictive of the whole carcass to warrant its use. Depth of backfat measured over the rib-eye may be reasonably predictive of total fat, but evidence presented in Chapter 6 with regard to breed differences in intermuscular and subcutaneous fat ratios could lead one to suspect it would not be independent of breed effects.

Area of rib-eye muscle, in that it is an indicator of total muscle, may be independent of breed to a greater extent than weight or length of carcass. However, general skeletal structure (long or short) may influence rib-eye area even though the weight of the longissimus dorsi may remain proportionate to total muscle. In a prediction equation, it would seem wise to use rib-eye area before carcass weight. Rib-eye area is correlated to carcass weight and some of this association will be reflected in total muscle prediction. It might thus be possible to leave carcass weight out of the equation and make the prediction more generally applicable.

Weights of individual selected muscles should be reasonably predictive of total muscle weight independent of breed because of the relative constancy of muscle proportions. From theoretical considerations these should be better than rib-eye area for predicting muscle. Sexes differ in muscle weight distribution at normal slaughter weight (Chapter 5) and therefore the relationship of a particular muscle to total muscle may not be the same for each sex. However certain muscles which grow at the same rate as total muscle in each of the three sexes might be generally applicable.

The degree of precision sought in any study will be influenced by the use which will be made of predictions tempered by the cost involved. In research these costs should be considered in light of the considerable expense already incurred by the time experimental animals are slaughtered. It could well be that the extra expense of getting precise estimates of carcass composition may be a relatively small fraction of the total experimental costs (Carroll, 1972). Precision, as pointed out by Garrett (1968), can be achieved by replication as well as by more accurate techniques and the relative cost of these alternatives should be considered. The cost of modification of commercial cutting of carcasses should be investigated in any situation where greater accuracy of muscle weight prediction is sought with the view to using the weight of a large muscle such as the biceps femoris or longissimus dorsi. There should be little loss for example in the removal of the biceps femoris if this could be done at a stage of processing where the unit of trade is being reduced to cuts. Some idea of the relative value for prediction of the larger carcass muscles is given by Butterfield and May (1966).

Carcass appraisals in progeny testing schemes are subject to the same considerations as those from research programmes. The best combination of evaluation techniques and replication will be sought. Carcass evaluation as a routine process for grading or classification schemes must, however, be economical, rapid and not too disruptive of routine procedures. We must continually keep before us the role that technology could play in making relatively complex procedures quite workable. The most promising predictors of carcass composition available seem to be specific gravity, average backfat thickness, and individual muscle weights. Rib-eye area contributes in a small but positive way to overall precision if weights of selected muscles are not obtainable.

LIVE ANIMAL PREDICTION

General considerations

The search for accurate indicators of carcass composition on the live animal is a continuing process which has so far achieved little success. Such techniques would make it possible to follow changes in composition in experimental animals during growth without the necessity of slaughter. Breeders would find accurate live animal evaluation of great benefit in breeding superior strains of cattle. Market cattle are sold on a live basis in many countries and accurate live assessment could prove very beneficial in pinpointing the most desirable animals for particular situations.

Live animal evaluation is caught between two blunt horns of a dilemma shackled by the tradition dominated show-ring, and mesmerized by gadgetry, the computer and pseudo-scientific discourse. We have discussed the difficulties of predicting composition from methods useable on the commercial carcass. Live animal assessment is one step further removed and must take into account the loss which occurs from live animal to carcass. Hide, head, feet and viscera all become redundant. A disproportionate increase in any of the noncarcass parts reduces dressing percentage.

Effective live appraisal techniques must account for differences in dressing per cent and differences in composition of the resulting carcass. Whereas dressing percentage is involved only with the weight of the carcass, composition influences its ultimate value. The objective in live animal appraisal should thus be to estimate both weight and composition of the carcass or carried one step further the weight of muscle in the carcass. The percentage of live weight which is muscle tissue is the important consideration.

Subjective visual appraisal

Visual appraisal has had two aims, one relates to how well the animal will function, breed, graze and survive, the other relates to the kind of carcass which will be produced. Our purpose in this section will be concerned only with the latter—quantity, distribution and quality of meat produced.

The concept of what the shape of an ideal beef animal should be has gone through major evolution in the past few years. Harrington (1971) contrasted descriptions in the 1958 and 1970 editions of the Meat Judging Handbook of the National Livestock and Meat Board, Chicago. The 1958 edition stressed uniformity—'extreme thickness from the hind shank to the chuck, for this is the area providing the more desirable steaks and roasts'. The 1970 edition states.

the idea that has prevailed for many years that smooth, blocky, short, deep and compact beef animals produce the most desirable beef carcasses has proven to be an erroneous concept. A heavily-muscled, properly finished beef carcass will be somewhat irregular in contour because of the variation in architecture of individual muscles in different parts of the carcass. For example, the round and chuck in the desirable carcass will be comparable in width whereas the loin and rib will be more narrow as a result of natural shape and form of muscles in these locations. This, along with a slight depression, is especially noticeable at the junction of the sirloin and short loin.

The general acceptance of the need for a change in the concept of what an ideal shape should be has been very rapid. There seems a danger, however, of losing sight of the purpose for the change. The net result and goal should be to produce a carcass with a high proportion of muscle, an acceptable optimum of fat and a minimum of bone. We have seen that muscle weight distribution is quite fixed and that fat is the tissue that is moved around when we start to change the shape of the animal. Advocates of live judging, recognizing that short and deep have proven wrong have now jumped on terms such as long and stretchy, particularly in the loin and rump regions of the high-priced cuts. There is no evidence in favour of length as an indicator of merit and there is no evidence that a disproportionate length in the high-priced regions will be beneficial. Rather than length and stretch it would seem more sensible to concentrate on the end point—muscle—and perhaps, if ways can be found accurately to estimate it, muscle as a proportion of live weight.

If shape is important in a carcass it will probably be in relation to muscle thickness. Traditional thickness was found to be mostly influenced by fatness (Harrington, 1971) and therefore many now shy away from thickness. Thickness related to muscling, however, should be advantageous.

Lewis *et al.* (1969) used trained and untrained judges to estimate dressing per cent, fat thickness, loin-eye area, quality grade and cutability grade (USDA). They concluded that—trained appraisors accounted for more than half of the variation in carcass traits and three-quarters of the variation in fat thickness. Fat thickness estimate seemed to be related to other traits. Loin-eye area was not easily measured nor was quality grade (i.e., marbling). On the other hand Dinkel and Busch (1973) concluded 'Visual appraisals such as conformation score and muscling score did not appear useful as predictors of animals genetically superior in the production or carcass traits studied'. Also Busch *et al.* (1969) found visual estimates added little to prediction formulae for predicting amount of edible product.

Barton (1967) in summing up a review of 'Live Animal Conformation and the Carcass of Cattle' concluded:

The conformation and size of cattle have been changed by selection. The modern beef animal is generally smaller and more compact than formerly, but this trend has not increased the proportion of lean in the carcass or changed its distribution. Thus emphasis on conformation in the showyard has been largely misdirected ... Further evidence that the beef-type conformation does not produce carcasses of high cutability or beef of superior eating quality comes from the numerous studies comparing dairy-bred with beef-bred animals, or unimproved with improved cattle.

It seems obvious that if visual appraisal of carcass composition is to be of any use, new guidelines have to be developed. Some proficiency can be developed in assessing fatness which is of primary importance in determining carcass composition. Estimating muscling independent of the influence of fat would be a second important criterion. An experienced judge could probably broadly classify

live animals on the basis of carcass composition; small differences will be very difficult to detect.

Live animal measurements

Numerous measurements including length, width, height, circumference, etc. have been made on live animals and correlated with measures of carcass merit. Taylor and Craig (1967) outline some of the problems of obtaining reliable live animal measurements and present data showing what contributes to variance in such measurements. Live weight has shown some relationship with muscle or retail cuts yield. Busch *et al.* (1969) used eighteen body measurements in an attempt to find some that were predictive of edible product. Body measurements added only 2 to 4 per cent to slaughter weight alone in accounting for differences in edible product. Batra *et al.* (1973) found five live measurements accounted for between 14 and 22 per cent of variation in lean, fat and bone of the carcass. Skelley *et al.* (1972) correlated bone weights, measurements and specific gravity to carcass measures and found a low but significant association between bone weights and trimmed cuts percentage.

It seems reasonably obvious that routine live animal measurements are of very little value in predicting carcass composition. Therefore caution should be exercised in attempting to change the shape or dimensions of animals in the hope of improving carcass composition.

Ultrasonic probes

The principles of the use of ultrasonics for estimating composition in animals were outlined by Stouffer (1963). 'Ultrasonics' refers to sound waves above the frequency audible to the human ear. Equipment has been designed which focuses a nearly parallel beam of sound waves which can be directed into the tissues. Speed of transmission is sensitive to density of material and changes in density result in reflection of waves back to the instrument. Thus obstructions, interphases between tissues, etc. can be recorded and mapped. Newer modifications incorporate a Polaroid camera with which a picture of the profile can be quickly obtained. Ultrasonics have long been used to measure flaws in metals and other solid materials. They have been used in medicine to outline cysts or tumors not detectable by X-ray techniques and in determining foetal outlines.

The first report of the use of ultrasonics to measure backfat in cattle was by Temple et al. (1956) and in swine by Dumont (1957).

Research in the use of ultrasonics has concentrated mainly on the measurement of backfat as a measure of fatness and on the depth or cross-sectional area of the longissimus dorsi muscle as measures of muscling. Most of the relationships reported correlate ultrasonic fat measurements or longissimus dorsi area with those subsequently made on the carcass (e.g., Watkins *et al.*, 1967; McReynolds and Arthaud, 1970). The ultimate usefulness of the technique must be assessed by how well it predicts carcass composition, not other measurements. Neimann-Sørensen (1972) related ultrasonic measurements on the live animal to per cent separable meat and fat of the carcass. By using meat:fat ratio (determined from areas outlined by ultrasonics) he was able to obtain a reasonable correlation with per cent meat, per cent fat, meat:bone ratio and per cent meat in the pistol cut.

There is every indication that accuracy and usefulness of ultrasonic techniques for assessing carcass composition are improving. Many problems in the application of the technique have been recognized and at least partially overcome. Experience is very important in interpretations involving boundaries of hide, fascia tissue, fat and muscle. The skill of the operator is important in achieving proper machine adjustment, etc. Equipment design will no doubt reduce errors previously associated with machine operation. The possibility of three dimensional scanning where quantitative measures of volume of specific muscles or fat depots can be measured is a challenge to design engineers.

The choice of what to measure on the live animal has not been resolved. Most measurements have been made at the point where the carcass is separated in normal commercial practice so that comparison could be made between live and carcass measurements at the same point. If carcass fat and muscle are used as more logical end points then what? Experiments can be designed to compare alternative sites for ultrasonic scanning. For instance, it may be less difficult to measure longissimus dorsi area in the lumbar region where possible interference from the spinalis dorsi which overlies the longissimus dorsi to a variable degree at the 12–13th rib is overcome. Three dimensional scanning of the middle gluteal or semitendinosus muscles may be feasible. Various sites for measurement of fat thickness should be tried.

There are very good reasons why considerable research effort should be expended in attempting to develop more precision and accuracy in ultrasonic predictions of carcass composition. The

technique is non-destructive and non-harmful to the animal or the product. It can be used on the live animal at any age or stage of development. It appears that the costs of obtaining useful measurements will not be excessive with respect to both time and equipment rental. Portability of the equipment is a further significant advantage. Information available to date indicates that ultrasonic measurements, properly taken and interpreted, could be useful in assessing comparative composition of live animals. Indications are that the usefulness of the technique will improve with further research and development.

Potassium 40 counting

Whole-body counting of the naturally occurring radioactive isotope of potassium (⁴⁰K) is being studied as a possible method for predicting the amount of muscle mass in the live animal (e.g., Frahm et al., 1971). 40 K has a long half life (3 × 10° years) and it occurs at a relatively constant proportion of total potassium. Potassium is found in the body, predominately within the cells. Muscle tissue contains a high proportion of the total potassium of the body. Lohman and Norton (1968) found the potassium distribution in the body of cattle to be as follows: 53.4 per cent in the standard trimmed lean, 12.4 per cent in the skeleton and 16.4 per cent in the gastro-intestinal tract and contents. There should be no K in neutral fat but some will be present in fat depots because of blood and connective tissue (Pfau, 1965). It has thus been reasoned that the amount of potassium in the animal's body might relate directly to the amount of muscle tissue and that it should be possible to measure the amount of K by measuring the ⁴⁰K isotope. Rather small quantities of K and thus of ⁴⁰K are found in the body which makes measurement a little more difficult.

To measure ⁴⁰K whole body counting chambers have been constructed. Such chambers are usually shielded with 4 to 8 inches of steel to cut down extraneous background radiation. Gamma rays produced by disintegrating ⁴⁰K are detected by scintillating counters of basically two types—liquid and solid. Considerable information on the counters and their use can be found in the Publication 1598 of the National Academy of Sciences, Washington 1968, on Body Composition in Animals and Man.

Technical problems involved in ⁴⁰K counts are associated with equipment calibration, elimination of background interference, accuracy of measurement, and repeatability. Size and shape of animals being measured affect the readings. Considerable progress seems to

have been made in resolving these technical issues. Other problems are more of a biological nature, such as: even if total K in the body can be measured, what does it mean? The concentration of K in the organs and tissues differs as does the ratio of nitrogen or protein to K in various organs. Widdowson (1968) lists ratios of mili equivalents of K per g of intracellular protein in man to be 5.0 for brain tissue, 1.4 for skeleton, 3.4 for muscle and 2.7 for liver. The organs and tissues differ in their contribution to the total body as the animal grows and so does their contribution to the total body potassium. In man, Widdowson (1968) listed muscle as accounting for 33 per cent of the K at birth and 62 per cent in the adult. As we have seen the body is not homogeneous, nor are tissues, nor are the cells that make up tissues. There is some evidence that the K concentration decreases in cattle as live weight increases (Lohman and Norton, 1968). The measurement of ⁴⁰K can also be influenced by the amount of K in the diet (Johnson et al., 1973b; Judge et al., 1969).

In spite of the problems enumerated above, the critical assessment of the usefulness of whole body counting will depend on how well it can predict total muscle mass. Experiments to date indicate reasonably good accuracy. Frahm *et al.* (1971) predicted total fat-free muscle with a standard error of 3.8 kg in young bulls averaging 145 ± 7.4 kg of fat-free muscle. This represented an error of 2.8 per cent.

The equipment is costly to build and to operate and it lacks portability. However, it is a nondestructive technique and if enough accuracy can be achieved it would undoubtedly find a useful place provided, of course, that no better or cheaper methods are available.

Dilution techniques

Dilution techniques for estimating body composition are based, as are other methods, on the assumption of reasonable constancy of the fat-free body. One of the major components, usually water, is estimated by introducing an easily analysable chemical in a known quantity which equilibrates with the body water. A sample of body fluid (usually blood) is drawn and analysed for the chemical from which the total fluid volume can be estimated as:

Volume (ml) = $\frac{g \text{ added}}{g \text{ (ml in solution)}}$

Radioactive substances have been adapted to dilution techniques in which case volume is measured as follows (Hansard, 1963)

Volume (ml) = $\frac{\text{counts/minute added}}{\text{counts/minute/ml}}$

The chemical used should be distributed rapidly and uniformally throughout the body, it should be non-toxic, it should remain stable long enough to permit sampling and its excretion from the body should be slow. Rapid and convenient methods should be available for its analysis (Hansard, 1963; Pearson *et al.*, 1968). Radioisotopes present a further problem of ultimate disposal.

Antipyrene and several of its derivatives including radioactive (I-131) antipyrene have been extensively used to estimate body water. These substances satisfy the conditions listed above quite well. There are indications that there is some difference in the behaviour of the various antipyrenes in how they equilibrate with the body metabolic pools, for example, with rumen and tissue fluids (Hansard, 1963; Bensadoun *et al.*, 1968).

Estimation of body composition by dilution of hydrogen isotopes has been reviewed by Panaretto (1968). Deuterium oxide (heavy water) satisfies the requirements quite well: it is not radioactive, it distributes quite rapidly and uniformly without being metabolized or causing toxicity in the amounts used (Flynn *et al.*, 1968). Tritiated water (TOH) using radioactive tritium is favoured by many researchers because of the ease of analysis of the radioactive form. TOH space has been reported by several groups to give reliable estimates of total body water and from this reliable estimates of other body components (Little, 1972; Searle, 1970; Searle & Graham, 1972).

One of the problems of using estimated total body water for estimating body composition relates to the constancy of water in the body. Water in the fat-free tissue decreases with maturity, but for practical purposes this may not be important after four to six months of age.

Undernutrition or fasting can affect the water content in the fat-free empty body. Farrell and Reardon (1972) found that undernourished sheep had a significantly higher water content in the fat-free empty body than well-nourished sheep. A large variable is introduced by water in the gut which is subject to great fluctuations. Some of the chemicals used equilibrate with the gut water, others apparently do not. Attempts have been made to use more than one chemical or drug in order to increase the accuracy of estimation (Bensadoun et al., 1968).

Changes in amount of ingesta can affect the measure of empty body weight according to Reid *et al.* (1963) by 5 to 30 per cent of the body weight. They suggest that shrunk body weight (with water but without feed) can be used to accurately estimate empty body weight. Reid et al. (1963) gave the following procedure for estimating body composition.

- estimate empty body weight from 'shrunk' body weight; 1.
- estimate water (or fat) and predict the one from the other; 2.
- 3.
- estimate fat-free dry matter as 100 (% fat + % water); compute protein and ash in fat-free dry matter from the ratio 4. of 80.3:19.7.

Reid et al. (1963, 1968) and Bensadoun et al. (1968) found empty body weight to be a better predictor of empty body water in sheep than estimates by any combination of two forms of antipyrene and creatinine. However, a combination of empty body weight and the dilution methods proved to be the most reliable predictor of body composition.

Use of dilution techniques to estimate body composition appears quite promising. Their use in research will undoubtedly increase. Little attempt has been made to adapt any of these techniques for industry use such as for selecting breeding animals or live market appraisal. Use of any of the radioactive diluents for industry use may not be acceptable. However, dilution techniques in conjunction with other live evaluation techniques should be fully explored with the goal of obtaining reliable and useful estimates of body composition of live animals.

CONCLUSIONS

Measuring and predicting carcass composition, either from techniques used on the carcass or the live animal will continue to receive much attention from researchers and various groups in the beef industry. Reliable methods will aid producers in making breeding and selection decisions and will provide a basis for establishing values for carcasses as they move through various segments of the beef trade. Traditional visual appraisal or judging of both live animal and carcass are gradually giving way to technology and objective methods of assessment. In this day of scientific achievement it should be possible to determine the composition of live animal body or of carcass to any desired level of precision. To perfect such techniques it will be necessary to allocate sufficient resources into research with the goal of developing accurate and economically feasible methods of characterizing carcass composition. A firm knowledge of factors which affect growth and development of the major tissues—muscle, fat and bone—as we have attempted to describe in this book, should assist in interpretation of the results of any composition predictions. Knowing normal patterns expected in growth and distribution, particularly of muscle and fat, and knowing how these patterns can be altered by feeding, breeding or management, should extend the range of applicability of any successful prediction technique.

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