New Concepts of Sheep Growth

Rex M. Butterfield

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THE ROAD TO HAHNDORF (Watercolour) 1921 Hans Heysen

Sheep have formed a part of many paintings by Sir Hans Heysen. They have drawn little if any recorded comment. I have enjoyed Heysen's sheep for many years and marvelled at his ability to capture the characteristic inelegant postures of the grazing Australian Merino. "Road to Hahndorf" is an outstanding example and I am deeply indebted to Mr T. Barr-Smith for permission to photograph the watercolour, Mr David Heysen for permission to use it, and Mr Colin Thiele for his advice.

I also thank Mr John Storey for his expert photography.

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Forward by N.M. Tulloh

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THE AUSTRALIAN MEAT RESEARCH COMMITTEE

The Australian Meat Research Committee (A.M.R.C.) made the writing of this monograph possible by continuous financial support since 1963, dating from the establishment of the original Australian Cattle and Beef Research Committee and continued by its successor, A.M.R.C.

I wish to express gratitude to the Committee and through it to the Industries and Governments which supported it, for funding of projects which, being based in the most ancient of all science disciplines, must have seemed far removed from the immediate problems of the animal and meat industries.

My particular thanks go to the succession of Chairmen: Mr. J.L. Shute, Mr R.M. Watts, Colonel Sir Malcolm McArthur, Mr R.G. Jones and Mr. P.D.A. Wright; and to the successive Executive Officers: Mr A.J. Vasey, Dr M.C. Franklin, Dr R.B. Dun and Dr M.A.S. Jones, who all demonstrated that they clearly understood that applied research must be nourished by so-called basic studies with no apparent relationship with temporal problems. I also thank Mr. Neil Allison who, as secretary to the Committee, smoothed many paths.

Rex Butterfield

FOREWORD

Professor Butterfield is to be congratulated on the production of this book. It is one which covers his own work and that of his graduate students during the past 25 years, and this work has been placed in the context of the world literature. He uses mature size as the basis for studying the growth and body composition of sheep. Using this approach, it is possible, at any stage in the life of an animal, to express the growth of any one part as a proportion of its own mature size and to compare this proportion with that achieved by any other part or parts of the animal, or of any other animal at the same or other stages of development.

The book is concerned with postnatal growth and most of the data presented have been obtained in investigations involving the seriatum killing of sheep as they grew, either from birth or from weaning, to mature liveweight. Both carcase and non-carcase parts have been dissected with meticulous care to provide relative growth studies concerned, particularly, with individual and groups of muscles, bones and fat partitions.

The method of handling the results mathematically involves the use of constrained quadratic equations to describe maturing patterns of growth. A description of how this has been done is clearly explained in one of the appendices. Each equation contains a constant 'q' called a maturity coefficient which, although quite different from Huxley's relative growth ratio (growth coefficient), can be used in a similar way to interpret differences in relative growth rates.

The book begins with a study of Merino rams. This forms the bench mark for studying the effects on growth of castration and of differences between sexes and between genotypes. The text and the appendices provide an immense amount of information and, for this reason alone, the book will remain a reference for many years to come.

The book will be sought after by academics in universities and colleges of advanced education, and by other scientists interested in the growth and body composition of farm animals. All students seriously interested in the subject should read it. Multiple copies are likely to be required in teaching libraries and single copies in research libraries. Many academics, research scientists and graduate students will buy personal copies; some institutions will use it as a prescribed textbook. It will be widely used throughout the world but, particularly, in English-speaking countries.

N.M. TULLOH

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PREFACE

"... if we liken the organism to a piece of music, the growth of all parts at the same rate would be unison, and their growth at different rates harmony ..." Needham and Lerner (1940).

"New Concepts of Cattle Growth" by Berg and Butterfield was published in 1976 and reprinted in 1978. The title of that monograph precluded further reprinting without substantial revision and so "Cattle Growth" was allowed to go out of print. This monograph, while based on a different species, provides an update of concepts many of which are applicable to both our most common domestic ruminants.

Since the cattle book was written more emphasis has been placed on the relationship between the mature size of animals and the growth of those animals and of their integral parts. The approach in this book is therefore very different with heavy emphasis on maturing patterns measured in proportions of mature size. The growth process has not changed, only the approach to its study.

A great deal of the work on which this book is based was carried out by postgraduate students and research assistants and by collaborators from other research establishments. All of these people appear in the bibliography, however, they merit special mention, as without their efforts the information on which much of this book is based would not have been available. Those who worked with me in the Department of Veterinary Anatomy included Carl Lohse, Geoff Warren, Mohamad Hilmi, Javier Zamora, John Thompson, Tony James, Ian Gardner, Yvonne Pinchbeck, Ken Reddacliffe, Mark Pearson, Sandy Brown, Jonathon Graham and Frank Moss. Scientists from other organisations who assisted in many ways were T.S. Ch'ang, Tom Searle, Jean Williams, Diana Perry, and Tony Kempster.

Special mention must be made of three mathematical gentlemen who guided my uncertain steps. Dr David Griffiths now Professor of Statistics at Wollongong University, and formerly of Commonwealth Scientific and Industrial Research Organisation (CSIRO), Division of Mathematical Statistics; Dr St. C.S. Taylor of The Animal Breeding Research Organisation, Edinburgh and Dr John Parks, Department of Animal Husbandry, University of Sydney. David Griffiths devised the constrained quadratic function which has become the basis of our most usual methods of analysis. Clair Taylor, through many patient sessions in the most unlikely venues, has coaxed and goaded to ensure that my mathematical inadequacy did not lead me into too much harm. John Parks, particularly by his influence on one research student; John Thompson; steered the progress of our work towards his young ideas.

Several people have kindly read drafts of chapters and I thank them for their efforts and advice. These people, who cannot be held responsible for any of the errors in the text, which are entirely mine, are Dr St. C.S. Taylor, Dr Alan Kirton, Mr Tom Searle, Dr John Thompson, Dean Roy Berg, Dr Don Charles, Dr Margaret Sabine, Dr Alan Frost and Dr Paul Hopwood.

In the preface of "New Concepts of Cattle Growth" we stated: "In manipulation of the growth process in cattle towards 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." The same statement could well have been made at that time about sheep meats and particularly lamb, although the commercial scene in 1987 suggests that the "manipulation of the growth process" in sheep has been neither fast enough nor drastic enough. The sheep industries have found it difficult to make the transition necessary to produce the meat of the extreme leanness being urged on red meat consumers. In Australia, where production of sheep meat is largely a by-product of the wool industry, changing of meat characteristics is perhaps more difficult than in those countries where meat is the primary aim and wool an almost undesired by-product.

In the sheep industries of many countries, the successful interaction of genotype and environment to ensure survival and fertility must decide the type of sheep which can be used. Hence the "quality" of meat (and wool) is that which results after the production criteria are met. This situation is unlikely to change, and so the future will depend on the continued use of this meat in its traditional form in its traditional markets in which the definitions of "quality" fortunately span a huge spectrum. However, it is within those sections of the meat animal industry, where environmental demands are less rigid and the production of meat is the prime aim, that competition from other species is greatest. Here considerable change will be needed towards the production of carcases with high muscle content if sheep meat is to retain its share of the market.

The ideal carcase in any market will remain as that with the maximum of muscle, the minimum of bone and the optimum of fat for that market. The challenge of the future is to approach the ideal carcase as closely as the economics of animal production will allow. These economic factors will be associated primarily with the process of growth. We can take the example from the cattle industry where it is profitable, under particular circumstances, to push the process of growth to what many would see as ridiculous extremes. I refer to the utilisation of "double-muscled" animals, particularly in Europe, where breeds such as the Piedmont and Belgian Blue are economically viable despite the production problem of a high proportion of Caesarian Sections. These breeds are profitable because their meat demands a price far greater than that of meat produced by normal cattle. There is little chance that an ideal sheep carcase will approach such extremes in currently visible markets.

Most consumers still demand a little fat in prime lamb. However, this level of fat continues to fall and we must look to future lambs being more muscular and less fat. To approach the future with confidence we need to understand the principles of growth. Maybe, this book will help a little.

Some readers may find it a little difficult to grasp the "mature size" approach in this monograph and I must therefore attempt to explain my enthusiasm. For the last couple of decades we have been impressed with the advantages of the fast-growing animal and it certainly has seemed logical that this should be so. However, there were many factors which differentiated the fast-grower from the slow-grower when measured in simple terms of gross weight. Quite simply the major factor in many cases was the final, genetically-determined, mature size of the animal. All else being equal it seems that genetically-large animals within a species grow fastest. Selecting for growth rate was, therefore, selecting for bigger animals and this may or may not have been desirable depending on a range of economic factors. And yet there are, among our populations, animals of similar genetic size which grow at different rates. The problem, therefore, now seems to be to select, not simply the fastest-growing animals, but rather the fastest-growing animals among those of the same mature size, if it is decided that larger breeding animals are not desired. All of this is, of course, far beyond the scope of a simple anatomical growth study. Yet maybe, by description of maturing patterns of tissues we can, from our basic discipline of anatomy, provide some help to animal breeders who are faced with the question of how big is the optimum breeding animal for their enterprise.

It would be nice to say that I have adopted the maturity approach because of these practical considerations, yet this is not so. Largely because of the stimulus of other people, I came to realise that an understanding of the influence of final size was perhaps the most important factor in understanding growth. However, it was not until I had played with data in simple graphs in which the units were not grams or pounds or percentages but were units of mature weight, that I fully realised the potential of studying growth in this way. I hope that through this book I can infect some other workers with enthusiasm for studies based on mature size.

The introduction into this book of the concept of using mature weight as the basis of study of growth has made it necessary to look closely at the terminology which serves our discipline of growth and development. I have felt uneasy with some of our terminology for a long time and take the opportunity to express my problems in the appendices of this book. The appendices are somewhat large, however, they are necessary to explain to the reader why terms such as "early maturing" and "late maturing" which are liberally sprinkled throughout almost all growth and development literature, will not be found in this text, except in quotes. Those who are interested in terminology and in the derivation of the maturing rate coefficient may care to read the appendices before the main text. Others may use them for reference when puzzled.

Very few people will read this book from cover to cover, but rather the scientist will dip into it for specific information. For this reason I have not shied from repetition where it was necessary to ensure the clarity of any section. Such repetition it is hoped will make for easy reference rather than boredom.

I make no apology for the heavy bias towards the musculature in this work. As J.Z. Young wrote in his preface to "The Life of Mammals": "I have tried to cover the ground but have had no hesitation in lingering longer in the fields that have interested me especially." In my case it is fortunate that the musculature is not only the tissue most desired by the consumer, but also the tissue which presents the most exciting growth phenomena. Hence, I make no excuse for more complete discussion of the musculature than of the other tissues.

No attempt is made to present a review of the literature of growth and development of sheep or other meat animals. Rather, I have selected those references which contribute in a positive or negative way to the development of the concepts I have presented. Most of the references relate to sheep but I have not restricted the examples used to sheep when there have been more appropriate references in other species.

A problem which confronted me in writing this book was that a considerable proportion of the work incorporated had been done in our own laboratory and published under my senior authorship. To have repeatedly acknowledged the source of each piece of information would have led to a most unattractive text. Accordingly, acknowledgement to original publications from this laboratory is largely made through tables and figures with a comment at the end of each chapter on the major literature sources of that chapter.

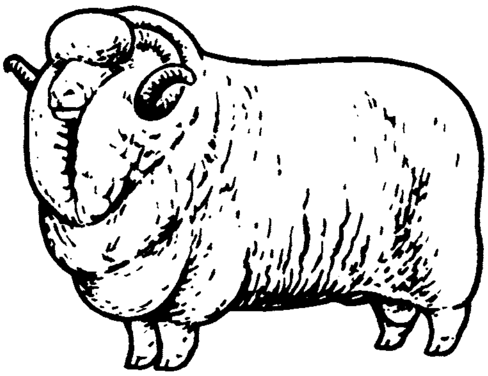
I return to those who have helped in the preparation of this text. Lynette Hicks, who was a major force in the production of "New Concepts of Cattle Growth" has again made a significant contribution, along with her word processor, in bringing together this more complex text. To her I extend my gratitude. Jenny Young did the bulk of the final art work from the first drafts which Sandy Brown produced from the data. Bozena Jantulik designed the dust cover and the comparative figures at the start of each chapter. Without the continued help of my back-up staff the "concepts" presented here would have been considerably less "new".

Grateful thanks are extended to Mr W.A. Crawford of "Sierra Park" Victoria Valley, Victoria, for the supply of the picture which adorns the dust cover and to Mr R. MacDonald, Registrar of the Australian Superfine Wool Growers' Association for his help in contacting Mr Crawford.

My thanks to Glen Davison of Griffin Press for his great help in printing the book.

CHAPTER 1

GROWTH OF A SINGLE SHEEP



"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." (Hammond, 1932).

"Elucidation of the laws governing growth and development of the animal body permits us to take useful advantage of its plasticity and resiliency to mould its conformation and composition of bone, muscle and fat in any desired direction." (McMeekan, 1969).

INTRODUCTION

In this chapter some aspects of the growth of a single sheep are described, using data derived from dissection programmes. As many of the measurements required for such a description can be obtained only by dissection of dead sheep, it is necessary to build up the story with data accumulated from large numbers of animals. In The University of Sydney over the last twenty years we have produced "total" dissection data from several hundred Merino sheep and it seems appropriate to start this monograph by using this data to describe as accurately as possible the growth of a typical sheep.

Some aspects of this attempt will be based on better information than others. For example the data on muscles for several reasons is much more comprehensive and more precise than that on fat. Most of the data come from sheep which were reared up to weaning under variable pastoral conditions and this limits the value, particularly of fat growth data. Nevertheless, for all its imperfections the story is presented in the belief that it provides a useful description of the growth of a single sheep, some variations from which, within the species, will be explored in the chapters which follow.

It will be left to the geneticists and comparative anatomists to decide how closely the growth of a single sheep can be used as an index of the growth of other mammals, for it seems that, with the current enthusiasm for genetic size scaling (Taylor, 1985a), there will be more interest in understanding similarities across breeds and across species as an essential prerequisite to the understanding of apparent and real differences between animals.

An appropriate starting point for such a description is to fix the mature size which it is required that the sheep should reach, as this mature size is the genetic size factor which can be seen in operation in every stage of growth (Taylor, 1985a). "Mature liveweight can, in certain situations, provide a reasonably comprehensive measure of mature size." (Taylor 1965), and so it is appropriate to use mature weight as our index of mature size. A mature weight of 100 kg, which is within the range of many sheep breeds, is chosen for this description. However, any such value is meaningful only if the conditions under which it is achieved are defined and Taylor (1985a) summarized the conditions for any specified genotype in the statement: "A definition of mature body weight that meets most purposes is the body weight of a normally grown, skeletally mature, normally active adult animal, maintained in a state of body weight equilibrium on a standard diet, in a thermo-neutral, disease-free environment with, or adjusted to, a chemical body fat of 20%". He went on to say that other levels of fat may be more suited for some comparisons. (See Appendix 1 page 123)

The sheep which we discuss in this chapter meets all of Taylor's criteria except the restriction on the level of fat. In this instance the level of fat will be that actually achieved by a sheep judged to be mature by the criteria of Thompson (1985b) which are essentially embraced by an assessment that the sheep has stopped growing. (See page 124)

I have chosen to describe a Merino ram as there is more information available on the growth of Merinos than on any other breed and because the growth process in rams is a more complete phenomenon than in the other "sexes". This is particularly so in the musculature as will be demonstrated in later chapters.

The nutrition chosen is *ad lib* feeding in pelleted form of the most nutritious food available following weaning from pasture. The best possible feeding regime is chosen as Hammond, many years ago, drew attention to the need for optimum nutrition to ensure the maximum expression of genetic characteristics. A suitable ration which has been used by many workers in CSIRO and The University of Sydney is shown in Table 1.I.1.

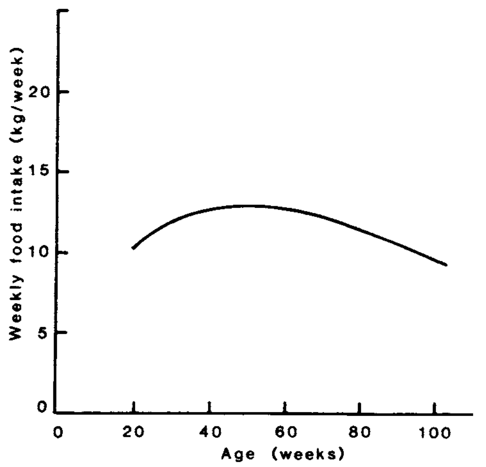


Figure 1.a.1.
Weekly food intake of a Merino ram up to a mature weight of 100 kg when fed *ad lib* on highly nutritious food.

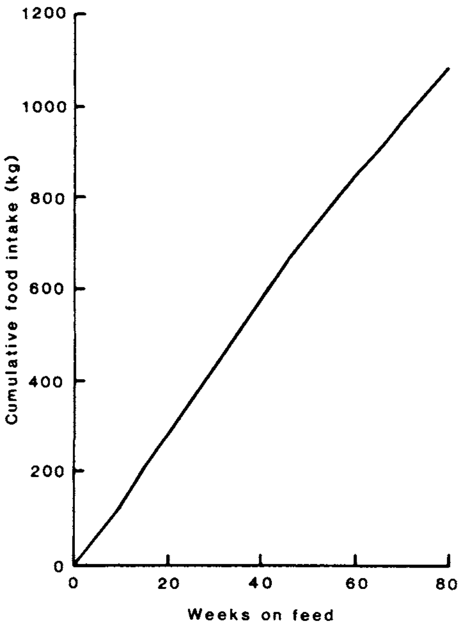


Figure 1.a.2.
Cumulative food intake of ram from 6 months to 2 years in acquiring a mature weight of 100 kg when fed *ad lib* on highly nutritious food.

Table 1.I.1. The contents and composition of a pelleted ration used to feed Merino rams

Contents (g/kg)*		Composition of dry matter (g/kg)	
Lucerne	500	Organic matter	938
Wheat grain	200	Crude protein	176
Oat grain	100	Crude fibre	180
Linseed meal	100	Nitrogen-free extracts	582
Coconut meal	100	Metabolizable energy (MJ/kg)†	10.83

* To 100 kg of this ration is added 1 kg finely ground limestone, 250 g salt, and 1 g ammonium molybdate.
† From Graham and Searle (1972).

a. FOOD INTAKE AND LIVEWEIGHT GROWTH

Food intake and therefore the whole process of growth can be influenced by many factors. In this section it is presumed that none of those factors is operative and our ram is in a Utopian environment, having been weaned when five months old and after a period of equilibration commenced his idyllic existence when six months old.

The pattern of post-weaning food intake is shown in Figure 1.a.1., and can be described as an exponential increase followed by a linear decline which shows that the ram reaches a peak of about 13 kg of pelleted food per week when about 70% mature at about one year old, and declines to an intake of about 10 kg per week at maturity. During feeding over an 18 months period (from six months old to two years) the ram eats about 1050 kg of pellets. The cumulative food intake is shown in Figure 1.a.2.

The growth in liveweight can be illustrated by the well-known sigmoid curve which is representative of so many mammals as shown by Brody (1945) and many others (Figure 1.a.3.)

Probably the most informative way to look at liveweight growth is to plot the growth rate in kg/week against stage of maturity (Figure 1.a.4.).

Brody (1945) described the "self accelerating stage" up to the inflection point in the liveweight curve as representing a "vegetative" phase; and the "self inhibiting or decelerating" phase after the point of inflection as being the "procreative" phase. It seems appropriate for us to use descriptive terms which are more in line with the anatomical growth process. Brody's self-accelerating phase is the period of an animal's life when it makes immense anatomical changes to ensure its survival by fitting it to the external environment, which is so different from the uterine environment from which it has been so recently expelled. It is, therefore, a "survival phase" during which there is not only an accelerating gain in weight, but also an intense ferment of differential growth of internal structures, so that both the size and form of the animal become appropriate to ensure the survival which is essential to allow the animal to enter the next phase.

To describe the next phase as procreative as proposed by Brody, is appropriate in a physiological sense as reproduction is the physiological goal but this is usually achieved prior to the growth goal of maturity. The animal is well and truly procreative while the growth process is far from complete and, although in wild animals the right for male animals to procreate may depend on the accumulation of sufficient mass to compete for the opportunity to mate, procreative ability is achieved far from the end-point of the growth process. Because of the continuation of the "decelerating phase" right through to maturity it is appropriate to embrace the whole of the period of growth past the point of inflection into a single phase which we will call a "maturing phase", and, as will be apparent throughout this monograph, it is possible to describe the growth of most anatomical structures during this period in a simple manner relative to their mature weights.

We will, therefore, refer to a "survival phase" up to about 20% mature followed by a "maturing phase" throughout much of which procreation is possible but in honour of which it is not named.

An alternative way of looking at the liveweight changes is by plotting the increments over given time intervals as shown in the histogram in Figure 1.a.5. It is clear that the further the animal proceeds towards maturity, the smaller its increments of liveweight in any time interval become. However, as discussed by Fitzhugh and Taylor (1971), Fitzhugh (1976), Parks (1982) and Thompson and Parks (1983), weight increase is a function of food intake rather than of time and as the animal approaches maturity the liveweight increase declines relative to the food eaten. This is also shown by plotting gross feed efficiency (liveweight/food weight) against degree of maturity in Figure 1.a.6.

It is apparent that, as the animal approaches its mature weight, the increments of liveweight become smaller on both a time and food intake basis and, if it is necessary to make a decision on when maturity is achieved, then appropriate criteria must be defined. Thompson *et al.* (1985) suggested a definition of maturity for *ad lib* feeding programmes as:

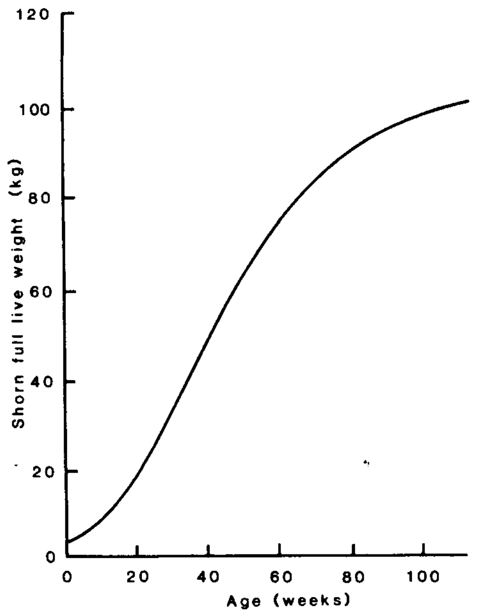


Figure 1.a.3.
Liveweight curve of a Merino ram to reach a mature weight of 100 kg when fed *ad lib* on highly nutritious food.

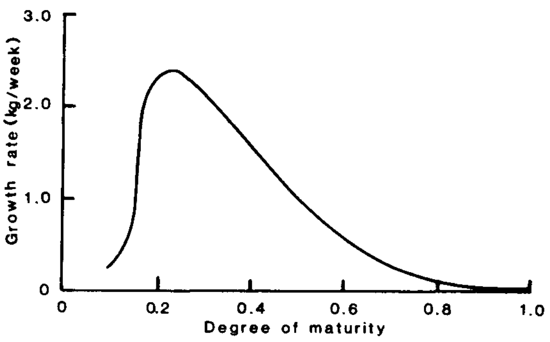


Figure 1.a.4.
Weekly growth rate of a Merino ram commencing from a birth weight of 4 kg to maturity at 100 kg when fed *ad lib* on highly nutritious food.

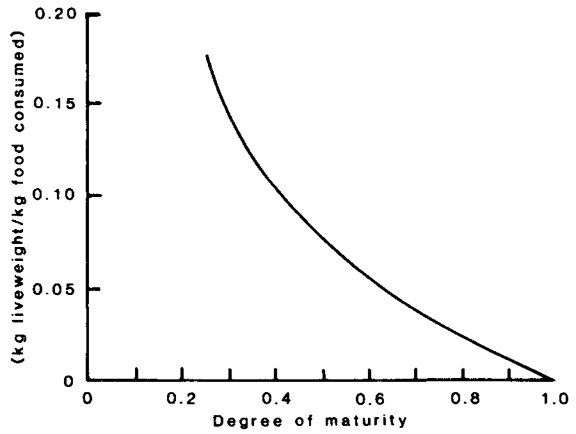


Figure 1.a.6.
Food efficiency during progress to maturity of a 100 kg ram when fed *ad lib* on highly nutritious food.

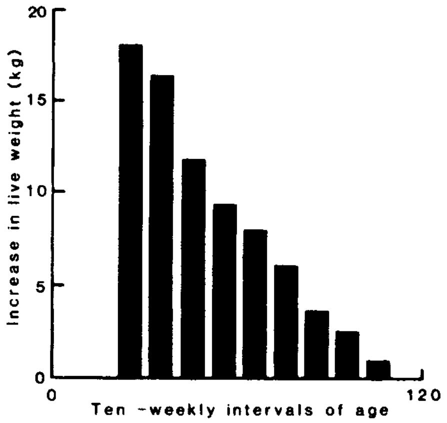


Figure 1.a.5.
Liveweight increments of a Merino ram to reach a mature weight of 100 kg when fed *ad lib* on highly nutritious food.

> ". . . an animal was accepted as mature when it had reached at least 0.85 of its asymptote for the exponential relationship between body weight and cumulative food consumed, and the average weekly increment in body weight for at least 10 weeks prior to slaughter was not significantly different from zero ($P < 0.05$)."

This is but one method of defining mature weight and other definitions are discussed later (page 123).

b. GROWTH OF CARCASE TISSUES

"Those who investigate the phenomena of life are as if lost in an inextricable jungle, in the midst of a magic forest, whose countless trees unceasingly change their place and their shape."
Carrel (1958)

SELECTION OF THE INDEPENDANT VARIABLE

Because the carcase is the commercial package in which the major salable portions of meat animals are merchandised, there is a tendency to regard its growth as an appropriate basis for study of the growth of its component tissues. This is not ideal for biological comparisons as the carcase is little more than an arbitrarily-chosen portion of the whole animal, the separation of which, divides anatomical tissues in a biologically meaningless way. The task of understanding the principles which govern the growth of tissues and organs is made very difficult when studies are based on the carcase rather than the whole animal.

In addition to the biological problems associated with studies within the carcase, there is also the simple arithmetic problem associated with the expression of composition changes within the carcase as proportions of that carcase. For most commercial purposes it is very appropriate to express carcase composition as proportions (or percentages) of the whole carcase, but it is of little value as a means of biological comparison as each change in the proportion of a tissue must be compensated by appropriate changes in the proportions of other tissues. As the carcase is merely an artifact within the total body it is far more desirable to use the total body as a basis for study of compositional growth as its use allows the compensatory changes resulting from change in organs, structures and tissues to be absorbed within the total biological system.

The removal of gut-fill from consideration of body composition has become usual, with most meat animal studies relying on empty body weight and the practical reasons for this are easy to accept. However, such a procedure does remove a large mass from the body, particularly from ruminants, which is vitally concerned in the physiological processes and anatomical structure of the animal. It is considered, therefore, that much more emphasis should be placed on full body weight than in the past, wherever it can be shown that short-term variation in gut-fill is not inappropriately affecting the consideration of the features of interest.

Butterfield, Griffiths, Thompson, Zamora and James (1983a) decided that with animals under controlled conditions full liveweight at a specified standard time of day was the measure of animal size which was most appropriate in a study aimed at finding biologically-sensible answers. Full liveweight has been used in several subsequent studies by the Sydney group. Ledger (1963) and others had previously used full liveweight for animals taken from open range "shot between first light and 8.30 a.m." Full liveweight will also allow comparison with zoological and human studies where "body weight" usually means the whole animal including gut-fill. A further major advantage of full liveweight is that it is a non-destructive measurement which can be recorded at frequent intervals throughout life as well as at slaughter.

Problems associated with wool growth and shearing require that wool weights be recorded at shearing and prior records of liveweight be adjusted for estimated wool growth up to the time of weighing if shorn weight is required. This is not a difficult undertaking and one which can be achieved with sufficient acccuracy for most studies of body composition by assuming that wool growth is linear, or by using length measurements of samples of wool plucked at each weighing to allocate final wool weight to the interim liveweights between shearings (Searle, Graham, Donnelly and Margan, 1986). These continuing records of liveweight can be particularly useful in studies of the growth of body components if non-destructive methods of assesssing the weights of tissues during growth are available (e.g., tritiated water (Panaretto, 1963, 1968; Searle, 1970a, b)).

A further factor in favour of full liveweight over starved liveweight which is also often used, is that no decision has to be made about the possible physiological differences in the effect of starvation on animals of different ages and sizes. Fourie *et al.* (1970) fasted lambs and sheep over a spectrum of time from 8-24 hours according to age in an attempt to cope with different effects of fasting on animals of different ages. This procedure is avoided if full liveweight is used.

There is a need to recognise the marked difference in the commercial value of those tissues contained in the carcase compared with sections of the same tissue in other parts of the animal, and this relates particularly to fat. And so, although we study carcase fat and carcase muscle in relation to liveweight as though they were complete systems, we later look at the total body fat (See 1.e.P ?) when studying changes within the adipose tissues. The small amount of skeletal muscle not contained in the carcase is ignored.

Shorn full liveweight is, therefore, chosen as the most desirable independant variable for the study of growth of carcase tissues.

GROWTH OF CARCASE MUSCLE, BONE AND FAT

The weights of the carcase tissues in a 100 kg mature Merino ram are set out in Table 1.b.1. It is apparent that the carcase portion of a mature Merino ram consists of approximately equal quantities of muscle and fat and that the total of the carcase tissues constitutes about 50% of the liveweight of the animal.

Using proportions of mature liveweight as the most appropriate base on which to describe the growth of carcase tissues, and by converting weights of the carcase tissues into proportions of their own mature weight, the actual liveweight of 100 kg becomes irrelevant (Figure 1.b.1.) and by the use of maturity coefficients (See Appendix 4) the pathways followed by the tissues in their progress to maturity may be specified by a single value. Table 1.b.2. shows the maturity coefficients ('q') and Figure 1.b.2. shows the maturing patterns for muscle, bone and fat.

Bone has the lowest growth impetus ('q' = 1.4) followed by muscle ('q' = 1.3) and as both of these tissues have lower growth impetus than the whole animal they decline as proportions of liveweight as the ram proceeds to maturity. Fat with a 'q' of only 0.07 has a high growth impetus and therefore constitutes an increasing proportion of liveweight as the animal matures.

Several studies (e.g. McClelland, Bonaiti and Taylor, 1976) have indicated a steady relationship between muscle weight and liveweight over narrower ranges of progress to maturity. It seems that it is probably only in advanced fattening that the proportion of muscle declines relative to liveweight. It may well be that an animal taken to maturity on a lower plane of nutrition will retain a more constant muscle proportion

Table 1.b.1. The weights of carcase tissues and these weights as percentages of liveweight in a mature 100 kg Merino ram

	Weight (kg) and Percentage of liveweight
Muscle	22.5
Bone	5.5
Carcase fat	21.8
Carcase weight	49.8
Liveweight	100.0

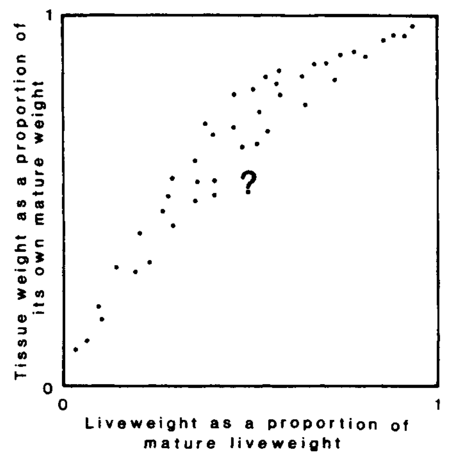


Figure 1.b.1.
The method of comparison of progress to maturity of body structures.

Table 1.b.2. Maturity coefficients of carcase muscle, bone and fat relative to liveweight from birth to 20% mature ('q*') and from 20% mature up to maturity('q') of a Merino ram proceeding to a mature weight of 100 kg

Tissue	Maturity coefficients 'q*'	'q'
Muscle	1.05	1.25
Bone	1.66	1.41
Fat	0.44	0.07

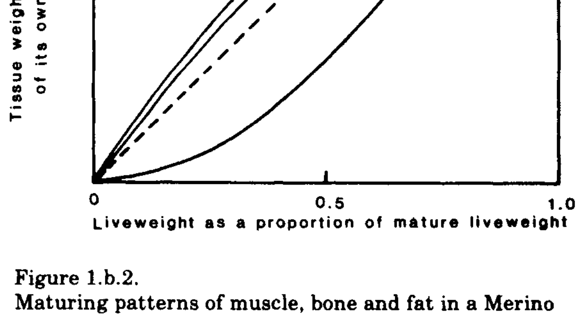


Figure 1.b.2.
Maturing patterns of muscle, bone and fat in a Merino ram.

throughout and hence have a 'q' not different from 1.0.

The approximate constancy of muscle growth relative to liveweight in sheep has drawn frequent comment in recent years and it is apparent that it is not just a feature of Merinos. It is shown to be a feature across breeds by Tulloh (1963) and across sexes and breeds by Fourie, Kirton and Jury (1970); Lohse (1971); McClelland *et al.* (1976); Lohse (1978) and Thonney, Taylor and McClelland (1986c). The last-named authors also included feral goats.

For ease of reference the maturing patterns from birth to maturity can be converted to tabular form as in Table 1.b.3. from which it can be readily seen, for example, that when liveweight is 60% mature, muscle is 66%, bone is 70% and fat 38% mature.

Table 1.b.3. The progress of carcase tissues of a Merino ram to maturity at 100 kg liveweight relative to the progress to maturity of shorn full liveweight

	Percentage Maturity										kg
Liveweight	4	10	20	30	40	50	60	70	80	90	100=100
Carcase muscle	5.0	12.3	24	35	46	56	66	75	84	92	100=22.5
Carcase bone	8.1	17.7	27	39	50	60	70	79	87	94	100= 5.5
Carcase fat	0.6	1.8	5	10	18	27	38	50	65	82	100=21.8

From the values in Table 1.b.3. it is simple to calculate the actual weights of tissues at any chosen liveweight and a range of values is presented in Table 1.b.4. from which it can be seen, for example, that, when the liveweight is 60 kg, muscle weighs about 15 kg, bone about 4 kg and fat about 8 kg. The information from the maturing patterns can be readily converted into proportions of liveweight.

Of critical interest to the economics of modern meat production is the amount of muscle being produced relative to the food consumed and this changes dramatically throughout the maturing process. Using the available information from Section 1.a. it is possible to combine this with the information in this section as the basis for some economic calculations throughout post-weaning growth. First it is necessary to determine the composition of the weight increments of the liveweight of the animal and these are shown in Figure 1.b.3. where it can be seen that the proportion of muscle declines slightly in each increment and the proportion of bone also declines and the proportion of fat in each increment increases as the animal matures. It is possible to formulate the amount of feed required for muscle growth from the information in Figure 1.a.1. This is shown in Figure 1.b.4.

The feed costs of production of muscle increase as the animal becomes more mature and with most meat markets of the world demanding high proportions of muscle it is becoming increasingly important to produce that muscle from animals in the earlier stages of the maturing process.

Table 1.b.4. The progress to maturity at 100 kg liveweight of actual weights of carcase tissues of a Merino ram relative to progress to maturity of liveweight

					(kg)						
Liveweight	4	10	20	30	40	50	60	70	80	90	100
Carcase muscle weight	1.12	2.8	5.4	7.9	10.4	12.7	14.9	16.9	18.9	20.8	22.5
Carcase bone weight	0.45	1.0	1.4	2.1	2.7	3.3	3.8	4.3	4.8	5.2	5.5
Carcase fat weight	0.12	0.4	1.1	2.3	3.9	5.8	8.2	11.0	14.2	17.8	21.8

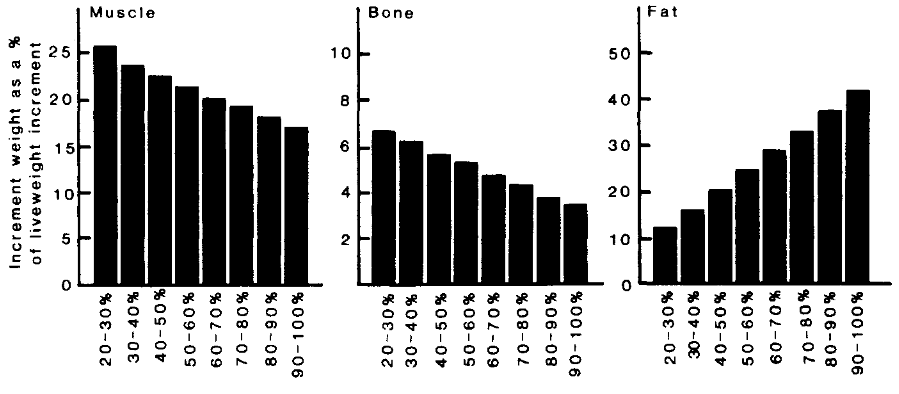


Figure 1.b.3.
Increments of muscle, bone and fat of a ram during 10% increments of mature liveweight when fed *ad lib* on highly nutritious food.

MUSCLE:BONE RATIO

Considerable interest has been generated at times in the use of muscle:bone ratio as a guide to carcase merit (Hankins, Knapp and Phillips, 1943; Berg and Butterfield, 1966; Berg and Butterfield, 1976) and also as an index of maturity (Davies and Kallweit, 1979).

Muscle:bone ratio according to Kempster, Croston and Jones (1981) is potentially the most important function of conformation. (for Kempster's definition of conformation see p.?) The influence of muscle:bone ratio on external appearance of both live cattle and their carcases is clearly apparent in the increasing numbers of later-maturing types of cattle now being used in many countries. However, as will be discussed in Chapter 5, the differences in muscle:bone ratio seen in the commonly-used breeds of sheep do not profoundly affect conformation.

Throughout the maturing process in a Merino ram this ratio increases from about 2:1 at birth, 3:1 at 10% mature up to about 4:1 at 60% mature. The ratio then appears to increase only very slightly until mature liveweight is reached (Figure 1.b.5.) The changes occurring in muscle:bone ratio are therefore of importance in the yield of muscle relative to bone in animals slaughtered at light weights up to about 50-60% of mature weight. However, once animals have reached this stage there is only small gain in this characteristic by taking them to heavier weights.

MUSCLE:FAT RATIO

Muscle:fat ratio has received little attention in the literature as it is rarely allowed to "run free" in comparisons of slaughter animals. Nevertheless, it is an important characteristic of meat animals, particularly to the final consumer, and one in comparisons of which it is necessary to understand the changes during growth. It is shown in Figure 1.b.6. that muscle:fat ratio declines progressively as the animal grows. It is apparent that with muscle a desired tissue and fat a less-desired tissue, that once an optimum has been reached that further decrease in this ratio heralds declining desirability of a carcase to the consumer.

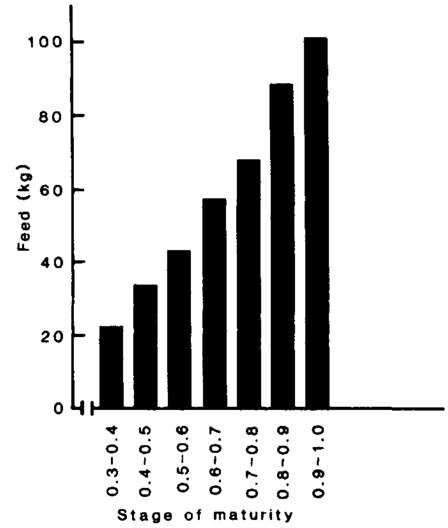


Figure 1.b.4.
Amount of feed required for each kg of muscle laid down by a Merino ram at various stages of progress to maturity when fed *ad lib* on highly nutritious food.

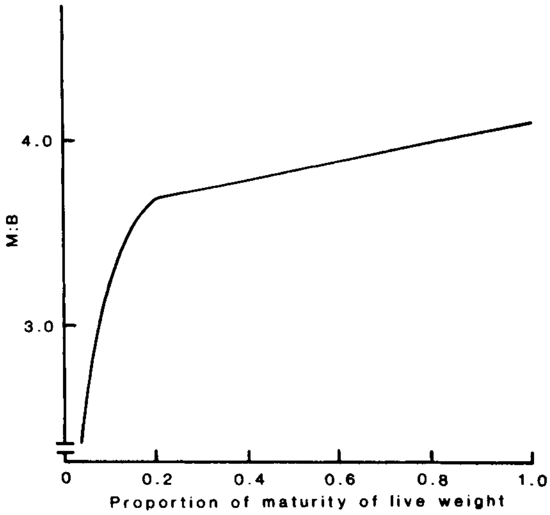


Figure 1.b.5.
The muscle:bone ratio (M:B) of a Merino ram proceeding to a mature weight of 100 kg expressed relative to progress to maturity of liveweight when fed *ad lib* on highly nutritious food.

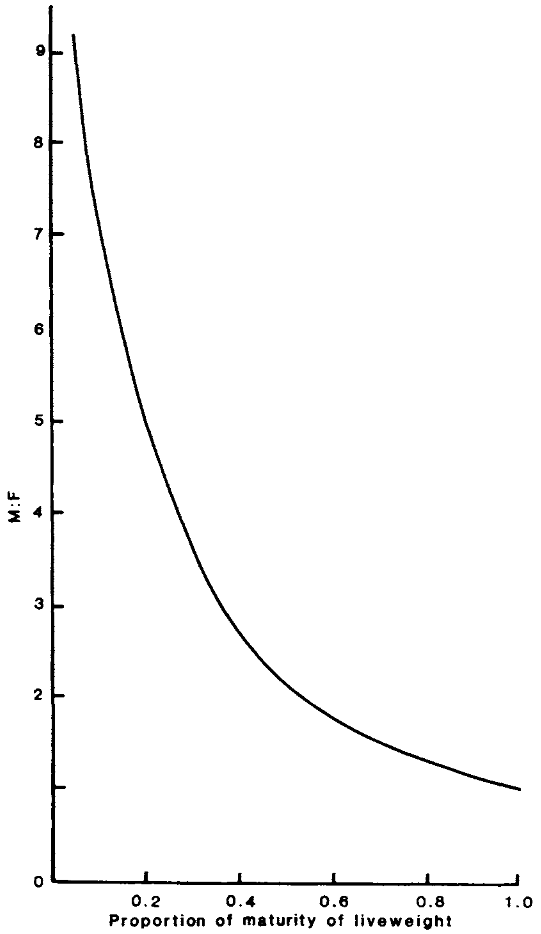


Figure 1.b.6.
Muscle:fat ratio (M:F) of a Merino ram proceeding to a mature liveweight of 100 kg when fed *ad lib* on highly nutritious food.

c. GROWTH WITHIN THE MUSCULATURE OF A MERINO RAM FROM BIRTH TO MATURITY AT 100 KG LIVEWEIGHT

Hammond (1932) described differential growth of the musculature of the hind leg of sheep and in the last twenty five years there have been several studies of muscle-weight distribution in cattle (Butterfield, 1963; Butterfield and Berg, 1966a, b, c; Seebeck, 1966a; Bergström 1978; Berg and Mukhoty, 1970; Charles and Johnson, 1976; Johnson, Pryor and Butterfield, 1973; Berg, Andersen and Liboriussen, 1978b; Pirchner, 1984;) in pigs (Richmond and Berg, 1971b; Davies, 1974b) and in sheep (Fourie, 1965; Seebeck, 1968b; Jury, Fourie and Kirton 1977; Lohse, 1973; Lohse, Moss and Butterfield, 1971; Thompson, Atkins and Gilmour, 1979; Taylor, Mason and McClelland, 1980; Wolf, 1982; Thonney *et al.*, 1986c; Perry, Thompson and Butterfield, 1987).

The growth of each individual muscle of sheep may be expected to be related to its activity. The activities of most skeletal muscles are primarily concerned with locomotion, however, mastication, urination, defeacation and particularly reproduction make differential demands within the anatomical spectrum of the musculature. At birth it is necessary that the lamb can stand, walk and suckle. As it grows, the activities become much more athletic so that the lamb is capable of quite vigorous frisking and of travel over long distances. From about weaning, functions change little for the rest of life for wethers and ewes except that the muscles of the abdominal wall of ewes assume greater load during pregnancy. In rams, the achievement of adulthood embraces the biological need to contest with other rams the right to mate with the available females. This contest takes the form of fighting which demands, in addition to total mass, especially-robust muscles of the neck, particularly the more dorsal muscles. As will be shown in this section, the changes in the development of the musculature are closely aligned to the activities of sheep.

THE IMMEDIATE POST-NATAL SURVIVAL PHASE

Early work in cattle showed that it was during the doubling of birth weight that most of the differential growth of muscles occurred (Butterfield, 1963). The work of Lohse (1971) and Lohse *et al.* (1971) showed that there was still some considerable change up to and possibly beyond four times the birth weight of lambs. It is during this phase from birth to about four times birth weight that the musculature is adapting from the relative inertia of intra-uterine life to its active role in the mobility of the lamb in the external environment. Those muscle groups which have to be well-developed at birth to ensure immediate post-natal survival, need to grow less rapidly as the other groups, which have minimal use in the neonate, catch up. This may be expressed in a different manner. Those muscles which are most important for survival in the immediate post-natal period have already achieved, at birth, a greater proportion of their mature weight than has the total musculature and must, therefore, necessarily grow relatively slowly at some stage post-natally. This relatively slow growth occurs particularly in the immediate postnatal period when other muscles, which, relative to their ultimate mature size, had grown slowly before birth, are frantically catching up.

THE ADOLESCENT AND MATURING PHASE

The adolescent and maturing periods are considered together as they are amenable to the same mathematical representation. During the adolescent phase only minor differences occur in relative muscle growth. However, following puberty in what we are calling the maturing phase the second assortment of differential growth gets under way in the entire male as the need to mate becomes urgent.

It is the order of things in nature that only those males which are physically best able to copulate should be able to mate with the female population, and it is the imposition of man's will on this natural law which is what modern animal breeding is all about. The physical ability to win the right to mate in our meat animals, should they be left to fight it out, would be largely concerned with the musculature, as physical mass which is extra-musculoskeletal is of limited use in a fight.

MATURING PATTERNS FROM BIRTH TO MATURITY

Analysis of relative growth of units within the musculature is most logically based on the growth of the total musculature (Wallace, 1948).

This section shows the growth from birth to maturity of the "Standard Muscle Groups" and is based on three studies. The early post-natal stage uses the data of Lohse (1971) and Lohse *et al.* (1971) while the remainder of the growth to maturity is based on the study of Butterfield, Zamora, James, Thompson and Williams (1983b). The methods used for the calculation of the value 'q*', which describes the muscle growth up to 20% mature, and the value 'q' up to maturity are set out in Appendix 4.

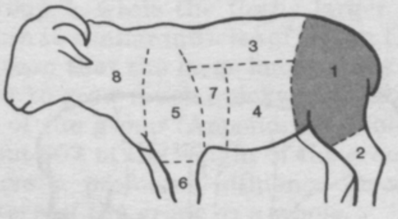
The composition of the musculature of the mature 100 kg ram which is the basis for the calculation of the maturing patterns of the musculature is set out in Table 1.c.1. The grouping is that originally proposed for cattle (see p. 130) and is based on individual muscle weights assembled according to anatomical location.

Table 1.c.1. The weights and percentages of the total musculature comprised by the "Standard Muscle Groups"* in a mature 100 kg Merino ram

Muscle Group	Weight (kg)	% of total muscle weight
1. Proximal hind limb	5.61	24.9
2. Distal hind limb	0.98	4.4
3. Surrounding spinal column	3.50	15.5
4. Abdominal wall	2.38	10.6
5. Proximal forelimb	2.43	10.8
6. Distal forelimb	0.62	2.8
7. Thorax to forelimb	1.93	8.6
8. Neck to forelimb	1.72	7.6
9. Neck and thorax	2.80	12.4
Scrap	0.57	2.5
TOTAL	22.54	100.0
Expensive muscle group (1+3+5)	11.54	51.2

* Butterfield (1964b)

GROWTH FROM BIRTH TO MATURITY OF "STANDARD MUSCLE GROUPS"



Standard Muscle Group 1 – The muscles of the proximal hind limb

It is no doubt essential for the ease of the birth process that the growth of this group is restrained antenatally. However, the group is sufficiently developed at birth to play a role in simple, tentative, locomotion. Immediately following birth large muscles in the group, in particular the biceps femoris (Footnote: strictly M. gluteobiceps of *N.A.V.* 1983), the middle gluteal and the semimembranosus muscles, grow much faster than the musculature as a whole and hence the group soon assumes a higher proportion of total muscle weight than was the case at birth. Considerable development of this muscle group is essential for optimum locomotory performance in the adolescent and adult animal.

When the lamb and its musculature are around 20% of their mature weight, this group has assumed its highest proportion of total muscle weight, and the lamb is now able to travel and frisk with a high degree of efficiency. For the remainder of life this group retains its functional role, however, when assessed relative to the total musculature, it is seen to be declining slowly in relative weight. All of the major muscles within the group, and the group as a whole, have maturity coefficients greater than 1.0, from around 5 kg total muscle weight (i.e., about 20 kg liveweight) to maturity (Figure 1.c.2. and Appendix 5 Table 1), indicating that the relatively high impetus growth of this group immediately following birth is gradually

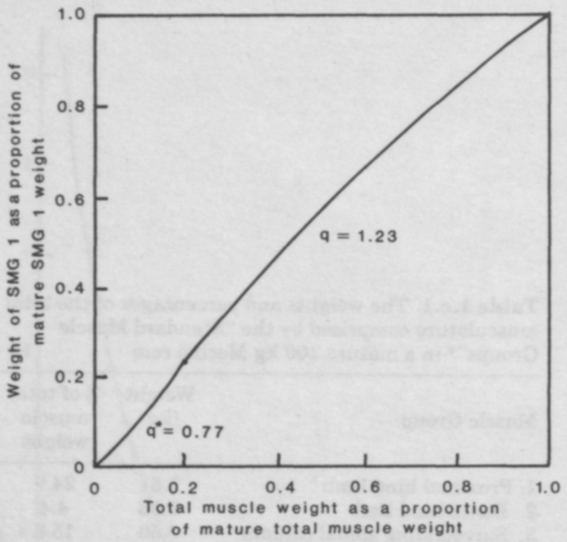


Figure 1.c.1.
The progress to maturity of the weight of muscles of the "proximal hind limb" relative to the progress to maturity of total muscle weight. (SMG = "Standard Muscle Group" 1.)

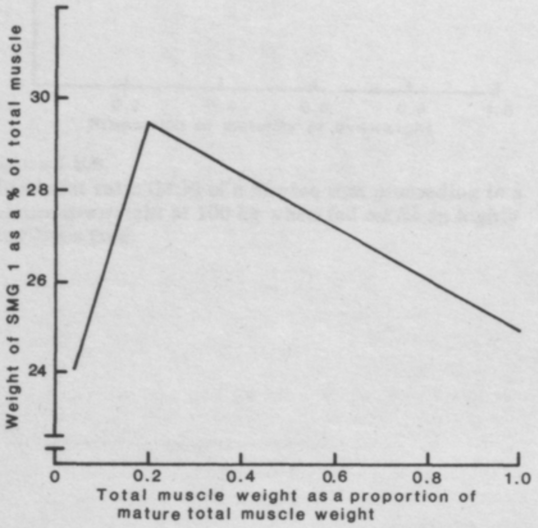


Figure 1.c.2.
Muscles of the "proximal hind limb" (SMG 1) as a percentage of total muscle weight at various stages of maturity of total muscle weight.

overtaken by the musculature as a whole as other groups make rapid growth to meet new functional requirements.

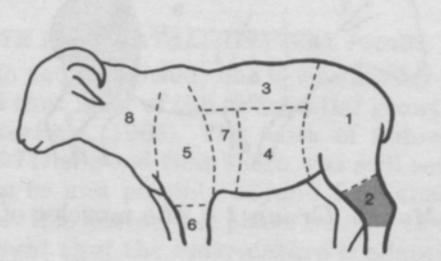
As this group comprises the bulk of the musculature of the "gigot" (hind leg) of United Kingdom terminology and, as will be shown, the remainder of the hind leg muscles mostly grow at a low impetus, it is not surprising that Jackson (1969) found that the "gigot" musculature was a declining proportion of total muscle weight in Scottish Blackface castrated males. (It is noted in Chapter 3 Table 3.b.5. that castration does not significantly alter the maturing patterns of the hind leg muscle groups.)

Thonney *et al.* (1986c) also showed that for their range of breeds (see p. 106) muscles of the hind limb were, in general, "early maturing" thus implying a lower growth impetus than that of total muscle. Surprisingly, Lohse (1971) classified this group as having a monophasic high impetus growth pattern. Although his 'b' value of 1.08 was significantly greater than 1.0 the magnitude of the difference was very small.

The whole pattern of growth and development of this group can best be expressed by two mathematical functions:

(a) Immediately post-natal a high impetus phase of growth with a coefficient, 'q*', of 0.8
(b) From about 20% of mature weight a low impetus phase with a maturity coefficient, 'q', of 1.2

Using Butterfield and Berg's (1966b) impetus classification, this group would be classified as "high/low impetus". The progress to maturity of the weight of this group of muscles relative to the progress to maturity of total muscle weight, is shown in Figure 1.c.1. The effect of the biphasic impetus pattern on the percentage of muscle weight comprised by this group at various stages of maturity of the total muscle weight commencing from birth is shown in Figure 1.c.2.



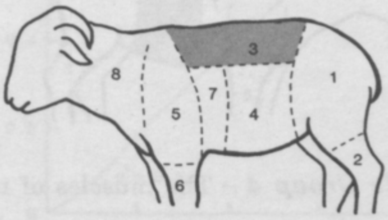
Standard Muscle Group 2 – The muscles of the distal hind limb

It is essential that this group be relatively well-developed at all stages of growth in order that it can play its part in locomotion of all degrees of efficiency. Its function is the same throughout life and therefore there are no dramatic changes as the animal passes through the functional demands of its post-natal lifespan. It is further advanced in its growth than most other groups at birth but this produces no problems to the birth process as the group is small and consists largely of multipennate, fibrous muscles bound tightly by deep fascia to the related bones, principally the tibia.

Having already progressed to a high level of efficiency at birth this group then grows slower than the total musculature and hence is found throughout postnatal life to be a progressively smaller proportion of total muscle weight. Its functional efficiency in no way declines; it is merely that the other muscle groups which are less developed and less efficient at birth catch up at various stages.

The phase of growth of this muscle group from birth to about 20% mature can be described by a 'q*' of 1.1 and the rest of the progress to maturity by a 'q' of 1.3, which indicates a low impetus pattern throughout post-natal growth in line with the

Lohse *et al.* (1971) classification of monophasic low impetus. Figure 1.c.3. shows the progress to maturity of this group and Figure 1.c.4. the changes in its proportion of total muscle weight. There is a general decline in its proportion of total muscle weight which is faster in the immediate postnatal period than later.



Standard Muscle Group 3 – The muscles surrounding the spinal column

A great deal of interest has been centred on this group for many years as it is of such commercial value and because it is widely used as an index of the musculature as a whole by both industry and science. The muscles within the group display a spectrum of growth and maturing patterns and perhaps this should be expected, as the muscles vary widely in physical structure and function: from the physically weak, fusiform, psoas major muscle; to the strong, multipennate, iliocostalis; from the massive, fleshy, longissimus to the tiny, fibrous, multifidus.

This group can be seen to be functionally similar to the combined groups of the hind leg. The deeper more fibrous muscles being akin to the Group 2 muscles, and the deeper muscles of Group 1, while the fleshy larger more superficial muscles are akin to similar muscles of Group 1. In line with this thinking it is seen that the large longissimus and psoas major muscles appear to grow much quicker immediately after birth than the rest of the group (Appendix 5 Table 1) and as they constitute about 60% of the weight of the group, their patterns of growth have a profound influence on the growth and maturing pattern of the group as a whole.

A majority of the muscles in this group have maturing patterns which are not different from that of the total musculature and these patterns align with a steady functional role throughout life. However, the two big fleshy muscles (M. longissimus and M. psoas major) enjoy an early post-natal spurt, much as the major muscles of the hind leg, before settling to a pattern of slow relative decline in growth impetus as the animal grows. The tendency of large muscles to grow on a higher impetus in the immediate post-natal period than small muscles was discussed by Berg and Butterfield (1974) in cattle where they showed a very strong relationship between muscle size and growth impetus. The overall effect of this is that the group as a whole declines slightly (see Figure 1.c.6.) from its peak percentage of total muscle weight which is achieved at about four times birth weight.

Lohse *et al.* (1971) classified this group as having a diphasic high/average impetus pattern. However, the bulk of evidence from other studies suggests that within male animals (including castrates) there is a declining growth impetus in this group following the initial growth spurt.

The total growth span of this muscle group from birth to maturity can be adequately described by a 'q*' value of 0.7 up to about 20% of mature weight representing a phase of high growth impetus followed by a 'q' of 1.2 for the remainder of post-natal growth. The impetus pattern of the group can therefore be described as "high/low" which is largely a reflec-

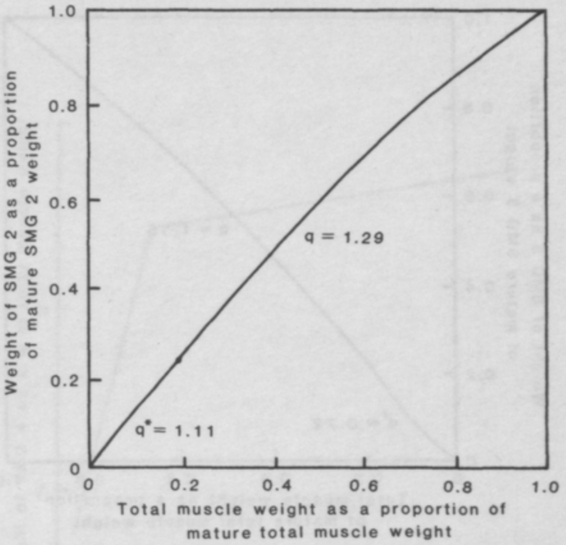


Figure 1.c.3.
The progress to maturity of the weight of the muscles of the "distal hind limb" (SMG 2) relative to the progress to maturity of total muscle weight.

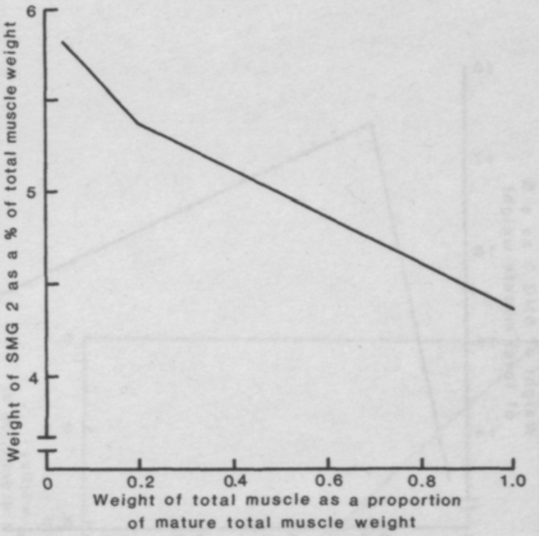


Figure 1.c.4.
Muscles of the "distal hind limb" (SMG 2) as a percentage of total muscle weight at various stages of maturity of total muscle weight.

tion of the patterns of the two largest muscles but different from many of the smaller muscles in the group. Figure 1.c.5. shows the maturing pattern and Figure 1.c.6. the changing proportions of the total muscle weight of this group.

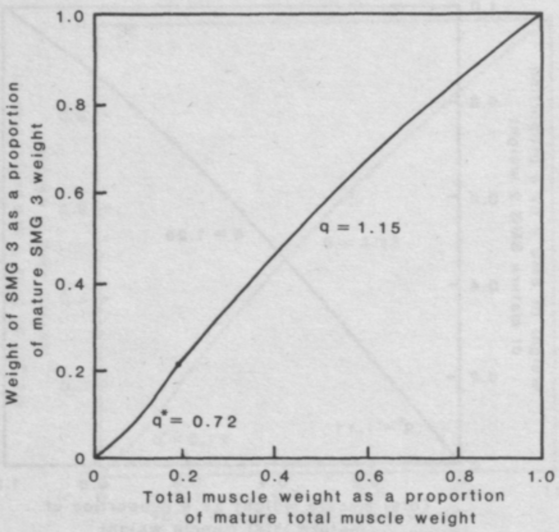


Figure 1.c.5.
The progress to maturity of the weight of the muscles "surrounding the spinal column" (SMG 3) relative to the progress to maturity of total muscle weight.

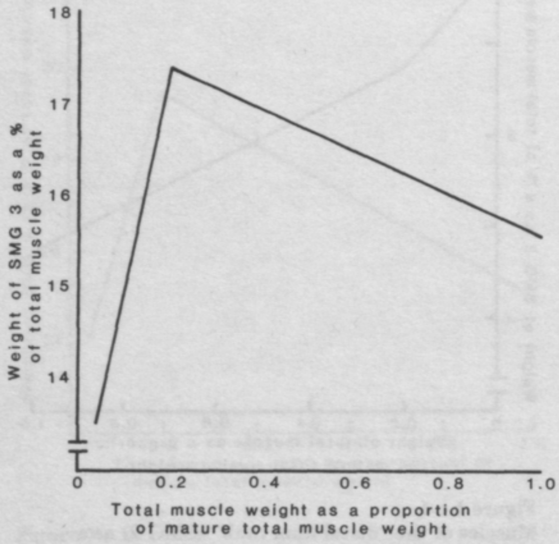
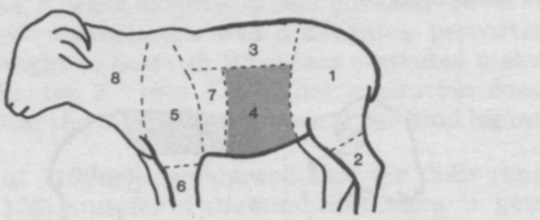


Figure 1.c.6.
Muscles "surrounding the spinal column" (SMG 3) as a percentage of total muscle weight at various stages of maturity of total muscle weight.



Standard Muscle Group 4 – The muscles of the abdominal wall

There is little functional demand on this group of muscles at birth as their prime function is to contain and support the abdominal viscera. The gastrointestinal tract comprises a high proportion of the viscera and is relatively poorly developed at birth and, in addition, has no appreciable content. This is fortunate for the ease of the birth process. There is rapid change, first by the intake of milk and soon by the intake of solid food of a bulky nature.

It is easy to postulate that the abdominal wall should grow relatively very fast to meet its changing post-natal function. It is also easy to imagine that the relative rate of growth could be readily modified by the rate and nature of food intake as demonstrated in calves by Butterfield and Berg (1966c) and Butterfield and Johnson (1971), and in adult cattle by Bergstrom (pers. comm. 1984).

There is a period of high impetus growth during the preweaning phase. Butterfield *et al.*'s (1983b) animals, in the post-weaning phase, were fed on a uniform *ad lib* intake of pellets which did not vary in physical characteristics and the 'q' values for the group and for all the muscles except one, did not vary from 1.0 in this post-weaning phase. The expectation is that increasing gut fill would result in a high growth impetus such as occurred with the pasture-fed sheep of Lohse (1971).

Comparison of Dorset Horns and Merinos in a later chapter (p. 107) will show marked differences in the growth of the abdominal wall muscles. This difference appears to be a genuine breed difference with the possible proviso that some difference in preweaning nutrition may have had some influence on this environmentally sensitive group.

Surprisingly Thonney *et al.* (1986c) classified the muscles of the abdominal wall as "early maturing" in rams indicating a declining proportion of total muscle weight. It is possible that this unexpected result was due to the *ad lib* artificial feeding regime of their lambs from about 10 days old resulting in much earlier development of the abdominal wall in response to functional demand.

The foregoing references to work on other breeds and to a range of experiments have been made to indicate the sensitivity of this group of muscles to various influences and therefore to suggest that the impetus patterns may be very different in different circumstances. However, although under many conditions, this group may grow on a monophasic high impetus pattern (Lohse *et al.*, 1971; Perry *et al.*, 1986) the pattern presented here is based on a 'q*' of 0.58 and a 'q' of 0.92 and is high/average, in line with the results of Butterfield *et al.* (1983b) and the appropriate progress to maturity and changes in proportion of the total muscle weight by this group are shown in Figures 1.c.7. and 1.c.8. respectively.

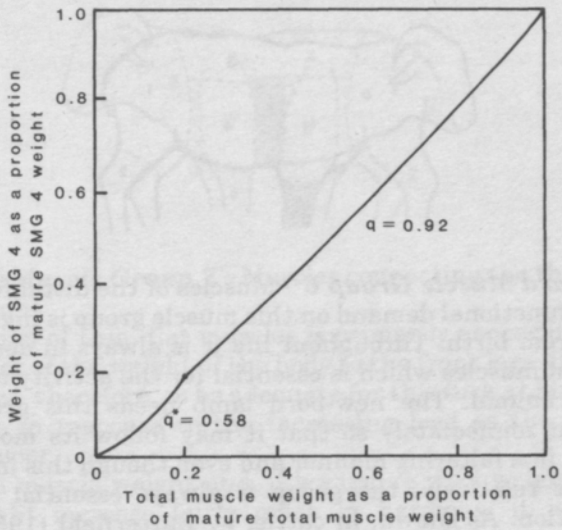


Figure 1.c.7.
The progress to maturity of the weight of the muscles of the "abdominal wall" (SMG 4) relative to the progress to maturity of total muscle weight.

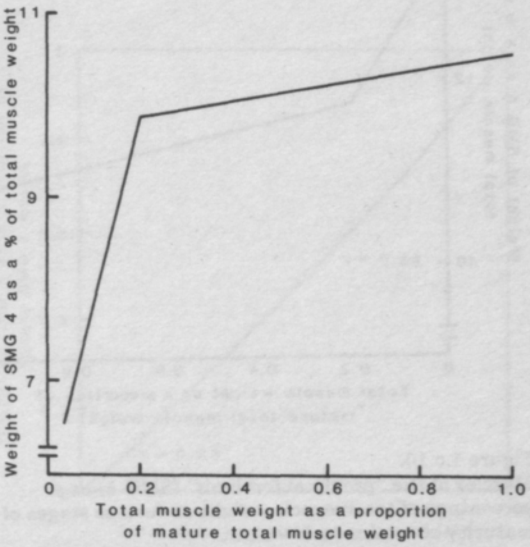
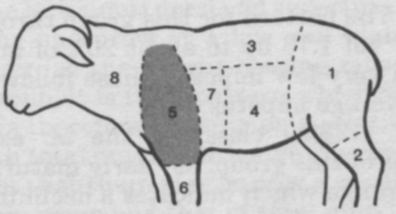


Figure 1.c.8.
Muscles of the "abdominal wall" (SMG 4) as a percentage of total muscle weight at various stages of maturity of total muscle weight.



Standard Muscle Group 5 – Muscles of the proximal forelimb

In order that the new-born lamb may be sufficiently stable on its front legs to suckle, this group may need to be relatively more advanced at birth than the corresponding group in the hind limb (Group 1). Accordingly, there is no immediate post-natal spurt of rapid relative growth in the muscles of the proximal forelimb. This group at first grows at a considerably slower rate than the whole musculature as also do most of the larger individual muscles within it, then, after about 20% mature weight is achieved, it grows a little faster relatively, but still slower than the total musculature, so that as a proportion of total muscle weight it first declines rapidly then slowly throughout progress to maturity.

This pattern of growth is in line with the rather special immediate post-natal function of propping the cranial end of the trunk during suckling to be followed by its whole-of-life role in simple locomotion.

Thonney *et al.* (1986c) agree that across their variety of breeds this muscle group is "early maturing" indicating a declining proportion of muscle weight. However, Lohse *et al.* (1971) suggested a period of average impetus followed by low impetus growth based on 'b' values which, although appropriately significantly different, were neverthelesss not substantially different from 1.0.

The pattern of growth of this group can be characterized by a 'q*' value of 1.14 and a 'q' value of 1.11. This is expressed, therefore, as a low impetus pattern. The progress to maturity and changes in proportion of total muscle weight by this group are shown in Figures 1.c.9. and 1.c.10. respectively.

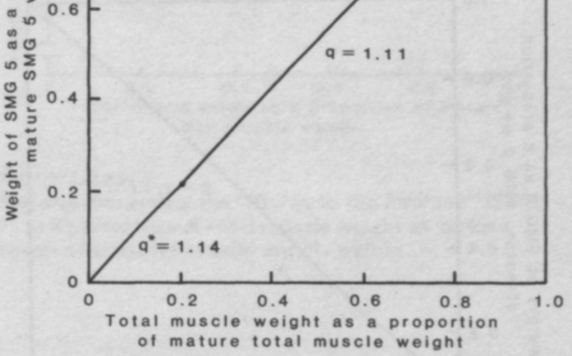


Figure 1.c.9.
The progress to maturity of the weight of the muscles of the "proximal forelimb" (SMG 5) relative to the progress to maturity of total muscle weight.

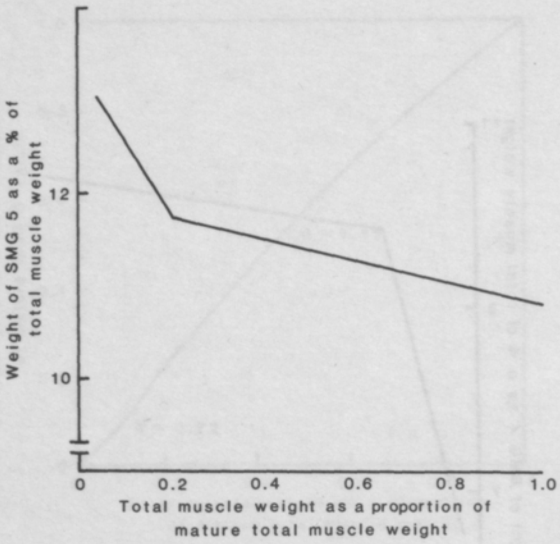
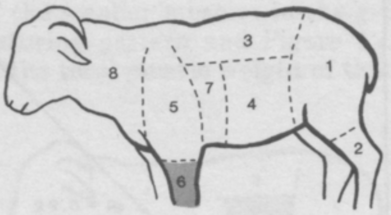


Figure 1.c.10.
Muscles of the "proximal forelimb" (SMG 5) as a percentage of total muscle weight at various stages of maturity of total muscle weight.



Standard Muscle Group 6 –Muscles of the distal forelimb

The functional demand on this muscle group is high immediately from birth. Throughout life it is always in demand as a group of muscles which is essential for the activity or survival of the animal. The new-born lamb needs this group to be efficient immediately so that it may follow its mother even though in a faltering manner and even though this importance declines relatively, the group is always essential to simple locomotion. As shown, in cattle, by Butterfield (1966a), even when animals have lost considerable muscle weight due to malnutrition, this group loses little weight as it is essential for the locomotion needed to survive.

Immediately post-natal, the muscles of this group almost all have low growth impetus according to Lohse *et al.* (1971), yet subsequently, many of the muscles grow at about the same rate as total muscle. The antenatal development of this group is well ahead of that of the total musculature so that it can meet its functional obligations immediately after birth, and then is able to grow at a lower impetus than total muscle in the early postnatal period. The pattern for this group throughout life is expressed by a 'q*' of 1.73 up to about 20% of mature weight which indicates a very low impetus phase followed by a 'q' of 1.11, a phase of average impetus.

Thonney *et al.* (1986c) classified the M. extensor carpi radialis, a member of this group, as "early maturing" over the 40-70% maturity range which indicates a declining proportion of total muscle weight. This is a little surprising as both the Merino and Dorset Horn data of Butterfield *et al.* (1983b, 1984b) and the Merinos of Lohse (1971) over a wide maturity range of approproxately 20–100% classified this muscle as exhibiting average impetus.

The progress to maturity and change in proportion of total muscle weight by this group are shown in Figures 1.c.11. and 1.c.12.

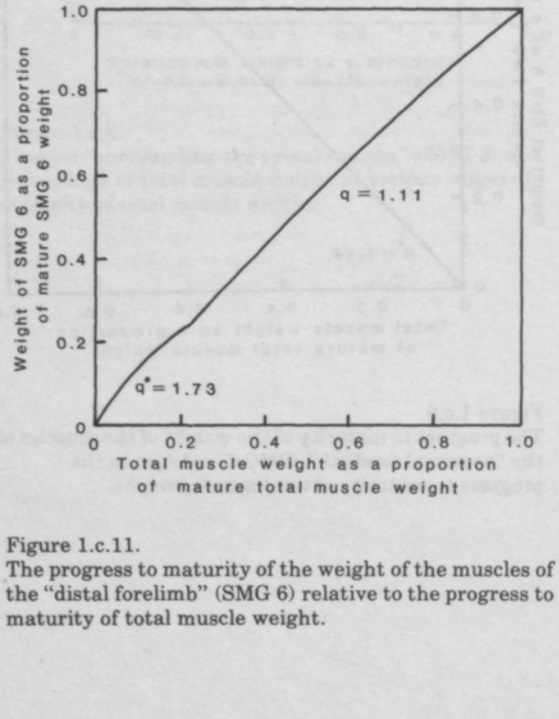


Figure 1.c.11.
The progress to maturity of the weight of the muscles of the "distal forelimb" (SMG 6) relative to the progress to maturity of total muscle weight.

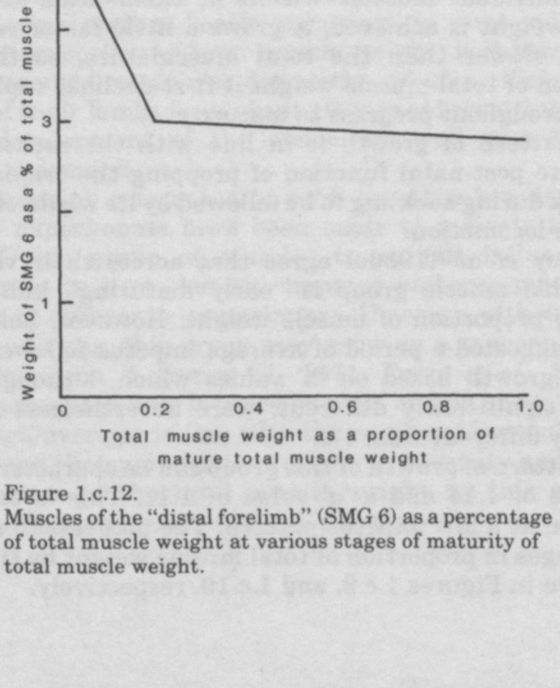
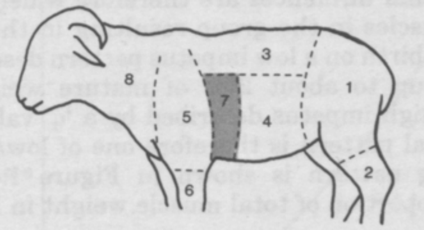


Figure 1.c.12.
Muscles of the "distal forelimb" (SMG 6) as a percentage of total muscle weight at various stages of maturity of total muscle weight.



Standard Muscle Group 7 – Muscles connecting the thorax to the forelimb

This group of thin, flat muscles is primarily concerned with the transfer of the weight of the body to the front legs. It would be expected, therefore, to be adequate for this task at birth and to develop in response to the increasing load as the animal grows heavier.

As total muscle weight and, if we ignore wool weight, total body weight increase fairly much in harmony, it is to be expected that the weight-bearing muscles in this group would grow and mature in a manner not greatly different from total muscle weight. However, total muscle weight declines slightly relative to total body weight plus wool weight and hence becomes a progressively smaller proportion of body weight during progress to maturity. It is not, therefore, surprising that the three weight-bearing muscles in this group grow at a high impetus which could be seen to be a reaction to increased function as body plus wool weight becomes proportionately larger relative to total muscle weight. Two of the muscles in this group, the latissimus dorsi and superficial pectoral, are not weight-bearing and grow at a low and high impetus respectively. However, as the weight-bearing muscles comprise the bulk of the group, it is their pattern which dominates and the whole group is therefore growing on a relatively high impetus compared with total muscle, although the results of Perry *et al.* (1987) suggest that there may be only a small difference in the impetus of this group and that of total muscle.

Using Lohse's (1971) and Butterfield *et al.*'s (1983b) data the group commences with a high impetus phase described by a 'q*' value of 0.58 up to about 20% of mature weight to be replaced by a less high impetus phase which is described by a 'q' = 0.9. The maturing patterns and proportions of total muscle weight comprised by this group are shown in Figures 1.c.13. and 1.c.14.

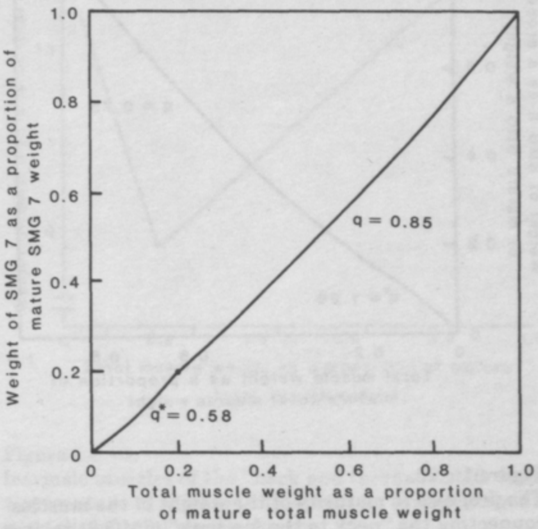


Figure 1.c.13.
The progress to maturity of the muscles connecting the "thorax to the forelimb" (SMG 7) relative to the progress to maturity of total muscle weight.

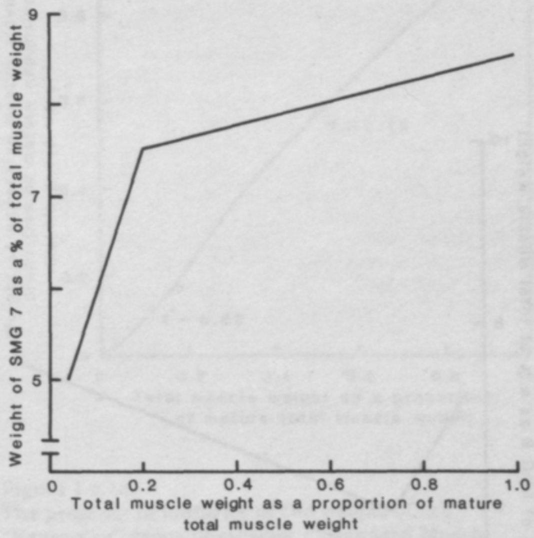
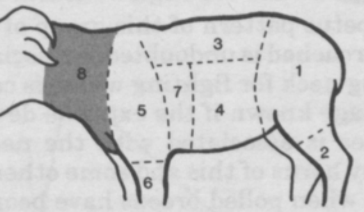


Figure 1.c.14.
Muscles connecting the "thorax to the forelimb" (SMG 7) as a percentage of total muscle weight at various stages of maturity of total muscle weight.



Standard Muscle Group 8 – The muscles connecting the neck to the forelimb

This group of muscles is dominated by the heavy serratus ventralis muscle which contributes about half of the weight of the group. As this muscle is a weight-bearing muscle it is similar in function and maturing pattern to those weight-bearing muscles discussed in the previous group. The late development of the other muscles in the group is possibly more associated with the process of masculinization. The rhomboideus muscle is very clearly identified with male characteristics in some species such as Bos indicus cattle (Butterfield and May, 1966) and the rhomboideus and "ventral neck muscles" were shown by Brännäng (1971) to be inhibited by castration in cattle.

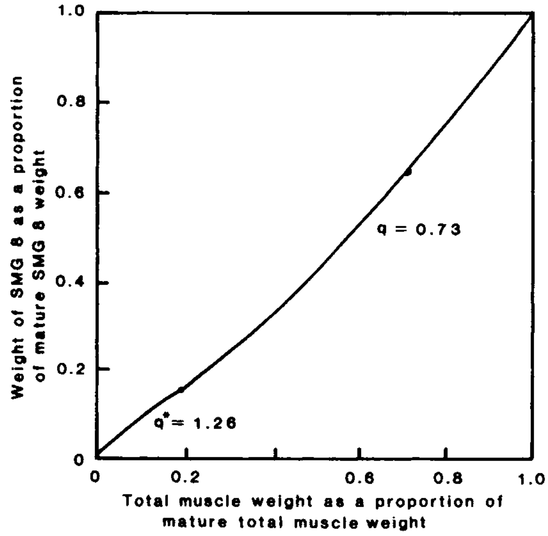


Figure 1.c.15.
The progress to maturity of the weight of the muscles connecting the "neck to the forelimb" (SMG 8) relative to the progress to maturity of total muscle weight.

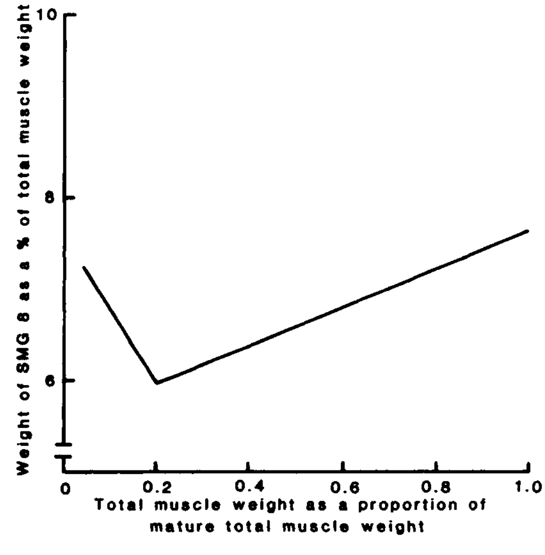
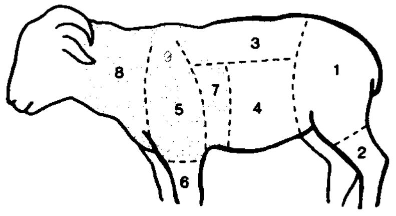


Figure 1.c.16.
Muscles connecting the "neck to the forelimb" (SMG 8) as a percentage of total muscle weight at various stages of maturity of total muscle weight.

The functional influences are therefore widely different for individual muscles in the group resulting in the whole group starting from birth on a low impetus pattern described by a 'q*' value of 1.3 up to about 20% of mature weight and then changing to high impetus described by a 'q' value of 0.7. The total post-natal pattern is therefore one of low/high impetus. The maturing pattern is shown in Figure 1.c.15. and the changes in proportion of total muscle weight in Figure 1.c.16.



Standard Muscle Group 9 – Intrinsic muscles of the neck and thorax

This group of muscles is of particular interest in entire male animals.

Immediately following birth and throughout adolescence, there is nothing unique about the functional demands on the group. Most of the muscles are very small and buried deep in the neck and thorax. It is expected, therefore, on the basis of Butterfield and Berg's (1974) discussion of the relationship between muscle weight and growth impetus, that these muscles would grow relatively slowly throughout life. This expected low impetus growth occurs up to about 20% mature, however the influence of male hormone obviously modifies this pattern as the maturity coefficients from 20% mature until maturity for the whole group and for many of the individual muscles in the Merino ram show that these muscles grow faster than total muscle weight as the animal matures.

The splenius muscle and the complexus muscle which are relatively large, both influence the group markedly, particularly the splenius with a maturity coefficient of about 0.1 from 20% mature to maturity demonstrating a very high impetus growth pattern. The extreme pattern of the splenius demonstrated by Lohse (1973) is in line with Brännäng's (1971) findings in bulls.

The high impetus pattern of this group of muscles as sexual maturity is approached is undoubtedly associated with the need for a very strong neck for fighting which is common in rams. It is not at this stage known if the extreme development of some of these muscles is associated with the need to support the extremely heavy horns of this and some other breeds. This may become clearer when polled breeds have been studied.

There is no doubt, as shown by Brännäng (1971) in bulls, that the splenius muscle is very special in the masculinization process. It has been shown by Tan (1981) in New Zealand that, at birth, the splenius muscle of Jersey bulls contains approximately double the number of muscle fibres compared with the same muscle of females. There is an apparent triggering of the growth of these large number of fibres by testicular hormones after puberty as the crest development caused largely by this muscle is much retarded in castrates. (See Chapter 3.)

The relative growth of the group can be represented in our ram by 'q*' of 1.3 in early postnatal growth followed by 0.6. from around 20% mature. It is therefore a low/high impetus group. The maturing pattern of this group relative to that of total muscle weight is shown in Figure 1.c.17. and the changes in proportion of total muscle weight in Figure 1.c.18.

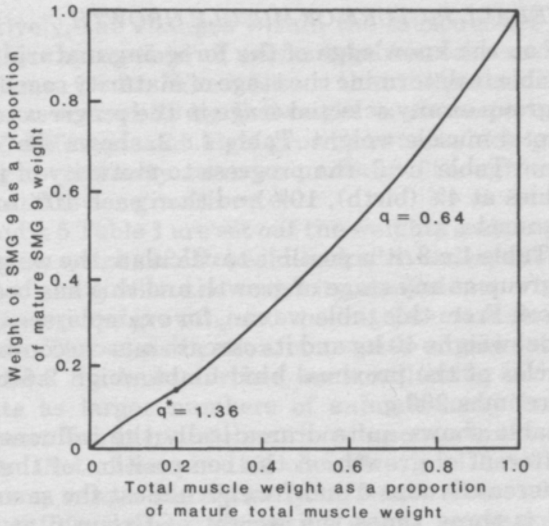


Figure 1.c.17.
The progress to maturity of the weight of the "intrinsic muscles of the neck and thorax" relative (SMG 9) to the progress to maturity of total muscle weight.

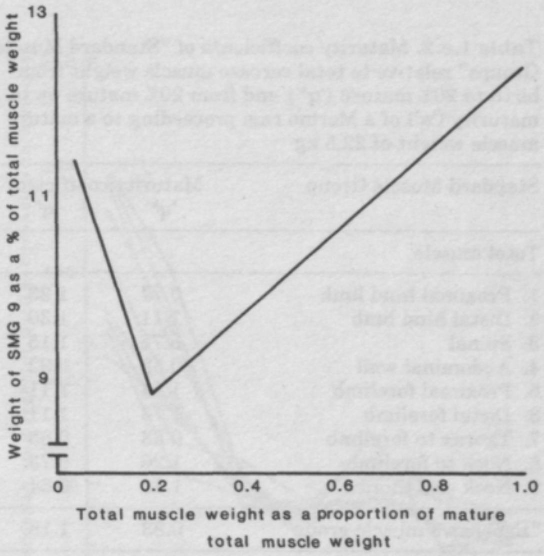
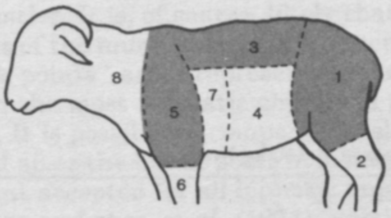


Figure 1.c.18.
Intrinsic muscles of the "neck and thorax" (SMG 9) as a percentage of total muscle weight at various stages of maturity of total muscle weight.



"Expensive muscle group"

This grouping of muscles first proposed for cattle (Butterfield, 1963) brings together approximately half of the musculature in the form of Standard Muscle Groups 1, 3, and 5 (Proximal hind limb, Surrounding spinal column and Proximal forelimb). The maturing pattern of the "Expensive group" reflects those of the two biggest constituent Groups, i.e., 1 and 3, so that from birth to about 20% mature it is represented by a q* of 0.83 and after 20% by a 'q' of 1.2, i.e., high impetus followed by low.

The progress to maturity of the "Expensive muscle group" is shown in Figure 1.c.19. The likely changes in the proportion of this group to total muscle weight are shown in Figure 1.c.20.

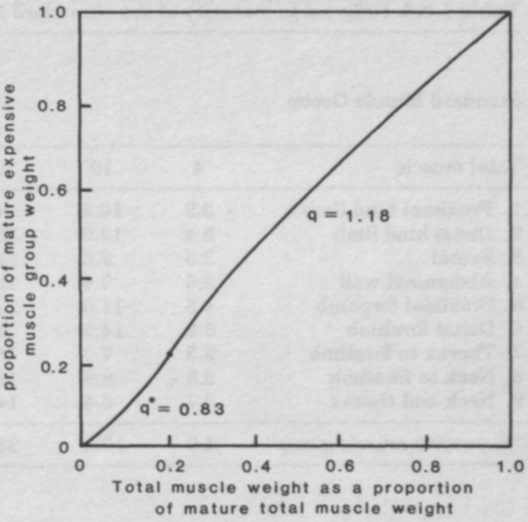


Figure 1.c.19.
The progress to maturity of the weight of the "Expensive" group of muscles ("Standard Muscle Groups" 1, 3 and 5) relative to the progress to maturity of total muscle weight.

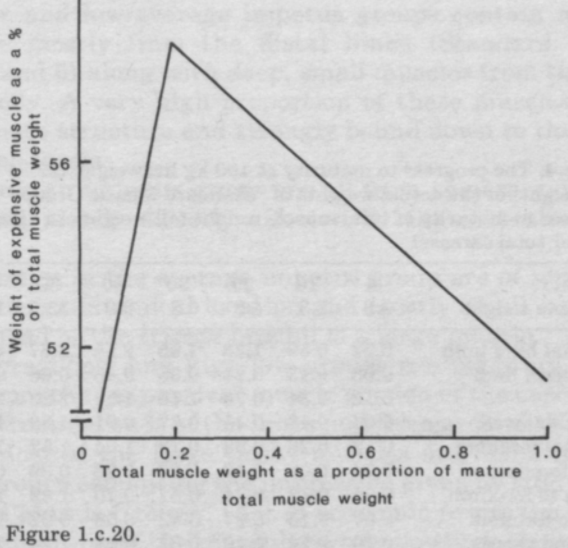


Figure 1.c.20.
The "Expensive group" as a percentage of total muscle weight at various stages of maturity of the total muscle weight.

Table 1.c.2. Maturity coefficients of "Standard Muscle Groups" relative to total carcase muscle weight from birth to 20% mature ('q*') and from 20% mature up to maturity ('q') of a Merino ram proceeding to a mature muscle weight of 22.5 kg

Standard Muscle Group	Maturity coefficient 'q*'	 'q'
Total muscle		
1. Proximal hind limb	0.77	1.23
2. Distal hind limb	1.11	1.30
3. Spinal	0.72	1.15
4. Abdominal wall	0.58	0.92
5. Proximal forelimb	1.14	1.11
6. Distal forelimb	1.73	1.11
7. Thorax to forelimb	0.58	0.85
8. Neck to forelimb	1.26	0.73
9. Neck and thorax	1.36	0.64
"Expensive muscle group"	0.83	1.18

THE OVERALL PICTURE OF MUSCLE GROWTH

Based on the knowledge of the foregoing maturing patterns it is possible to determine the stage of maturity reached by each muscle group at any selected stage in the progress to maturity by the total muscle weight. Table 1.c.2. shows the 'q*' and 'q' values and Table 1.c.3. the progress to maturity of the groups with values at 4% (birth), 10% and then each 10% to maturity of total muscle.

From Table 1.c.3. it is possible to calculate the weight of each muscle group at any stage of growth and this has been done in Table 1.c.4. From this table we can, for example, see that, when the animal weighs 40 kg and its carcase muscle content is 9 kg, the muscles of the proximal hind limbs weigh 2.6 kg and the distal forelimbs 260 g.

This table shows quite dramatically the influence of post-natal differential growth on the composition of the musculature. Whereas Groups 6 and 7 weigh almost the same at birth, Group 7 is three times the weight of Group 6 at maturity. Group 1 is 1.67 times the weight of Group 3 at birth and this is little changed at maturity at 1.60. Total muscle has multiplied in weight from birth to maturity by about 25 times whereas Group 6 has increased only 15 times and Group 9 has increased by 28 times.

Table 1.c.3. Progress to maturity of the "Standard Muscle Groups" of a Merino ram at 100 kg liveweight

Standard Muscle Group	% maturity										Maturity weight (kg)
Total muscle	4	10	20	30	40	50	60	70	80	90	100 = 22.54
1. Proximal hind limb	3.9	10.5	24	35	46	56	66	75	84	92	100 = 5.61
2. Distal hind limb	5.4	13.0	25	36	47	57	67	76	85	93	100 = 0.98
3. Spinal	3.5	9.6	22	33	44	54	64	73	82	91	100 = 3.50
4. Abdominal wall	2.5	7.4	19	28	38	48	58	68	79	89	100 = 2.38
5. Proximal forelimb	4.8	11.6	22	32	43	53	63	72	82	91	100 = 2.43
6. Distal forelimb	6.9	14.9	22	32	43	53	63	72	82	91	100 = 0.62
7. Thorax to forelimb	2.3	7.0	18	27	36	46	56	67	78	89	100 = 1.93
8. Neck to forelimb	3.8	8.9	16	24	34	43	54	64	76	88	100 = 1.72
9. Neck and thorax	3.7	8.4	14	22	31	41	51	62	74	87	100 = 2.80
"Expensive muscle group"	4.0	10.5	23	34	44	55	64	74	83	92	100 = 11.54

Table 1.c.4. The progress to maturity at 100 kg liveweight (22.54 kg total muscle weight) of the actual weights of "Standard Muscle Groups" relative to the progress to matúrity of total muscle weight (all weights in kilograms) (all weights for total carcase)

Liveweight Total muscle weight	4 0.9	10 2.3	20 4.5	30 6.8	40 9.0	60 13.5	80 18.0	100 22.54
1. Proximal hind limb	0.22	0.59	1.33	1.95	2.55	3.67	4.69	5.61
2. Distal hind limb	0.05	0.13	0.24	0.35	0.46	0.66	0.83	0.98
3. Spinal	0.12	0.34	0.78	1.16	1.53	2.23	2.88	3.50
4. Abdominal wall	0.06	0.18	0.45	0.67	0.91	1.38	1.87	2.38
5. Proximal forelimb	0.12	0.28	0.53	0.79	1.04	1.52	1.99	2.43
6. Distal forelimb	0.04	0.09	0.13	0.20	0.26	0.39	0.51	0.62
7. Thorax to forelimb	0.05	0.13	0.34	0.52	0.70	1.09	1.50	1.93
8. Neck to forelimb	0.07	0.15	0.27	0.42	0.58	0.92	1.30	1.72
9. Neck and thorax	0.10	0.24	0.40	0.63	0.88	1.44	2.08	2.80
Scrap	0.09	0.15	0.14	0.23	0.05	0.16	0.3	0.57

Alternatively, the changes within the musculature may be examined by the method of percentage increase and this is shown in Figure 1.c.21. Here it is seen that the period from 4 kg (i.e. birth) to around 20 kg liveweight is characterized by a ferment of different and high growth rates which give way from 20 kg to maturity to more uniform although not completely so, and lower growth rates.

In Appendix 5 Table 1 are set out the weights and proportions of total muscle weight of all the individual muscles, at birth and at maturity, along with the maturity coefficients which describe the patterns of growth, and the impetus classification for each muscle. This classification is a series of estimates from available data; no doubt further work will bring about some refinements as larger numbers of animals move borderline decisions more firmly in the direction chosen or in the opposite direction to that chosen in this classification. Those muscles which have q values significantly different from 1.0 can be regarded confidently as constituting either increasing or decreasing proportions of the total musculature. In Appendix 5 Table 1, and throughout this section, an arbitrary "break point" of 20 kg liveweight (i.e. 5.4 kg total muscle weight), or approximately five times birth weight, has been imposed, although it is realised that this will not be the actual breakpoint for all muscles. It is, of course, likely that the changes of relative impetus of the muscles and groups occur gradually and that the "break points" are a representation of "the abscissa values at which the most dramatic change in growth occurs." (Mellits, 1968). It is possible to compare the slopes of straight lines before and after the break point in a simple manner.

The breakpoint accepted for all biphasic muscles is probably a realistic choice as Lohse *et al.* (1971) classified over 2/3 of their biphasic patterns as having a breakpoint of 4 times birth weight and also as their data did not allow classification beyond 4 times birth weight.

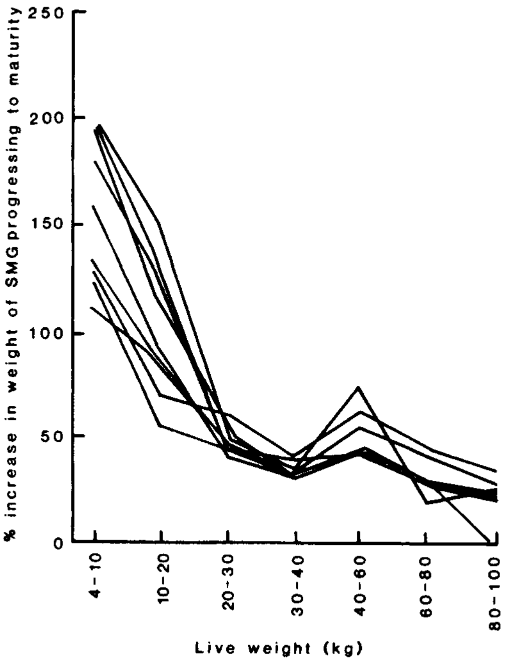


Figure 1.c.21.
The percentage increase of "Standard Muscle Groups" at various stages of liveweight increment during progress to maturity at 100 kg liveweight.

The grouping of muscles into "Standard Muscle Groups", or any other anatomical or regional conglomerates, results in the aggregation of muscles with different maturing patterns so that, although many muscles within a group may show similar patterns, those which are different from their larger neighbours are submerged. In order to overcome this problem Butterfield and Berg (1966a) grouped muscles according to their growth patterns when studying the effect of rate of growth on muscle-weight distribution. In Table 1.c.5. the individual muscles are grouped according to their growth impetus patterns.

The low and low/average impetus groups contain muscles which are mostly from the distal limbs (Standard Muscle Groups 2 and 6) along with deep, small muscles from throughout the body. A very high proportion of these muscles are of multipennate structure and strongly bound down to the skeleton by deep fascia.

The low/high impetus group are all from the cranial end of the animal, mostly directly affected by the masculinization process.

The muscles in the average impetus group are of somewhat heterogenous anatomical location and mostly small, although the long head of the triceps brachii is a large muscle.

The average/low and high/low groups are made up almost entirely from the "expensive" muscle portion of the carcase, i.e. from the proximal ends of the limbs and from around the spinal column. Most of the large fleshy muscles are found in these impetus groups cementing the impression given by study of the "Standard Muscle Groups" that in economic terms the proportional composition of the musculature is slowly declining from about 20% mature.

The average/high muscles are very small and of little conse-

Table 1.c.5. A classification of the growth impetus patterns of individual muscles in a Merino ram. Based on dissection data from Lohse et al. (1971) and Butterfield et al. (1983b)

Impetus group	Standard muscle group	Muscle name
Low	1	m. gemellus
	1	m. quadratus femoris
	1	m. popliteus
	2	m. extensor digitorum lateralis
	2	m. cranial tibial
	2	m. gastrocnemius
	2	m. peroneus longus
	2	m. flexor digitorum superficialis
	3	m. iliocostalis thoracis
	5	m. brachialis
	5	m. triceps brachialis (caput mediale)
	5	m. subscapularis
	6	m. extensor digitorum tertii
	6	m. extensor digitorum lateralis
	6	m. anconeus
Low/Average	1	m. sartorius
	2	m. extensores
	5	m. deltoideus
	6	m. flexor carpi radialis
	6	m. abductor pollicis longus
	6	m. extensor carpi radialis
	6	m. extensor digitorum communis
	6	m. ulnaris lateralis
	6	m. flexor carpi ulnaris
	6	m. flexor digitorum sublimis
	6	m. flexor digitorum profundus
	7	m. pectoralis superficialis
	9	m. multifidis cervicis
	9	m. transversus thoracis
Low/High	5	m. teres minor
	5	m. biceps brachii
	7	m. trapezius thoracis
	8	m. trapezius cervicalis
	8	m. omotransverse
	8	m. brachiocephalic
	9	m. splenius
	9	m. intercostales
	9	m. rectus capitis dorsalis major
	9	m. intertransversarius cervicis
	9	m. longissimus capitis et atlantis
	9	m. obliquus capitis caudalis
	9	m. complexus
Average	2	m. flexor digitorum longus
	3	m. longissimus cervicis
	3	m. quadratus lumborum
	4	m. obliquus externus abdominis
	5	m. triceps brachii (caput longum)
	5	m. infraspinatus
	5	m. teres major
	9	m. scalenus ventralis
	9	m. longus colli
Average/Low	1	m. pectineus
	1	m. rectus femoris
	1	m. obturatorii externus et internus
	1	m. vastus medialis
	1	m. gluteus accessorius
	1	m. iliacus
	2	m. flexor hallucis longus
	3	m. psoas minor
	3	m. multifidus dorsi
	5	m. coracobrachialis
	5	m. supraspinatus
	5	m. triceps brachii (caput laterale)
	7	m. latissimus dorsi
Average/High	3	m. spinalis dorsi
	4	m. cutaneus trunci
	5	m. tensor fascia antibrachii
High	7 & 8	m. serratus ventralis
	7	m. pectoralis profundus
	8	m. rhomboideus
High/Low	1	m. vastus lateralis
	1	m. semitendinosus
	1	m. adductor femoris
	1	m. biceps femoris
	1	m. tensor fascia latae
	1	m. semimembranosus
	1	m. gluteus medius
	3	m. psoas major
	3	m. longissimus thoracis et lumborum
High/Average	1	m. gracilis
	2	m. tibialis caudalis
	4	m. rectus abdominis
	4	m. transversus abdominis
	4	m. obliquus internus abdominis

quence whereas those of high impetus are the large, weight-bearing muscles associated with the support of the trunk between the front legs.

The high/average impetus group contains two small muscles and those large muscles of the abdominal wall whose pattern will be malleable according to the nature of diet.

The grouping together of "Standard Muscle Groups" into impetus groups is shown in Table 1.c.6. The distal limb muscle groups fall together in low impetus classification: the proximal hind limb and the muscles surrounding the spinal column in high/low and the muscles of the pectoral girdle in average/high. Each of the other three groups has a unique pattern.

Consideration of the current knowledge of the growth patterns of muscles should leave us in no doubt as to the importance of the functional influences. Yet we know little of just what degree of function is needed to ensure that each muscle will grow according to the pattern which is so clearly aligned with its function. Function must be only a moderator of the underlying genetic size factor (Taylor, 1985a) which

Table 1.c.6. A classification of growth impetus patterns of "Standard Muscle Groups" in a Merino ram. Based on dissection data of Lohse *et al.* (1971) and Butterfield *et al.* (1983b)

Impetus Classification	"Standard muscle group"	Muscle Group Name
Low	2	Distal hind limb
	6	Distal forelimb
Low/High	9	Intrinsic muscles of neck and thorax
Average/High	7	Muscles connecting thorax to forelimb
	8	Muscles connecting neck to forelimb
High/Low	1	Proximal hind limb
	3	Surrounding spinal column
High/Average	4	Abdominal
Average/Low	5	Proximal forelimb

operates throughout growth. It seems that even the locomotory muscles require only minimal exercise to provoke "normal" growth as calves restrained in small pens showed no difference in muscle-weight distribution at the end of the immediate postnatal phase of muscle growth from other calves which were vigorously exercised (Butterfield, unpublished). On the other hand, there are those muscles whose rapid differential growth is undertaken in anticipation of function rather than in response and this is brought about by testicular hormones, the removal of which has interesting implications for the musculature which will be discussed in Chapter 3.2

d. GROWTH WITHIN THE SKELETON

The contribution of the skeleton to body composition has usually been assessed by weight. Nevertheless, a great deal of the assessment of both live animals and meat carcases is based on an appreciation of the relationship between bone length and body weight. The same amount of meat around a longer bone is generally regarded as inferior, i.e., the animal or carcase is said to be of poorer conformation. Therefore, it is necessary to consider not only bone weight in assessment of meat carcases, but also bone length. The close relationship of the length of any one long bone, such as the tibia or femur, to the general length of skeletal long bones is such that we can use the tibia or femur or radius as an index of general skeletal size (Figure 1.d.1.).

The length of the metacarpus and metatarsus relative to the other long bones of the limbs is of no importance to the assessment of the carcase, however their length has a large influence in the perception of leg length in the live animal and there is little information on the relationship of distal leg length to the total leg length.

Even though bone length is important, it is the weight of bone which is the final concern of people desiring the maximum yield of edible meat from any carcase or cut of sheep meat.

A study of the growth of the weight of bones in the carcase includes all of the skeleton with the exclusion of that of the head, distal limbs and tail. The weight of the bones and their percentage weight of the skeleton are shown in Table 1.d.1. and their maturity coefficients, describing the patterns on which the bone weights mature relative to the whole skeleton, are shown in Table 1.d.2. The total 'q' for the bones of each limb and for the axial skeleton is also shown and indicates that the hind limb grows relatively more slowly followed by the forelimb and the axial skeleton (Figure 1.d.2.). This indicates that the proportion of the skeleton comprised by the limb bones falls progressively as the animal matures (Figure 1.d.3.).

The use of the weight of the bones of a limb as an index of total bone weight will be influenced by the stage of maturity and therefore it is imperative to understand the growth pattern of the weight of any bone before suggesting its use as an index of total bone weight unless the animals being compared are equally mature.

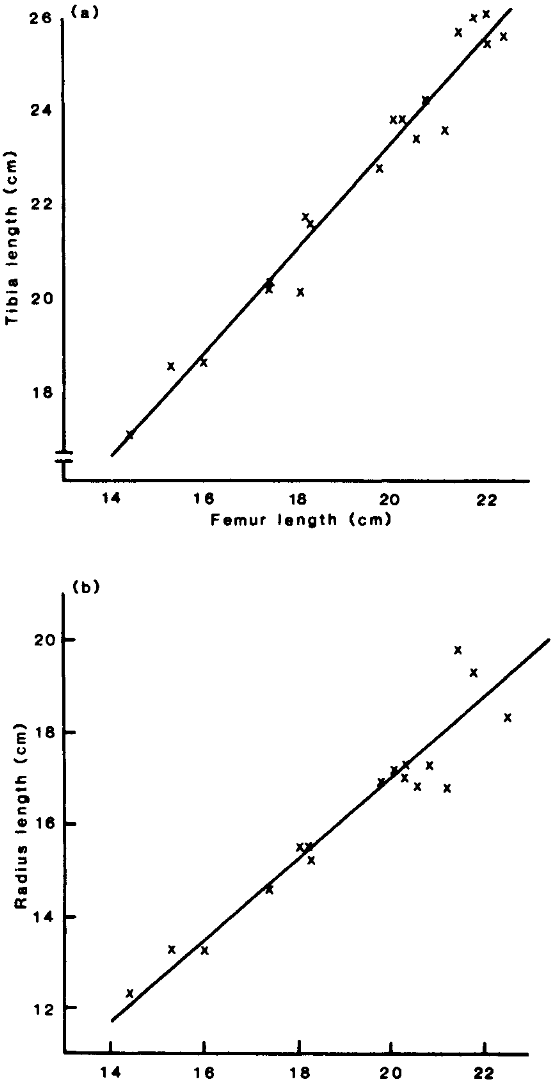


Figure 1.d.1.
Length of tibia (a) and radius (b) relative to femur length of a Merino ram. (Butterfield, unpublished.)

Table 1.d.1. Weights of bones and percentage of total half carcase bone weight of a 100 kg mature ram

	Bone weight (g)	% total bone weight
Hind limb		
Femur	217	7.9
Patella	14	0.5
Tibia	190	6.9
Tarsus	63	2.3
Axial Skeleton		
Pelvis	264	9.6
Lumbar vertebrae	242	8.8
Thoracic vertebrae and ribs	759	27.6
Sternum	159	5.8
Cervical vertebrae	349	12.7
Forelimb		
Scapula	140	5.1
Humerus	176	6.4
Radius and ulna	149	5.4
Carpus	28	1.0
TOTAL CARCASE BONE	2750	100

Table 1.d.2. Maturity coefficients for bone weights relative to total carcase bone from 20 kg to 100 kg liveweight of a Merino ram proceeding to a mature total bone weight of 5.5 kg

	Maturity coefficient 'q'	
Hind limb		
Femur	1.4	
Patella	1.5	1.4
Tibia	1.3	
Tarsus	1.4	
Axial Skeleton		
Pelvis	1.0	
Lumbar vertebrae	0.9	
Thoracic vertebrae and ribs	0.8	0.9
Sternum	1.2	
Cervical vertebrae	0.7	
Forelimb		
Scapula	0.7	
Humerus	1.2	
Radius and ulna	1.2	1.1
Carpus	1.3	

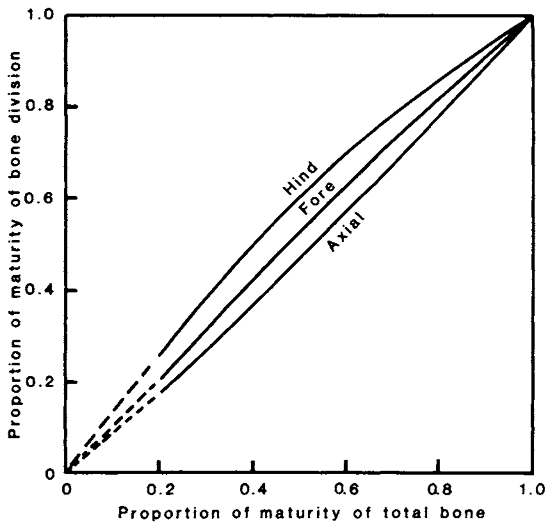


Figure 1.d.2.
Maturing patterns of the three major divisions of the skeleton of a Merino ram.

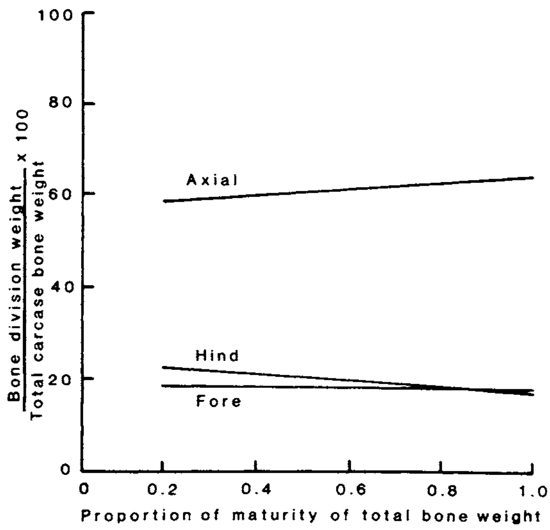


Figure 1.d.3.
Proportion of total skeleton represented by its three major divisions throughout progress to maturity of a Merino ram.

THE GROWTH OF SOME CARCASE BONES

1. *The femur*

The femur declines from about 10.2% of total bone weight when 20% mature to 7.9% at maturity. The decline can be represented by 'q' = 1.4.

Figure 1.d.4. shows the maturing pattern of the femur and Figure 1.d.5. shows the femur weight as a percentage of total carcase bone weight at various stages of maturity. It is of interest that the weight of the femur has a maturing pattern of similar low impetus to that of the muscle mass which enfolds it ("Standard Muscle Group 1") during the greater part of the postnatal progress to maturity.

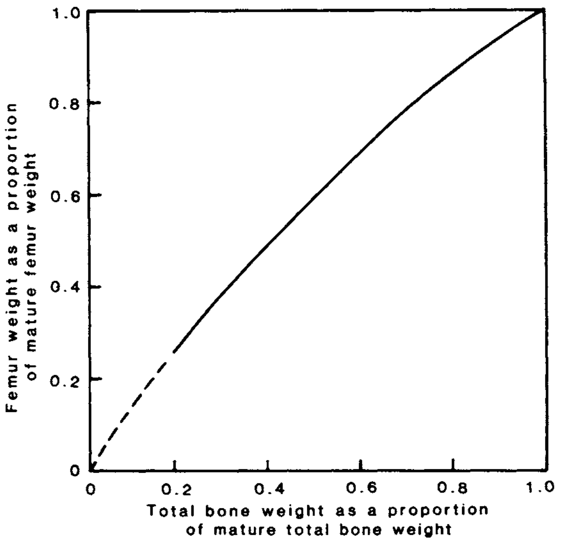


Figure 1.d.4.
The maturing pattern of the weight of the femur relative to total carcase bone weight from birth to maturity of a 100 kg Merino ram.

2. *The tibia*

The tibia declines from about 8.7% of total bone weight when 20% mature to about 6.9% at maturity. The decline can be represented by 'q' = 1.3.

Figure 1.d.6. shows the weight of the tibia as a percentage of total carcase bone weight at various stages of maturity. The low impetus growth of this bone is like that of the femur and in line with that of the surrounding muscle mass. It is tempting to suggest that it is necessary that this should be so. However, the next bone, the scapula, illustrates that there is not necessarily a link between relative bone growth and relative muscle growth of the associated muscles.

3. *The scapula*

The scapula increases from about 4.0% of total carcase bone weight when 20% mature to about 5.1% at maturity. This increased proportional weight by this flat bone varies from all the long bones of the limbs. Also, whereas the major muscles surrounding the scapula (i.e., the supra-and infra-spinatus and subscapularis) are, in total, a declining proportion of total muscle weight, the bone is increasing as a proportion of total bone weight.

The increase can be represented by 'q' = 0.7. Figure 1.d.7. shows the weight of the scapula as a percentage of the total carcase bone weight at various stages of maturity.

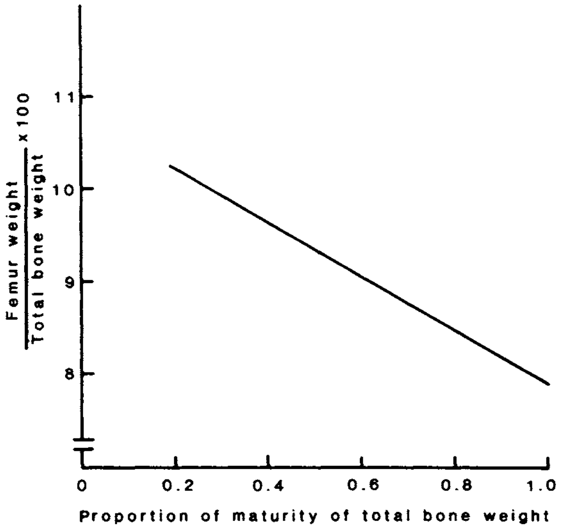


Figure 1.d.5.
The femur weight as a percentage of total carcase bone weight from birth to maturity of a 100 kg Merino ram.

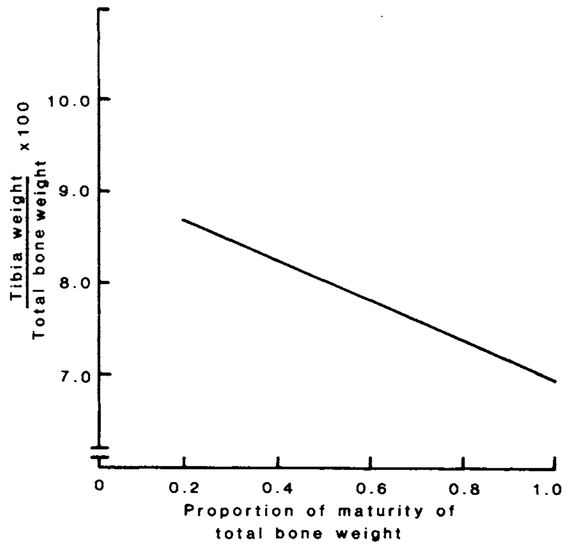


Figure 1.d.6.
The tibia weight as a percentage of total carcase bone weight from birth to maturity of a 100 kg Merino ram.

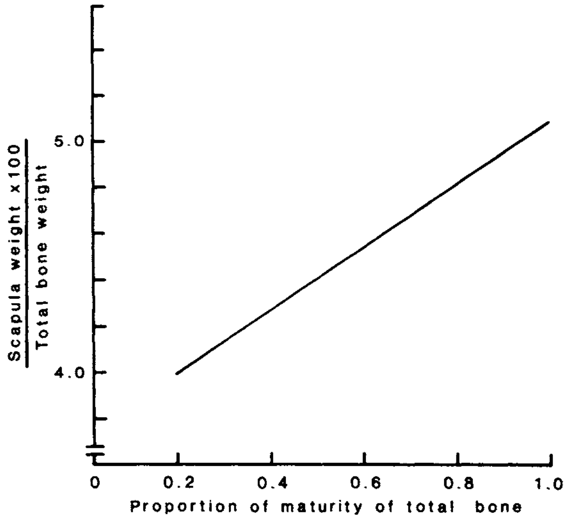


Figure 1.d.7.
The scapular weight as a percentage of the weight of total bone from birth to maturity of a 100 kg Merino ram.

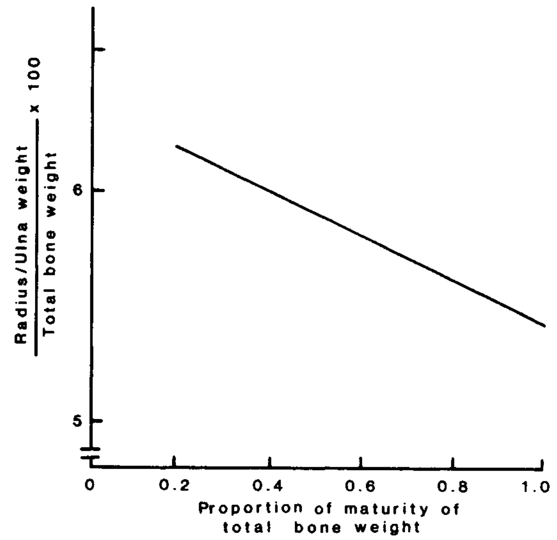


Figure 1.d.8.
The radius and ulna weight as a percentage of total bone weight from birth to maturity of a 100 kg Merino ram.

4. *The radius and ulna*

The weight of the combined radius and ulna declines from about 8.0% of total bone weight when 20% mature to about 5.4% at maturity. The decline can be represented by 'q' = 1.2. Figure 1.d.8. shows the radius and ulna weight as a percentage of total bone weight at various stages of maturity. The proportional decline by the weight of the radius and ulna is in line with the similar decline of the surrounding muscle weight relative to that of total muscle.

5. *Lumbar vertebrae*

The weight of the lumbar vertebrae increases from about 8.0% of total carcase bone when 20% mature to 8.8% at maturity. The increase can be represented by 'q' = 0.9. Figure 1.d.9. shows the weight of the lumbar vertebrae expressed as a percentage of total bone weight at various stages of maturity. The relative increase in proportional bone weight of this group is not mirrored in the growth of the surrounding muscles which mostly decline as a proportion of total muscle weight.

Based on the knowledge of the foregoing maturing patterns it is possible to determine the stage of maturity reached by each bone at any selected stage in the progress to maturity by total bone weight.

Table 1.d.3. shows the values at each 10% to maturity of total bone from 20 to 100%.

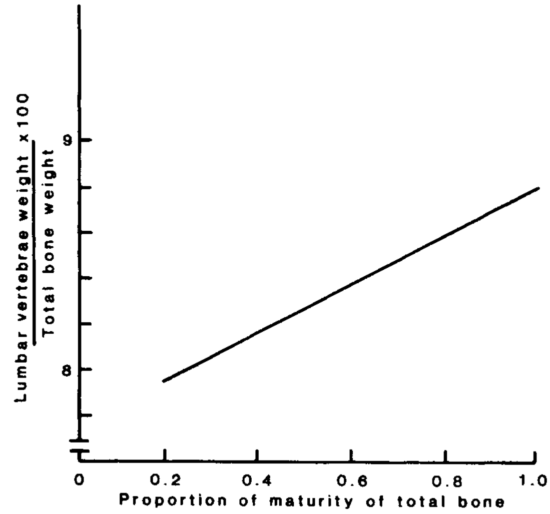


Figure 1.d.9.
The weight of the lumbar vertebrae relative to the weight of total carcase bone from birth to maturity of a 100 kg Merino ram.

Table 1.d.3. The progress to maturity of bone weights of a 100 kg Merino ram relative to the progress to maturity of total bone weight

	Percentage maturity								Mature Weight Grams (½ carcase)
Total bone	20	30	40	50	60	70	80	90	100 = 2750
Hindlimb									
Femur	26	38	49	59	69	78	86	93	100 = 217
Tibia	25	37	48	58	68	77	85	93	100 = 190
Patella	28	40	52	62	72	80	88	94	100 = 14
Tarsus	27	39	50	61	70	79	87	94	100 = 63
Whole limb	26	38	49	59	69	78	86	93	100 = 484
Axial Skeleton									
Pelvis + sacrum	20	31	41	51	61	71	80	90	100 = 264
Lumbar vertebra	18	27	37	47	57	67	78	89	100 = 242
Thoracic vertebra and ribs	17	26	36	46	56	66	77	88	100 = 759
Cervical vertebra	16	25	34	44	54	65	76	88	100 = 349
Sternum	23	33	44	54	64	73	83	91	100 = 159
Whole axial skeleton	18	27	37	47	57	67	78	89	100 = 1773
Forelimb									
Scapula	16	24	34	43	54	64	76	87	100 = 140
Humerus	24	35	46	56	66	75	84	92	100 = 176
Radius and ulna	23	34	44	55	64	74	83	92	100 = 149
Carpus	24	35	46	57	66	75	84	92	100 = 28
Whole limb	21	31	42	52	62	71	81	91	100 = 493

e. GROWTH WITHIN THE BODY FAT

In reviewing fat partitioning and distribution Kempster (1980) highlighted the paucity of information on this subject in meat animals. Of all areas of study of meat animal composition, fat most requires a major input from workers to whom very large numbers of animals and carcases are available. However, this input can be of general use only if the patterns of growth of the various fat depots and partitions emerge. Past comparisons of small numbers of animals of different breeds, of different inherent size, of different fatness, of different nutritional history, of different species, of different sexes and by different people using different dissection techniques and different statistical techniques, have all produced a conglomerate of results from which it is difficult to extract precise guidelines to fat growth. As Kempster stated: "Considerably more detailed information is required before accurate predictions can be made of fat development in practical circumstances for different breeds of cattle, sheep and pigs."

The relative growth of fat has been considered to be a major factor in the determination of the dressing percentage of animals since the work of Lawes and Gilbert in 1859. Callow (1944) reported that Mackenzie and Marshall (1918–19) had concluded in cattle that "... the correspondence between fatness and dressing out percentage was very inexact for most beasts and did not hold at all for fat and very fat cattle."

Callow's data on the relationship between carcase fat as a percentage of liveweight and dressing percentage is reproduced here in the figure from his paper (Figure 1.e.1.). There is no doubt that there was a relationship between the two values, however, it may be that this was coincidental rather than causal and this can be resolved only by knowledge of the relative growth of the carcase versus non-carcase fat. It may be that the relative growth of the internal body organs is a major factor in the determination of dressing percentage and the situation is not as Callow suggested "... it is clear that the dressing-out percentage of steers and heifers is closely related to the stage of fatness which the animal has reached, and that any other factors can affect dressing-out percentage to a minor extent."

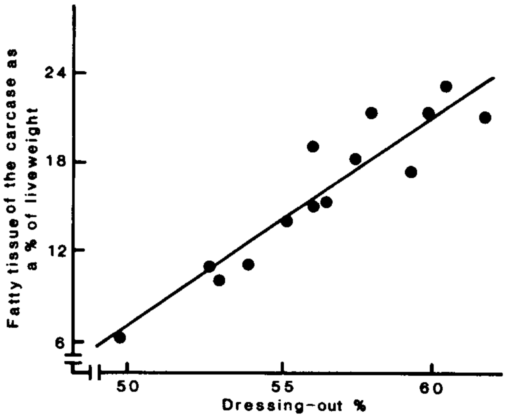


Figure 1.e.1.
The relation between dressing-out percentage and degree of fatness in cattle. (Adapted from Callow, 1944.)

A problem in gaining a clear picture of relative fat growth is that the definition of the carcase is often different in that the inclusion, or omission, of kidney and pelvic fat influences the balance of carcase and non-carcase fat. All of the dissectible fat in the body is considered in this section and the weights of the partitions and the proportions which they comprise of total body fat in mature rams are set out in Table 1.e.1. The composition of the partitions of fat are set out in Appendix 1 p. 129). A little over sixty percent of the fat is found in the two carcase partitions and this is almost evenly divided between the subcutaneous and intermuscular fat with a slightly higher proportion in the intermuscular partition. Under some trade conditions the kidney plus pelvic fat and scrotal fat are also traded with the carcase so that about 76% of total body dissectible fat then enters the retail trade.

Table 1.e.1. The weights and proportions of the total body fat comprised by the various fat partitions in a mature 100 kg Merino ram

Partition	Weight (kg)		% of total body fat	
Total carcase fat	21.8		62	
Subcutaneous		10.3		29
Intermuscular		11.5		33
Total non-carcase fat	13.6		38	
Kidney plus pelvic fat		4.0		11
Omental fat		5.5		16
Mesenteric fat		3.0		8
Scrotal fat		1.1		3
Total body fat		35.4		100

Nevertheless, there are considerable amounts of fat from within the body cavity which do not become part of the commercial carcase; the omental fat and mesenteric fat together constitute 24% of total fat weight, and so to understand the principles involved in the growth of all the fat partitions we need to take account of these quite large deposits.

Warren (1974), in pasture-reared Merinos, showed that there were dramatic changes in the immediate postnatal period in the proportions of the total fat located in the subcutaneous, intermuscular and internal partitions. Within 18 days of birth the subcutaneous partition changed from 5% to 30% of the total dissectible fat; intermuscular fat fell from 49 to 40% and internal fat fell from 46% to 30%. For the remaining 1000 days of Warren's study the proportions within the fat partitions varied little. It is apparent, therefore, that any growth coefficients calculated from birth will be very different from those calculated over later periods of growth. As Warren's sheep were grown at pasture and did not achieve high levels of fat, we cannot translate his results directly to our *ad lib* fed ram.

The results of Vezinhet and Prud'hon (1975) are similar to those of Warren in that their lambs "lack subcutaneous fat, at birth, ..." and that this depot reaches 30% of total body fat during the first 25 days of life. They also showed that intermuscular fat remained almost constant as a proportion of total body fat throughout growth. Vezinhet and Prud'hon made the important statement that "After the period required for the establishment of the different fat deposits, we could observe in lambs, . . . a relative growth which tends to become isometric with regard to the total fat deposits."

Using the values in Table 1.e.1. and additional data from immature animals it is possible to calculate the maturity coefficients of the various fat partitions and these are presented in Table 1.e.2.

Table 1.e.2. The maturity coefficients of the fat partitions relative to total body fat of a Merino ram (Based on data from Thompson 1983)

Partition	Maturity coefficient 'q'	Difference from 1.0
Total carcase fat	1.16	N.S.
Subcutaneous	1.05	N.S.
Intermuscular	1.26	Greater
Total non-carcase fat	0.77	N.S.
Kidney plus channel fat	0.75	N.S.
Omental fat	0.60	Less
Scrotal fat	1.23	N.S.
Total body fat	1.00	

The coefficients of the partitions vary little from 1.0 except for the intermuscular, kidney plus pelvic, omental and scrotal in most of which the variation is of the order of only 0.2 or 0.3.

An important influence on dressing percentage in cattle apparently comes from total carcase versus non-carcase fat (Geay, 1978). Butler-Hogg and Johnsson (1986), in Hampshire Down x Mule (Blue-faced Leicester x Swaledale) ewes showed an increase from 693 to 739 g/kg of total fat in the carcase (intermuscular plus subcutaneous) from 4 to 36 weeks of age. Yet, it is clear from the available data on Merino rams that increasing fat does not increase dressing percentage as carcase fat with a 'q' of 1.16 is declining as a proportion of total fat and therefore having a negative influence on dressing percentage.

Had kidney plus pelvic fat been included in the Merino carcase the 'q' for carcase fat would have been 1.08 and the changes in proportion of fat in the carcase and extra-carcase partitions would have been negligible. This calculation is an example of the use of the 'q' coefficient in simple problems of carcase composition:

SC + IM :	'q' = 1.16,	% total fat = 62
Kidney + pelvic fat :	'q' = 0.75,	% total fat = 11

$$\begin{array}{l} 1.16 \times 62 = 71.82 \\ 0.75 \times \underline{11} = \underline{\ 8.25} \\ \quad\quad 73 \quad 79.07 \end{array}$$

79.07 divided by 73 = **1.08** = 'q' for (S.C. + I.M.) + (Kidney + pelvic)

It seems that the causal relationship between increasing fat and increasing dressing percentage, first suggested for cattle by Lawes and Gilbert (1859): questioned by Mackenzie and Marshall (1918-1919) and supported by Callow (1944) may not be true for Merino sheep and particularly when very fat. There is probably a large species difference as Geay (1978) gave the non-carcase fat components of cattle as only 20-25% whereas Thompson's sheep (1983) had 38% in the non-carcase depots.

We draw on the study of Thompson (1983) to provide some information on the relative growth of the two major divisions of the carcase fat, namely subcutaneous and intermuscular. In his study, Thompson showed that subcutaneous fat had a 'q' of 1.05 and intermuscular of 1.26 in Merino rams under *ad lib* feeding and this is in line with the work of Thompson, Atkins and Gilmour (1979) and of Jones (1982) who studied fat partitioning within four major wholesale cuts (i.e., the carcase minus neck, breast and flank) in lambs from 24 to 62 kg liveweight and showed that relative to total fat in the cuts, subcutaneous fat had the highest 'b' value of 1.23 followed by kidney fat (1.05) body cavity (0.83) and intermuscular (0.74). (N.B. "Body cavity" should not be confused with "non-carcase" fat and would be part of intermuscular fat in our technique.)

Butler-Hogg (1984) using Southdown and Clun sheep obtained significantly different growth coefficients for the different fat partitions and ranked the partitions from lowest to highest growth impetus as: pericardial; intermuscular; perirenal-retroperitoneal; mesenteric; subcutaneous; and omental. This order is similar to the ranking in Butterfield and Thompson's Merino sheep except that they did not find that the growth impetus of the partitions were significantly different.

An important observation in the study of Butler-Hogg is his reference to the possible influence of events around weaning on the proportions of fat within each partition due to variable physiological activity.

The current situation of a hazy story of fat partitioning after many years of study in many species, highlights the need for a reappraisal of methods as suggested by Berg and Butterfield (1976). It maybe that a new approach is needed and it is suggested that the minor depots could be ignored as separate entities by incorporating them into the major partitions. Therefore, it is suggested that carcase fat versus non-carcase fat and subcutaneous versus intermuscular may be all that is needed to reveal all that is necessary of the relative growth of fat for commercial and most genetic purposes.

The variability of fat makes the detection of significant differences more difficult than for other body tissues. This variability may result from a lack of anatomical discreteness which is a far cry from the units of the musculature and the skeleton. From current knowledge we can conclude that relative to the growth of the total dissectible fat of Merino rams on high plane nutrition, the partitions grow on the following impetus patterns from about 20% mature to maturity:

Intermuscular: Low;
Subcutaneous: Average;
Carcase fat: Low;
Non-carcase fat: High.

The proportional changes are represented in Figures 1.e.2. and 1.e.3.; first with all partitions as percentages of total body fat throughout progress to maturity of total body fat and then carcase versus non-carcase on the same basis; and then subcutaneous versus intermuscular relative to total carcase fat.

Warren's (1974) work suggested that these patterns might extend from about 10% of maturity. However, there is a great need for further study of the early growth of fat.

f. GROWTH OF BODY ORGANS

"It is plain, then, that there is no simple and direct relation, holding good throughout life, between the size of the body and its organs; and the ratio of magnitude tends to change not only as the individual grows, but also with change of bodily size from one individual, one race, one species to another." D'arcy Thompson (1942).

Body organs do not form part of the commercial carcase and do not provide a direct clearly-identifiable financial return to the sheep producer. Hence, with the exception of the New Zealand study of Kirton, Fourie and Jury (1972) and our own (Butterfield, Zamora, James, Thompson and Reddacliff, 1983c; Butterfield, Zamora, Thompson, Reddacliff and Griffiths, 1984a), little attention has been given to their growth in modern sheep studies. Nevertheless, as stated by Kirton *et al.*, the knowledge of the likely yields of all the by-products of the meat industry is essential in the efficient planning of processing plants. Doornenbal and Tong (1981) highlighted the need for a knowledge of the relationship of the weights of body organs to the weight of the body in nutritional, biological and

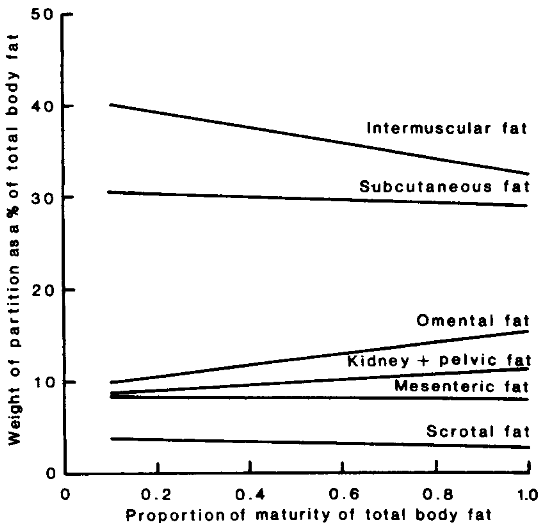


Figure 1.e.2.
The proportion of total body fat comprised by each fat partition throughout the progress to maturity of total body fat in a Merino ram. (Based on Thompson, 1983.)

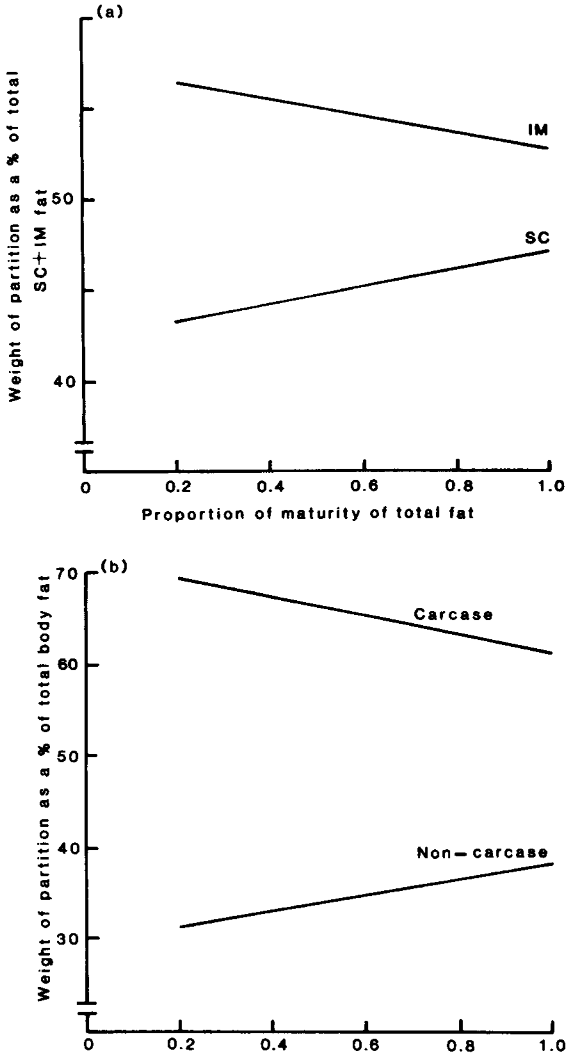


Figure 1.e.3.
Changing proportions within the fat partitions of a Merino ram within the carcase (a); within the whole animal (b). IM = Intermuscular; Sc = Subcutaneous (Based on Thompson, 1983.)

medical studies. Although this chapter and indeed this book does not dwell on the effects of body weight loss, it is well to note that certain organs are markedly affected by general body weight loss. Alaku and Moruppa (1983) demonstrated how the liver and skin were severely depleted in times of poor nutrition in goats. The skin dropping from about 7% of body weight to about 5% and the liver from 5.6% to 2.8%.

A proper understanding of the yield of carcase to non-carcase tissues can be achieved only if the changing proportions within the body tissues, including visceral organs, is known. There is a continuing search for non-carcase structures which can be readily separated and weighed at slaughter for use as indices of the weights of carcase structures (Kraybill, Hiner and Farnworth, 1954; Kirton, 1957; Johnson, 1979). For example, at various times high hopes have been held that the liver could be shown to have some special relationship with muscle weight, and this was investigated by Kraybill *et al.* (1954) who showed that it had only similar predictive value to other internal organs. The heart has been shown to have a close relationship to total body weight across many species (Brody 1945; Prothero 1979) when comparisons of mature animals are made.

The weights of the body organs in our 100 kg mature ram are set out in Table 1.f.1. and provide the basis from which the maturing patterns of the body organs can be developed in association with data from immature animals. The maturity coefficients are tabulated in Table 1.f.2. and provide the basis of the maturing patterns shown in Table 1.f.3.

Only some of the major organs will be discussed but should the reader wish to extend the information on other organs to provide a guide to their size or proportion at any stage this can be simply done by calculation from the data in Tables 1.f.1. and 1.f.3.

Table 1.f.1. The weights and percentages of mature liveweight of the body organs of a mature 100 kg Merino ram

Organs	Weight (g)	Percentage of liveweight
Oesophagus	75	0.075
Rumino-reticulum	910	0.91
Omasum	100	0.10
Abomasum	220	0.22
Small intestine	470	0.47
Large intestine	490	0.49
Total Alimentary Tract	2,265	2.27
Rumino-reticular content	4,240	4.24
Omasum content	145	0.14
Abomasum content	340	0.34
Small intestine content	570	0.57
Large intestine content	810	0.81
Total Alimentary Tract Content	6,105	6.10
Liver	1,010	1.01
Kidneys	190	0.19
Spleen	110	0.11
Heart	290	0.29
Trachea	70	0.07
Lungs	470	0.47
Thyroid	20	0.02
Pancreas	60	0.06
Total Major Internal Organs	2,220	2.22
Brain	100	0.10
Eyes	30	0.03
Total Brain and Eyes	130	0.13
Blood	3,420	3.42
Head	6,230	6.23
Hide	8,980	8.98
Distal limbs	1,490	1.49
Total Miscellaneous	20,120	20.12
Shorn Empty Liveweight	93,900	93.90
Shorn Full Liveweight	100,000	100.00

Table 1.f.2. The maturity coefficients and impetus classification of the body organs from 20% mature to maturity relative to total body weight of a Merino ram

Organs	Maturity coefficient 'q'	Impetus classification
Oesophagus	1.8	Low
Ruminoreticulum	2.3	Low
Omasum	3.4	Low
Abomasum	2.1	Low
Small intestine	5.7	Low
Large intestine	3.2	Low
Total Alimentary Tract	3.2	Low
Ruminoreticulum content	2.1	Low
Omasum content	2.9	Low
Abomasum	1.7	Low
Small intestine content	4.4	Low
Large intestine content	3.4	Low
Total Alimentary Tract Content	2.5	Low
Liver	2.5	Low
Kidneys	2.0	Low
Spleen	1.4	Low
Heart	1.8	Low
Trachea	2.5	Low
Lungs	2.3	Low
Thyroid	2.2	Low
Pancreas	2.1	Low
Total Major Internal Organs	2.3	Low
Brain	–	Very low
Eyes	–	Very low
Blood	1.6	Low
Head	1.3	Low
Hide	1.2	Average
Distal limbs	1.9	Low
Shorn empty body weight (live)	0.9	

Table 1.f.3. Progress to maturity of body organs in a 100 kg mature Merino ram

	Percent maturity									
Shorn full liveweight	20	30	40	50	60	70	80	90	100 =	kg 100
Alimentary tract										
Oesophagus	33	47	60	70	80	87	93	97	100 =	0.08
Ruminoreticulum	41	58	72	83	92	98	101	102	100 =	0.91
Omasum	58	80	97	109	117	120	119	112	100 =	0.10
Abomasum	38	54	67	78	87	94	98	100	100 =	0.22
Small intestine	96	129	153	168	173	169	156	132	100 =	0.47
Large intestine	56	77	94	106	114	117	116	110	100 =	0.49
Total	55	76	93	105	113	116	115	110	100 =	2.27
Alimentary tract contents										
Ruminoreticulum contents	38	54	67	78	87	94	98	100	100 =	4.24
Omasum contents	50	69	85	97	105	109	110	107	100 =	0.14
Abomasum contents	32	46	58	68	78	86	92	97	100 =	0.34
Small intestine contents	74	100	120	134	140	140	134	120	100 =	0.57
Large intestine contents	59	81	98	111	118	121	119	112	100 =	0.81
Total	44	61	76	87	96	101	104	103	100 =	6.10
Other major internal organs										
Liver	44	61	75	87	95	101	104	103	100 =	1.01
Kidneys	35	50	63	74	83	90	95	99	100 =	0.19
Spleen	26	38	50	60	70	78	86	94	100 =	0.11
Heart	33	47	60	71	80	87	93	97	100 =	0.29
Trachea	44	62	76	88	96	102	104	104	100 =	0.07
Lungs	41	58	72	83	92	98	101	102	100 =	0.47
Thyroid	40	55	69	80	89	96	100	101	100 =	0.02
Pancreas	37	52	66	77	86	92	97	100	100 =	0.06
Total	40	56	70	81	90	96	100	101	100 =	2.22
Central nervous system										
Brain	80	82	85	87	90	92	95	97	100 =	0.10
Eyes	68	72	76	80	84	88	92	96	100 =	0.03
Total	77	80	83	85	88	91	94	97	100 =	0.13
Miscellaneous components										
Blood	29	42	53	64	73	82	89	95	100 =	3.42
Head	25	35	47	57	67	75	84	93	100 =	6.23
Penis + bladder	23	34	44	54	64	74	83	92	100 =	0.09
Hide	22	33	44	54	64	73	82	91	100 =	8.98
Distal limbs	34	48	61	71	81	88	94	98	100 =	1.49
Total	25	37	48	58	68	77	85	93	100 =	20.21
Shorn empty liveweight	18	28	38	47	58	68	78	89	100 =	93.90

The Heart

The constancy of heart weight as a proportion of liveweight in mature animals has been reported across a wide range of species (Brody, 1945; Prothero, 1979). In a mature Merino ram it represents approximately 0.3% of liveweight and, because of its vital role in life, it is an early developing structure as indicated by its maturity coefficient of 1.8. This is represented in Figure 1.f.1.

Consistent with its maturing pattern the proportion of liveweight represented by heart weight falls steadily as the animal grows (Figure 1.f.2.)

The heart can be taken as representative of that group of vital organs which are essential to life, and so the following, which are all early developing, could be represented by similar but slightly different patterns of changing proportions within the body: liver, kidney, spleen, trachea and lungs and pancreas. The study of Butterfield *et al.* (1983c) left the thyroid in doubt with different 'q' values for each of two strains of sheep.

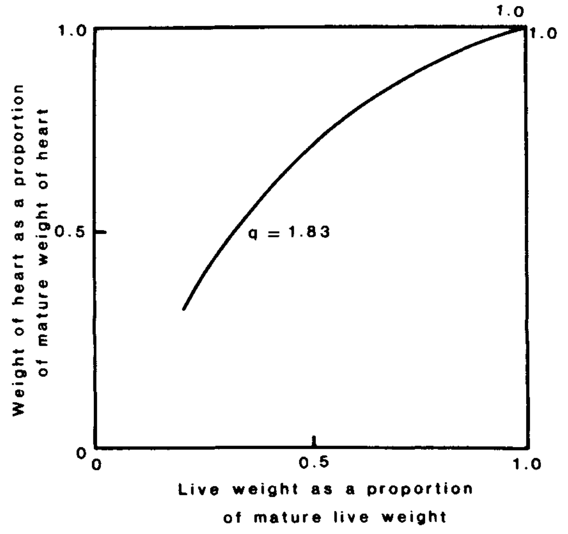


Figure 1.f.1.
Maturing pattern of the heart of a Merino ram.

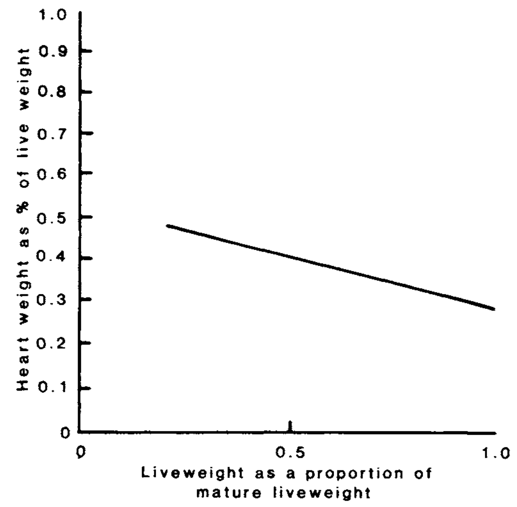


Figure 1.f.2.
The weight of the heart as a proportion of liveweight of a Merino ram.

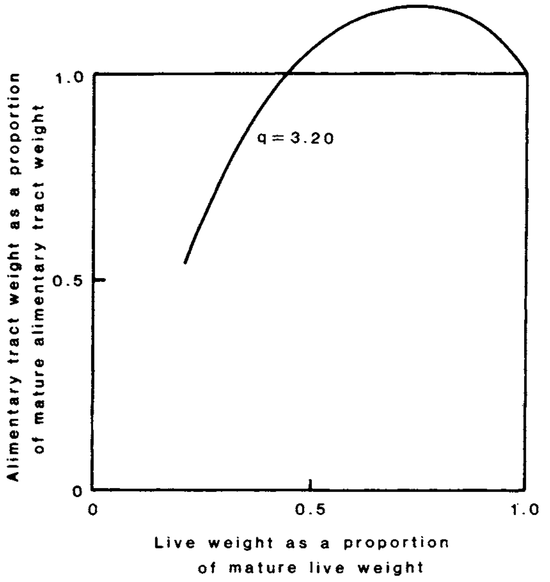


Figure 1.f.3.
Progress of the alimentary tract weight to maturity of a Merino ram fed *ad lib* on highly nutritious food.

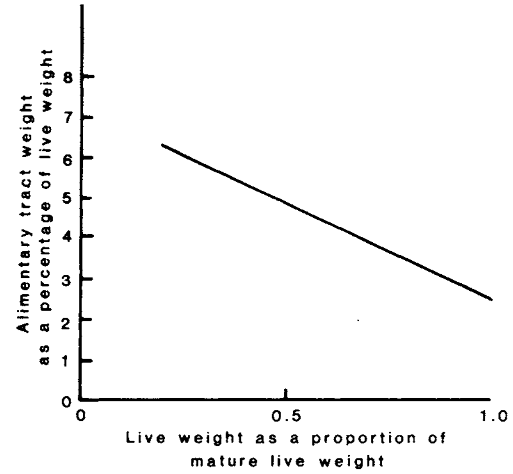


Figure 1.f.4.
The weight of the alimentary tract as a proportion of liveweight of a Merino ram fed *ad lib* on highly nutritious food.

The Alimentary Tract

The empty alimentary tract represents approximately 2.3% of the weight of the mature ram and developes early (q = 3.2). This is represented in Figure 1.f.3. and shows that the weight of the tract is greater during progress to maturity than in the mature animal.

From this maturing pattern can be derived the proportion of liveweight represented by the alimentary tract throughout life (Figure 1.f.4.)

All sections of the alimentary tract follow somewhat similar patterns to the total tract and reference to Table 1.f.3. allows comparison of the maturing patterns of the various sections. The most extreme pattern is that of the small intestine and this is shown in Figure 1.f.5. and 1.f.6.

The weight changes in intestinal contents align with the changes in the weight of the alimentary tract itself and hence have patterns which are broadly similar, although on average somewhat less extreme. The pattern for total alimentary tract contents is represented in Figures 1.f.7. and 1.f.8.

The knowledge that the small intestine weight increases rapidly after birth and then falls dates back to Hammond (1932) and Wallace (1948) who claimed that the absolute weight fell in the later stages of growth. Palsson and Verges (1952) were a little tentative with their claim that: "We are inclined to believe that the absolute weight has actually declined."

Palsson and Verges claimed a relationship between the growth of the thymus and that of the small intestine in sheep, however Wilson (1958) could not demonstrate a statistical relationship between the weights of the two organs in goats.

There is little doubt that the weight of visceral organs, particularly the liver and gastrointestinal tract, vary in response to nutritional experience, and liver and gut weights are highly correlated to feed intake (Ferrell and Jenkins, 1985).

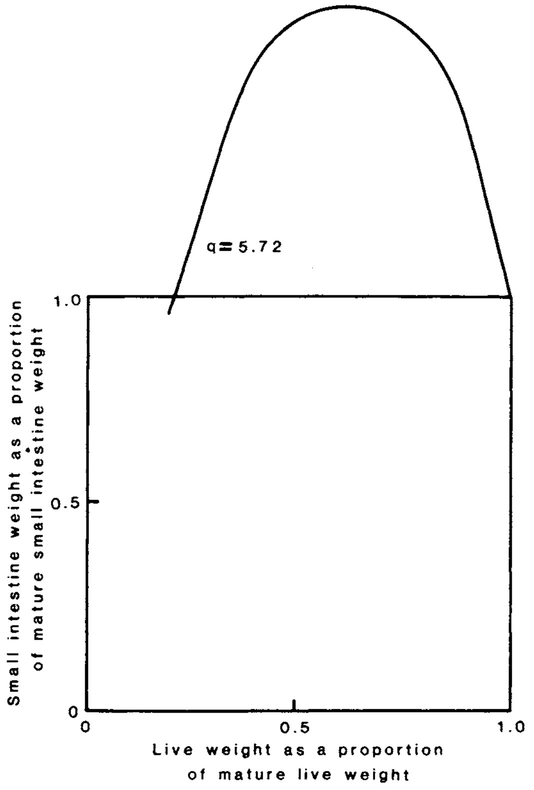


Figure 1.f.5.
Progress of the small intestine to maturity of a Merino ram fed *ad lib* on highly nutritious food.

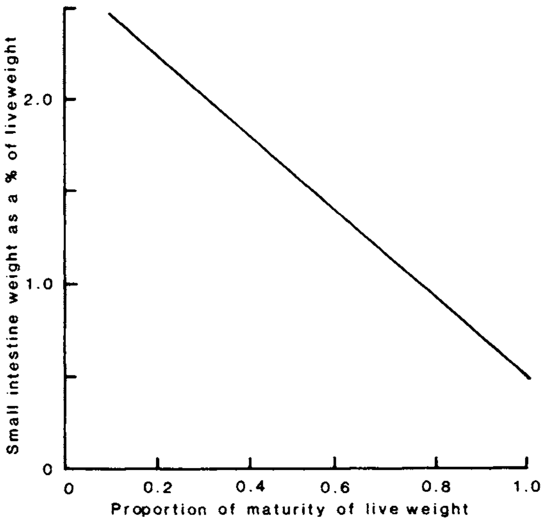


Figure 1.f.6.
The weight of the small intestine as a proportion of liveweight of a Merino ram fed *ad lib* on a highly nutritious food.

The Spleen

Wilson (1958) concluded by comparison with data of Palsson and Verges (1952) that there was a species difference in the relationship of the spleen and body weight growth between sheep and goats. He classified the spleen as late developing in the goat. Reference to Tables 1.f.2. and 3 show that in Merinos the spleen with a 'q' of 1.4 develops earlier than total body weight and declines as a proportion thereof.

The Liver

Baldwin and Black (1979) indicated an extremely variable relationship between liver weight and body weight, particularly at higher body weights, and it was shown by Wilson (1958) that data for liver weights of goats were "very variable". Wilson drew attention to similar variations in liver weight in the appendix tables recording data for McMeekan's pigs, Palsson's lambs and Wilson's chickens.

Figure 1.f.9. shows a simple plot of liver weights for Merinos and also shows the values for hearts in the same sheep for comparison. These plots show that the liver weights remained close to expected values up to about 80 kg liveweight in Merinos before scattering widely. Ferrell and Jenkins (1985) drew attention to the relationship of liver weight to feed intake along with a similar relationship of the gut to feed intake. However, the variability of liver weights in more mature sheep seems to be unrelated to variation in feed intake in *ad lib* fed sheep.

The Hide

The hide matures on approximately the same pattern as liveweight. If the hide was simply a covering for the body, it would be expected to be related to liveweight raised to the power 2/3 (Brody 1945) and would therefore be early developing relative to liveweight. That hide weight has an average impetus pattern would suggest that, in addition to an increase in surface area, other factors, such as an increase in hide thickness, must contribute substantially to increases in hide weight and this agrees with Gaili and Nour (1980) who showed that in Kenana cattle the hide as a proportion of body weight was constant from 100 to 400 kg liveweight. Alternatively, Hammond (1932) and Kirton, Fourie and Jury (1972) have both reported that the hide is an early-developing component of the body. However, it is difficult to compare their results with the

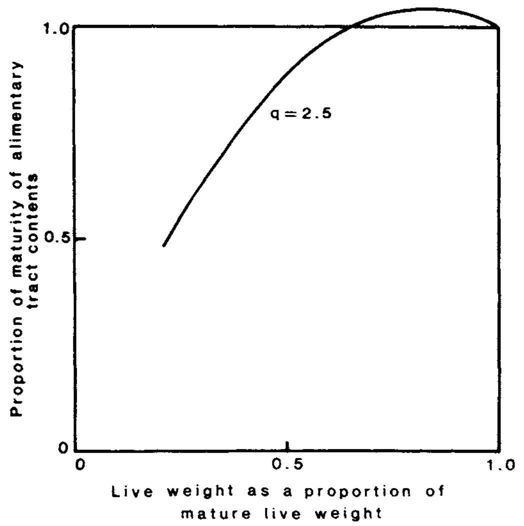


Figure 1.f.7.
Progress of the alimentary tract contents to maturity of a Merino ram fed *ad lib* on a highly nutritious food.

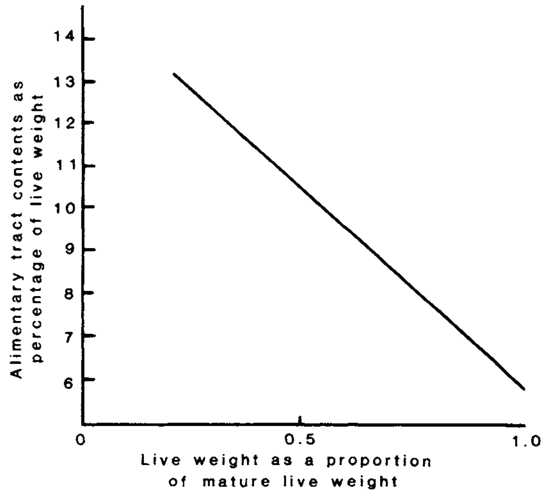


Figure 1.f.8.
The weight of alimentary tract contents as a proportion of liveweight of a Merino ram fed *ad lib* on a highly nutritious food.

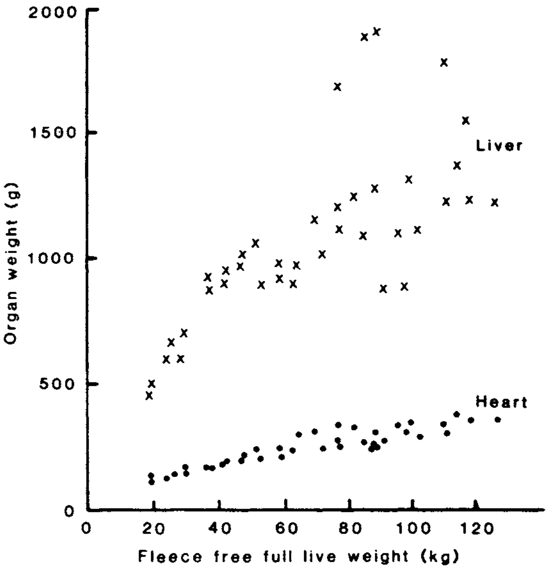


Figure 1.f.9.
The weight of the liver and heart relative to liveweight of Merino rams. (Butterfield, unpublished.)

present study as Hammond included the feet in the pelt weight and, as shown in this study, the feet were early developing, and Kirton *et al.* included the immediate postnatal period of growth for which we do not have data.

Wilson (1958) reported that the hide on goats falls from 12.4% at birth to 7.2% at 30 lb liveweight, which would result from very low impetus growth.

Although Merino data is highly variable, a 'q' of 1.15 is suggested. It seems likely that the true picture is one of somewhat lower growth impetus than the whole animal and that this may be a variable characteristic among breeds. However, it seems that skin weight may be a relatively constant proportion of body weight at the same degree of maturity in many animals as Grand (1983b) showed in six marsupial genera in Guyana.

Thymus

We have no Merino data, therefore the best estimation must come from other sheep breeds. Wallace (1948) found that the thymus had an increasing growth rate during foetal life, reaching its largest percentage of body weight at birth and continuing to be active up to 9 weeks, after which the growth rate of the neck thymus fell while the heart thymus growth rate continued to gain slightly up to 11 weeks and then declined.

It is presumed that the picture is similar in Merinos.

Miscellaneous Components

In this category we place structures such as head, brain, eyes, blood, distal limbs, etc., and in general the structures are early developing.

Brain and Eyes

Compared with other body structures the growth of brain and eyes relative to liveweight is highlighted by the fact that they, along with testes, are the only tissues the growth patterns of which cannot be reasonably explained by the use of a constrained quadratic equation (Butterfield *et al.*, 1983c). Butterfield et. al. found it necessary to use a linear regression constrained to maturity to enable them to describe the maturing patterns of the brain and eyes from 20% of the mature weight of the animal to maturity. This is shown for the brain in Figure 1.f.10.

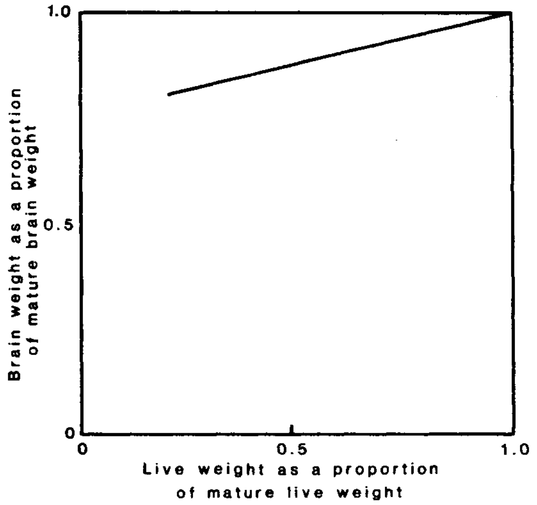


Figure 1.f.10.
Progress of the weight of the brain of a Merino ram to maturity.

The declining percentage which the brain comprises of liveweight is shown in Figure 1.f.11. Fourie (1965) plotted brain weight as a percentage of empty liveweight in sheep and this is shown in Figure 1.f.12., and is quite different from the brain changes in the human as presented by D'arcy Thompson (1942) (Figure 1.f.13.).

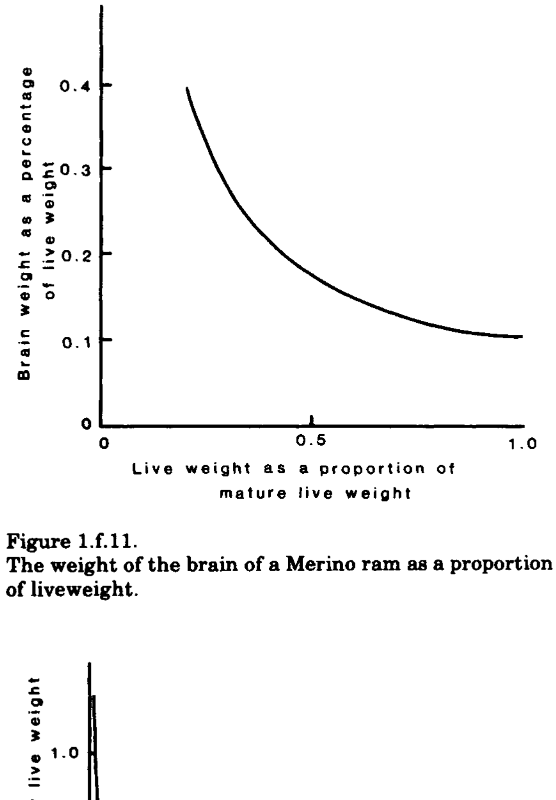


Figure 1.f.11.
The weight of the brain of a Merino ram as a proportion of liveweight.

The relationship of the brain to total body weight is markedly different across species and D'arcy Thompson (1942) illustrated this as follows: "Man and gorilla are born with brains much of a size; but the gorilla's brain stops growing very soon indeed, while the child's has four years of steady increase. The child's brain grows quicker than the gorilla's, but the great ape's body grows much quicker than the child's; at four years old the young gorilla has reached about 80 per cent. of his bodily stature, and the child's brain has reached about 80 per cent. of its full size." Therefore, if body weight is used as a basis for description of maturing patterns of brain weight, these patterns will be very different across the spectrum of mammals. However, the contrasts within the domestic species will not approach the starkness of man/gorilla comparisons.

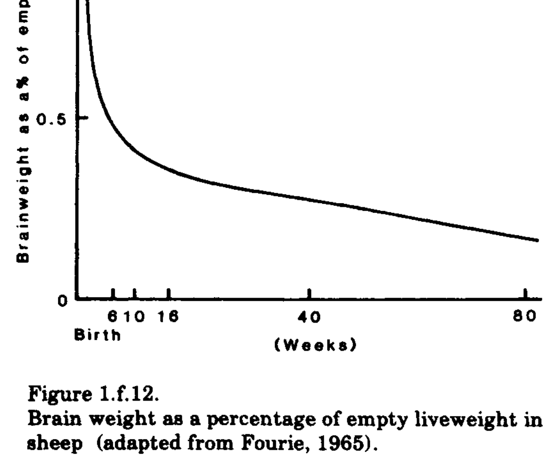


Figure 1.f.12.
Brain weight as a percentage of empty liveweight in sheep (adapted from Fourie, 1965).

General

The organs of the body each have their own unique pathway of weight gain from differentiation to maturity. These pathways are in some organs, such as brain and eyes, probably highly resistant to environmental change (Black, 1983), whereas others, such as the alimentary tract, will proceed largely according to the experience encountered. Therefore, any mathematical or graphical representation of the growth and maturing patterns of body organs will be more precise for some than for others.

In Summary

There is a wide range of maturing patterns for body organs during the post-weaning phase. At one extreme, organs grow rapidly very early and either exceed their mature weight when the whole animal is only 30 to 40% mature and then decline, as in the case of the small intestine; or remain below their mature weights, although close to them, throughout much of the maturing process, as does the brain. Other less early developing organs, such as the lungs, achieve their mature weight when the animal is about 70 to 80% mature, whereas most organs, such as the heart and kidney, continue to increase in weight up to the maturity of the whole animal. At the other extreme, the hide matures at about the same rate as the total body.

These patterns are shown by some examples in Figure 1.f.14.

g. THE MAJOR DEFICIENCY IN THE STORY OF THE GROWTH OF OUR 100 KG RAM

The major deficiency in this chapter is the lack of information on what would happen had our ram been grown at maximum potential from birth to weaning. Lambs in both Lohse's (1971) study and that of Butterfield *et al.* (1983) were reared on their mothers under pastoral conditions in Australia, and consequently grew at a pace which was set by the environmental conditions and the resultant milk supply of their dams; both of which were less than optimum.

The influence that this rearing had on the story told in this chapter is likely to be greatest on the low priority tissues, such as fat, and least on the high priority tissues, such as internal organs. If the information produced by Butterfield and Johnson (1971) in calves holds for lambs, and this seems highly likely, the influence of rate of growth in the early postnatal period on relative muscle growth would be negligible, although Hilmi (1975) and Murray and Slezacheck (1975) did show a minor effect in lambs.

It is hoped that a programme may be developed in which Merino ewes can be placed in an optimum environment and a serial slaughter programme developed which will embrace the entire postnatal growth span of their progeny.

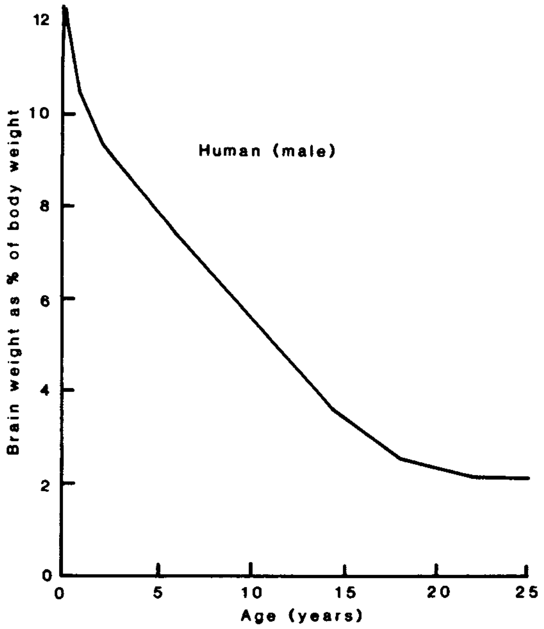


Figure 1.f.13.
Brain weight as percentage of body weight against age in a human male (adapted from D'Arcy Thompson, 1942).

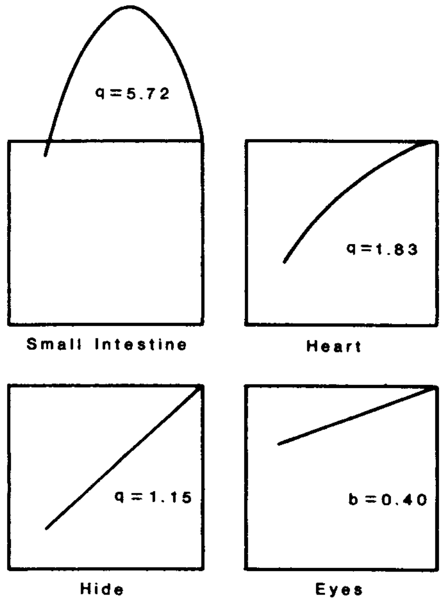


Figure 1.f.14.
Examples of the maturing patterns of body organs.

MAJOR REFERENCES FOR CHAPTER 1

Butler-Hogg (1984) "The growth of Clun and Southdown sheep: Body composition and the partitioning of total body fat"

Butterfield *et al.* (1983a, b, c, d) "Changes in body composition relative to weight and maturity in large and small strains of Australian Merino rams"

Kempster (1980) "Fat partition in the carcasses of cattle, sheep and pigs: A review"

Kirton, *et al.* (1972) "Growth and development of sheep. II. Growth of carcass and non-carcass components of the Southdown and Romney and their cross and some relationships with composition"

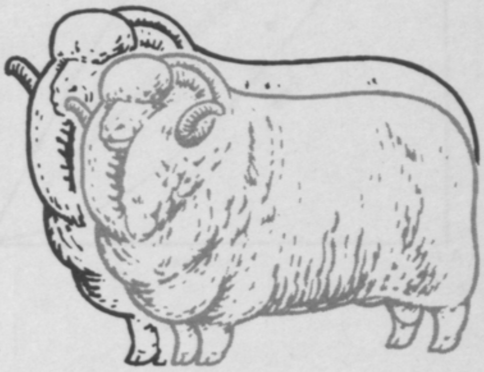
Lohse (1971) "Studies in the quantitative anatomy of Merino sheep"

Lohse *et al.* (1971) "Growth patterns of muscles of Merino sheep from birth to 517 days"

Wallace (1948) "The growth of lambs before and after birth in relation to the level of nutrition"

CHAPTER 2

THE INFLUENCE OF MATURE SIZE ON THE GROWTH OF SHEEP



"The size of an animal, as indicated by some measurement at some stage during its development, can theoretically be partitioned into two components: one describing the mature size . . . eventually attained or maintained, and the other describing the proportion, . . . of mature size reached at the stage in question." (Fitzhugh and Taylor, 1971)

a. INTRODUCTION

The range of mature weights in the sheep population of the world is not known, although it is certainly very wide from such miniatures as the Soay to large Lincolns, Border Leicesters and others within the breeds which are "conventional" in the English-speaking countries. However, there is a vast array of sheep on a world-wide basis as set out in Mason's "A World Dictionary of Breed Types and Varieties of Livestock" (1951). It is, therefore, likely that any comparisons made at equal age, equal weight or equal anything, other than degree of maturity, will give comparisons which have little bearing on the genetic body composition of the sheep being compared.

Goss (1976), in a chapter entitled "The Right Size", highlighted our lack of knowledge of the regulatory forces which fix the absolute size of the body and the relative size of its constituent parts. He posed the question: "Is body mass the point of reference for organ growth or is there a built-in limit to the growth of each organ which determines the size beyond which the body as a whole cannot grow?" In this section we do not move any closer to answering that question, however we do attempt to demonstrate the close relationship between the ultimate mature size at which the growth process of each body structure is aimed and growth characteristics of the structures throughout post-natal life.

Every animal has a genetically-determined mature size. Whether it is determined as a whole animal within which the "organs" are then apportioned shares; or as individual "organs" which add up to the total animal, is of little concern to those involved in meat animal research, although of considerable intrinsic scientific interest. Taylor (1982, 1985b) referred to "mature body weight, a" as a "genetic factor" which "is present from the earliest embryonic stage and the diverse modes of expression of this genetic size factor can be seen in operation at every stage of growth."

A major concern in meat animal production and research is: How to compare animal A with animal B, or breed A with breed B, or carcase A with carcase B or experimental group A with experimental group B? All workers in the field, as they look back on their own and other people's comparisons, must find that many conclusions have been reached in such comparisons without recognition of variables which they would now regard as important. In our own work on muscle-weight distribution we knew nothing of the possible influence of mature muscle weight and so compared animals in age groups (Butterfield, 1963, 1964b), which may or may not have represented approximately equal degrees of maturity as suggested by Butler-Hogg (1984). Later we decided that age was an inappropriate basis and switched to comparisons at equal weight (Butterfield and Berg, 1966a) which is still appropriate for many commercial comparisons.

Comparisons of meat animals to assess suitability to a particular market are relatively simple as the criteria of excellence of that market can be defined and the animals assessed relative to them. Unfortunately, "markets" are ephemeral and such comparisons are, therefore, of fleeting value both in commerce and in the long term of animal breeding. If comparisons of lasting value are to be made it is necessary to understand the growth process throughout as much of the lifespan as possible rather than to concentrate on the composition of animals in line with current market criteria. Nevertheless, comparisons at a single carcase weight or narrow range of carcase weights, are valuable if carcase weight is an important specification within a particular trade to which a comparison is related; or at equal fatness if level of fat is an important specification.

Preston and Willis (1970) argued strongly for between-breed comparisons to be made at equal carcase weight, dismissing the ideas of Taylor (1965) supported by Carroll (1966), that breeds be compared at weights proportional to their birth weight or mature weight. Preston and Willis claimed that both ante-and post-natal influences made birth weight unsatisfactory and that knowledge of mature weights rarely exists, and this is true. However, it is difficult to be convinced by their claim that "... between breeds, the comparison can only be on a fixed carcase weight basis." Neither Australian workers (Lohse *et al.*, 1971) nor European workers (Pirchner, 1984) have been discouraged by Preston and Willis and have used multiples of birth weight as a basis for comparison of meat animals. Time will reveal if this procedure is as unsatisfactory as Preston and Willis suggested.

Before a soundly-based comparison can be made of the proportion of a particular structure within an animal with the proportion of the same structure in another animal, it is necessary to understand how that structure grows relative to how the animals grow if the results are to be applicable at other than the one point of comparison. Similarly, it is necessary to understand the maturing pattern of intrinsic units, within a total system, such as individual muscles, within the total musculature, if soundly-based comparisons of the proportions within the system are to be made.

Until recent times "improvement" of body composition has been assessed mostly through subjective processes linked to eye appraisal of live animals. The modern trend is to assess body composition by objective means. To enable genetically-sensible comparisons of objective data to be made a great deal of information must be obtained regarding the process of growth. Techniques must be evolved to determine the real value of comparisons made on different bases, such as age, liveweight, tissue weight, proportion of maturity and others, as objective measurement could be an equally effective tool in reaching misleading conclusions as it could be in guiding us to the correct answers.

The simple reason why many tissues need to be compared at the same stage of maturity, rather than at the same weight, when assessing genetic, sex or other biological difference, in animals of different mature weight, is because they have maturing patterns which differ from the maturing pattern of the whole animal. Similarly this applies to within-tissue comparisons where either the mature weight of the tissue is different and/or units of the tissue follow different maturing patterns to that of the total tissue. As a consequence of a different maturing pattern to that of the whole animal a tissue will constitute different proportions of the animal at different weights or different stages of maturity. In Figure 2.a.1. two hypothetical tissues are shown each of which comprise the same proportion of the total animal at maturity but which achieve that proportion by different maturing patterns, one with a 'q' which is significantly greater than 1.0 and the other significantly less than 1.0. Part b. of the figure shows the changes in the proportion of the animal represented by each of the tissues throughout progress to maturity. If these extreme maturing patterns were representative of the same tissue in different animals (but this is rarely going to be the case) it is clear that comparisons at any and all stages of maturity would give different answers. What is far more important is to realise that a tissue will usually have similar, but not necessarily identical, maturing patterns in most animals, and that these may result in changing proportions which are closely related to the stage of maturity. Therefore, if the animals are of different mature size, comparisons may include differences which are made up of differences due to stage of maturity and mature composition when compared at the same weight.

In comparisons at equal body weight, difference in mature size will have a profound effect on the proportion of the whole represented by structures which proceed to maturity on patterns different from that of the whole animal, whereas the proportion represented by structures with maturing patterns which are the same as that of the whole animal, are unaffected by differences in mature size.

Taylor drew attention to the need for comparisons to be made at equal maturity in 1968 when the general trend was for comparisons to be made at equal weight. However, it was not until 1976 that McClelland, Bonaiti and Taylor published the first data on sheep relating genetic comparisons to degree of maturity. However, Taylor had stimulated considerable interest in the concept of comparisons at equal maturity and the need to define the mature animal before this time.

Animals which have been taken to their mature weights specifically for the purpose of providing a basis for comparisons at the same stage of maturity, have been reported only recently. Walstra (1980) reported a significant study in pigs. Butterfield *et al.* (1983, a,b,c, d); Thompson (1983) and Thompson *et al.* (1985/6) have reported the use of mature animals in the comparison of strains and sexes within the Merino breed. Butterfield et al (1984a, b, c) have compared Dorset Horn rams and wethers on the basis of their mature composition. And so the data are starting to accumulate.

Davies and Henning (1985) have made a very strong case for the use of the pig as a unique animal for study of differences related to size as within this species the mature size of breeds varies more widely than in any other domestic species commonly used for meat production. Weights of mature animals range from around 50 kg in the Gottingen mini-pig to around 300 kg in commercial breeds. Perhaps more importantly for studies of the musculoskeletal system the pig multiplies its birth weight far more than the other species in that it increases about 100 fold in body weight postnatally and is at a high peak of locomotory efficiency throughout almost the entire postnatal growth period.

Although this section will not answer Goss' question regarding the reference point of growth of body organs, it will, we hope, help in the development of methods of comparison of animals of different mature size and in so doing maybe define more clearly the relationship between organ size and body size.

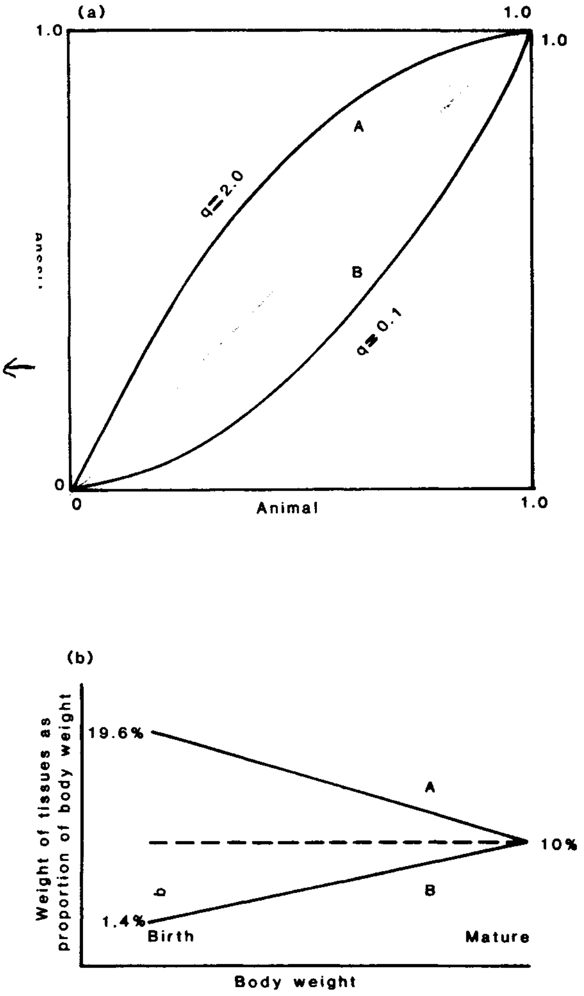


Figure 2.a.1.
Illustrating the effect of maturing patterns on body proportions at different stages of maturity.

a. Maturing patterns of 2 hypothetical tissues of which the 'q' values are 2.0 and 0.1 and which happen to comprise the same proportion of total weight of the animal at maturity, say, 10%.

b. Changes in proportion of total weight of the animal comprised by tissues A & B from a. above.

b. THE INFLUENCE OF MATURE SIZE ON THE GROWTH OF CARCASE TISSUES OF SHEEP

Without a great deal of experimental evidence being available it has long been considered as general knowledge that the mature size of animals influences the proportions of muscle, bone and fat which are to be found in the carcases of animals slaughtered at similar weights. This has been related to

Hammond's description of tissues as "early" or "late" maturing according to the sequence in which they reach their maximum absolute growth rates, which shows bone to be earlier maturing than muscle, which is earlier than fat. If these periods of maximum absolute growth rate occur at generally similar proportions of mature liveweight, it is apparent that any comparisons of composition at the same liveweights or the same carcase weights, will give different answers for small and large animals even if they share similar composition at maturity.

Much of the speculation regarding the influence of mature size on the proportions of muscle, bone and fat in animals and in carcases, has been developed in the general knowlege of which breeds are large and which are small, but with little precise knowledge of their mature weights or relative mature weights under various nutritional regimes or any same regime. Similarly, there has been little knowledge of mature composition achieved on the same rations as fed to slaughter stock, as few breeding animals are carried through to maturity on rations appropriate to slaughter stock. Despite the use of the terms "early maturing" and "late maturing" to describe periods of high growth impetus, there has been little knowledge of the complete patterns on which tissues mature relative to the manner in which the whole animals mature. In 1976 McClelland, Bonaiti and Taylor studied breed differences in the composition of equally mature sheep by estimating the mature weights of females from the dam weights of the flock, and of males by multiplying estimated female mature weight by 1.30. In 1983 Butterfield *et al.* fed Merino rams of two strains of different size in an experiment designed specifically to study the influence of mature size on the maturing process of body tissues. Thompson (1983) also fed Merino rams and ewes to maturity from flocks which had been selected for high and low weaning weights over thirty years and from a randomly-bred control flock maintained since the beginning of the selection.

Set out in Table 2.b.1. are the weights and in Table 2.b.2. the proportions of liveweight of the carcase tissues of large and small mature size Merino rams at maturity. From these tables it is seen that, although the two strains differed by about 25 kg in their mature liveweight, and also differed considerably in the actual yields of muscle, bone and fat, the proportions of muscle and bone relative to liveweight were almost the same and fat differed by only 2.3 percentage units. It seems from this result that simple difference in size need not be accompanied by dramatic difference in the proportions of liveweight of these three carcase tissues at maturity.

Table 2.b.1. Carcase tissue weights of mature rams of two strains of Merinos of different mature size (Data from Butterfield *et al.*, 1983a)

Whole carcase tissue	Weight (kg) Large n = 3	Small n = 3	Sig. of Diff.
Muscle	25.9	20.7	***
Bone	6.4	4.9	**
Fat	26.7	18.8	**
Liveweight	116.5	90.9	***

Table 2.b.2. Carcase tissues as percentages of shorn full liveweight of mature rams of two strains of Merinos of different mature size (Data from Butterfield *et al.*, 1983a)

Whole carcase tissue	Percent of liveweight Large n = 3	Small n = 3	Sig. of Diff.
Muscle	22.3	22.8	NS
Bone	5.5	5.4	NS
Fat	23.0	20.7	*
Liveweight	100.0	100.0	–

If the similarity in proportions of carcase tissues is also shown in the non-carcase fat depots, it would support the hypothesis of McClelland and Russel (1972) that "when animals of differing mature weight are slaughtered at the same stage of maturity, the proportion of fat in the body will be similar.", *provided* the maturing pattern of fat is also the same in the animals being compared. It would not be safe, however, to suggest that the proportion of fat in the body at equal maturity would also be the same when size is altered as a result of selection for growth rate for, as Thompson (1983) showed, selection for weight at weaning produced different maturing patterns of fat relative to body weight even though the proportion of fat in mature animals was not affected.

Fowler (1980b) pointed out that a superficial consideration of Brody's (1945) generalisation that "... as land animals grow, although weight tends to increase as a function of the cube of linear size, the strength of the muscles supporting the increased weight can increase only as the square of their linear size." would suggest that "larger animals need a disproportionately large musculature to support body weight." Fowler went on to show that the gross proportion of total muscle weight relative to liveweight bore no relationship to weight across six species on which data were available from a variety of sources (Table 2.b.3.).

Thompson *et al.* (1985b) showed that selection for weaning weight "increased the proportions of bone and ash in the body of mature animals", and this is shown for bone in Figure 2.b.1. This clear difference was in contrast, in their study, with the same relationship between bone weight and body weight within each of their strains and sexes of sheep. Also, Butterfield *et al.* (1983a) showed no difference in the proportion of bone in large and small strains of Merino rams at maturity, however Kayser and Heusner (1964) showed that over a wide range of species the proportion of bone increased with increased species size. However, Davies and Henning (1985) in their study on extreme size range of pigs concluded that larger pigs support their weight without need of a disproportionate development of supporting structures. The response shown by Thompson *et al.* may be in part a functional response to provide the relatively larger skeleton needed to support larger mature size but, in view of the relatively small difference in weight of his strains compared with the pigs of Davies and Henning, it seems rather unlikely.

In attempting to study the influence of any factor, be it mature size, sex, or whatever, on the growth of carcase tissues, it is necessary to first decide on the basis of comparison. Do we compare at equal age, equal carcase weight, equal empty liveweight, equal full liveweight or at some proportion of the maturity of any one of these values?

Carcase weight has certain commercial advantages but has little biological significance. Empty liveweight overcomes problems of variation of gut fill but is a condition which is difficult to achieve and very difficult to relate to real life. Age has little to offer because of the confounding effects of appetite and food intake. For these reasons it is decided that full liveweight is an appropriate measure, and the next problem is to find the best way in which to express it, such as actual full liveweight in kilograms, or percentage increase in liveweight, or proportion of mature liveweight. Of these the proportion of mature liveweight is favoured in all cases where mature weight is available as by its nature it removes the variation between groups being compared, caused by any differences in their mature size.

Using the composition of the mature sheep as in Table 2.b.1. and data from immature sheep, maturity coefficients can be calculated. Maturity coefficients for Merino rams do not differ (Table 2.b.4.) between large and small strains and so pooled values are presented.

That the maturing patterns are not different in sheep of such diverse mature weights, confirms that each tissue has an inherent maturing pattern which is coded from early life to the mature weight which it is to ultimately achieve. Therefore, we can gain additional understanding of the changes of proportions of the carcase tissues if we first acquaint ourselves with both mature weight and the maturing pattern of each tissue. This close relationship between the mature weights of tissues and their weight increments throughout the growth process provokes some thought in relation to the question posed by Goss with which this chapter was introduced. It seems to be much easier to accept that the necessary mechanism to achieve the correct increments of weight throughout is intrinsic to each tissue (and as will be shown later; to each unit within these tissues and to body organs) than that the final size of the whole animal is the determinant. Yet the final appropriateness of the size of each mature structure to the size of the mature animal suggests the existence of a whole animal influence. We are no closer to answering Goss' question!

Table 2.b.3. Muscle weight as a percentage of liveweight (From Fowler, 1980b).

	Liveweight (kg)	Muscle as percentage of liveweight
Cattle	593	32
Deer	100	39
Pig	91	32
Sheep	37	28
Dwarf goat	14	35
Rabbit	2	48

* Data from various sources quoted by Fowler.

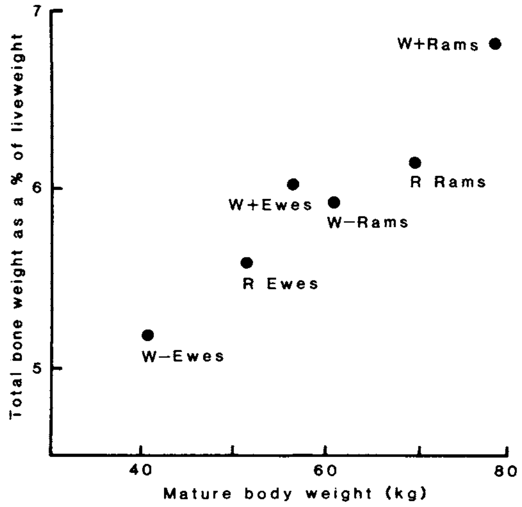


Figure 2.b.1.
Bone weight as a percentage of liveweight as a function of mature body weight for groups of rams and ewes from flocks of Merino sheep selected for high (W+) and low (W–) weaning weight and from a randomly bred control flock (R) (From Thompson *et al.*, (1985b).)

Table 2.b.4 Maturity coefficients for carcase tissues relative to liveweight of Merino rams (Data from Butterfield *et al.* 1983a)

		'q'*	
	Large (N = 20)	Small (N = 19)	Pooled
Muscle	1.31	1.18	1.25
Bone	1.33	1.48	1.41
Fat	0.07	0.08	0.07

* *No significant difference between strains.*
* *All values Significantly Different from 1.0.*

Table 2.b.5. Progress to maturity of carcase tissues of large and small Merino rams relative to progress to maturity of shorn full liveweight (Data from Butterfield *et al.*, 1983a)

	Percentage maturity									Mature weight (kg)	
										Large	Small
Liveweight	20	30	40	50	60	70	80	90	100 =	116.5	90.9
Muscle	24	35	46	56	66	75	84	92	100 =	25.9	20.7
Bone	26	39	50	60	70	79	86	94	100 =	6.4	4.9
Fat	5	11	18	27	38	51	65	82	100 =	26.7	18.8

The progress to maturity of each carcase tissue is tabulated in Table 2.b.5. and the progress of the carcase tissues relative to each other and to liveweight can be seen, so that, for example, when liveweight is 60% mature, muscle is 66%, bone 70% and fat only 38% mature irrespective of the mature size of the sheep.

With the information in Table 2.b.5. we are able to determine just what each tissue is likely to weigh in an animal of a particular weight. For example, when a large mature size ram weighs 58 kg it will be about 50% mature and hence will contain approximately 14.5 kg of muscle, 3.8 kg of bone, and 7.2 kg of fat, whereas at the same weight a small mature size ram will be 64% mature and contain 14.5 kg of muscle, 3.6 kg of bone and 8.1 kg of fat.

Having demonstrated that the growth of carcase tissues is closely related to mature size, and that in sheep of quite different mature size each carcase tissue follows the same pattern aimed at its own particular mature weight, and that these patterns differ significantly from that of liveweight, it is axiomatic that comparisons of genotypes of different mature size at the same liveweight will result in quite different answers from comparisons at the same degree of maturity. We therefore find that the differences in the proportion of liveweight comprised by the carcase tissues at the same weight are considerably altered when comparison is made at the same proportion of mature weight (Table 2.b.6. and Figure 2.b.2.) in genotypes which share similar although not identical composition at maturity. A similar situation would usually occur irrespective of the similarity or otherwise of mature composition, unless the differences in mature composition and the differences due to stage of maturity were mutually cancelling.

A most interesting point is that, in this comparison in Table 2.b.6., while the percentage fat is significantly greater in the small rams at the same weight, this position is reversed at the same proportion of maturity and hence it is apparent that comparisons of body composition of animals of different mature size at the same weight may result in quite different and even opposite, conclusions to those made at equal proportions of maturity. There is clearly, therefore, a danger in reaching conclusions and in making suggestions regarding inherent carcase composition of animals which are compared at any chosen weight without full knowledge of both mature composition and maturing patterns.

Table 2.b.6. Predicted means for carcase tissues as a proportion of live weight for large and small mature size Merino rams after adjustment to (i) the mean shorn full liveweight (70.0 kg), and (ii) the mean proportion of mature shorn full liveweight (0.68); of the available data (Data from Butterfield *et al.*, 1983a)

	At the same liveweight				At the same proportion of maturity			
Carcase Tissue	Large Mature	Small Mature	Difference	Significance	Large Mature	Small Mature	Difference	Significance
Muscle	24.5	24.1	0.4	NS	24.1	24.6	0.5	NS
NS Bone	6.4	5.9	0.5	*	6.2	6.1	0.1	NS
NS Fat	14.5	16.3	1.8	**	16.1	14.5	1.6	*

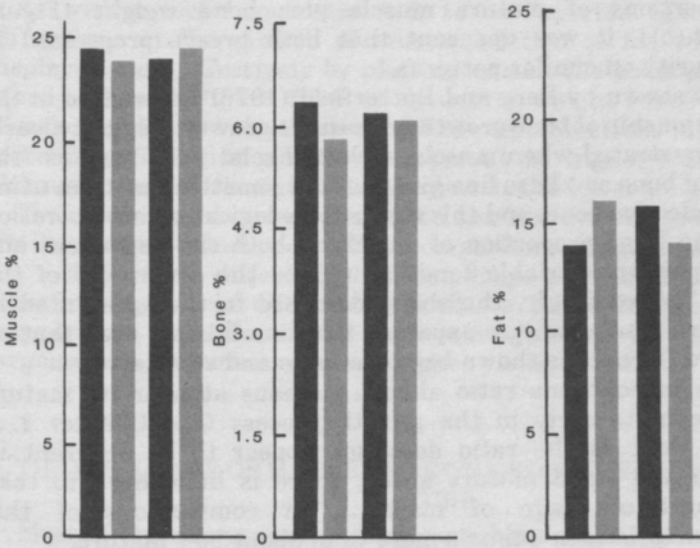


Figure 2.b.2.
Comparison of differences in percentage of liveweight of the carcase tissues of large and small mature size Merino rams on two bases. 1. Equal liveweight. 2. Equal maturity of liveweight.

In comparisons of Merino rams of different strains, differences in maturing patterns of each carcase tissue are likely to be small and of little importance and it is the relationship of the maturing pattern of the tissue to that of the whole animal which is of major concern. Muscle, which because its maturing pattern differs little from that of liveweight ('q' = 1.24), is likely to give only slightly different results when comparisons are made at the same liveweight from those made at the same degree of mature liveweight. Both bone and particularly fat, because their maturing patterns are less-closely related to that of liveweight, give answers which will differ more between the two bases of comparison. It seems, from the results of Thompson (1983), that selection pressure on body weight at an early age (e.g. at weaning) may alter maturing patterns of fat slightly. His three strains had 'q' values for carcase fat of 0.28, 0.18 and 0.14. and comparisons at a variety of stages of maturity would vary slightly and therefore for precise genetic comparisons it is necessary that both mature compostion and maturing patterns be known.

MUSCLE:BONE RATIO

It is important to understand if different bases of comparison of muscle:bone ratio (e.g., equal liveweight, equal carcase weight etc.) produce different interpretations (Berg and Butterfield, 1966) in animals of different mature size. Consequently the ratio is shown in Figure 2.b.3. against proportion of maturity of liveweight, against equal body weight and against equal muscle plus bone weight. There would be little difference in interpretation of the changes of muscle:bone ratio on these bases.

However, if the extremes of mature weight in two breeds of sheep were of the order which is found in the pig, then very different considerations would be necessary. For example, Davies (1984) and Davies and Henning (1985) presented a figure showing the muscle:bone ratio of Göttingen miniature pigs and German Landrace which were on the basis of equal muscle plus bone weight. This is shown in Figure 2.b.4.(a). From this figure it seems that the development of the muscle: bone ratio throughout the process of growth was very different in the two groups of pigs but when those data were replotted as proportions of mature muscle:bone ratio on the basis of

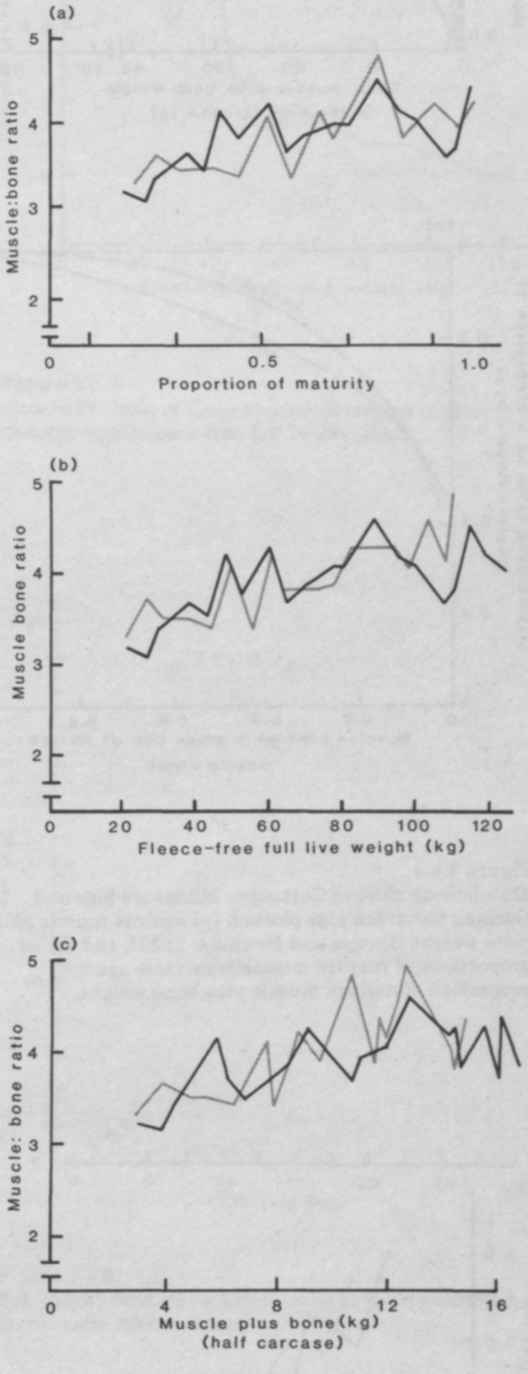


Figure 2.b.3.
Muscle:bone ratio of large and small mature size Merino rams on three bases of comparison. (Butterfield, unpublished.)

proportions of mature muscle plus bone weight (Figure 2.b.4.(b)), it was apparent that both breeds progressed to maturity on similar patterns.

As shown by Berg and Butterfield (1976) differences in the relationship of bone growth and muscle growth are most clearly demonstrated when muscle is plotted relative to bone as "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." Accordingly, the sheep data are further presented in Figure 2.b.5. and it is apparent that on all bases used that no real difference is shown between large and small strains.

As muscle:bone ratio almost plateaus at near its mature value quite early in the growth process (See Chapter 1... p. 7), and as the ratio does not appear to be different in large and small mature sheep, there is little need to take account of stage of maturity in comparisons of this characteristic in animals more than about 50% mature.

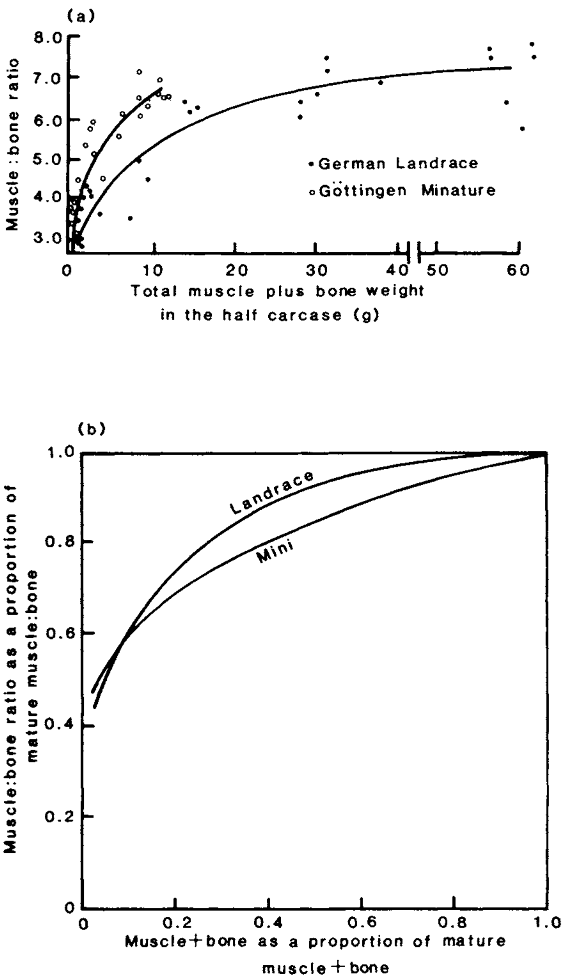


Figure 2.b.4.
Muscle:bone ratio of Gottingen Miniature pigs and German Landrace pigs plotted: (a) against muscle plus bone weight (Davies and Henning, 1985); and (b) as proportions of mature muscle:bone ratio against proportion of mature muscle plus bone weight.

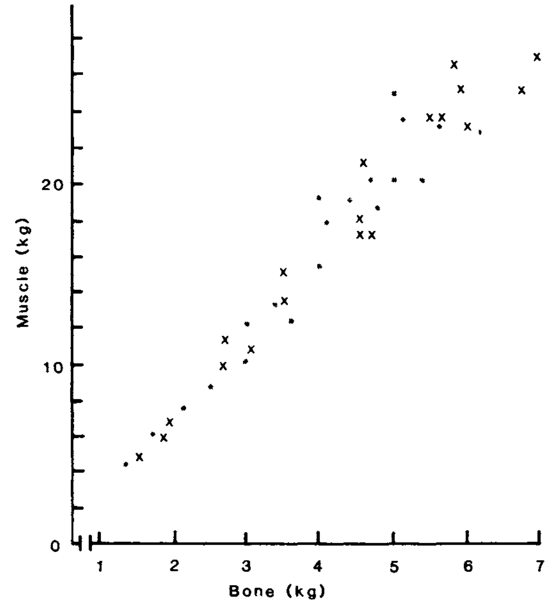


Figure 2.b.5.
Growth of muscle relative to growth of bone in large and small Merino rams (data from Butterfield *et al.*, 1983a).

MUSCLE:FAT RATIO

As with muscle:bone ratio it is important to understand the effect of the basis of comparison on the apparent similarities and differences revealed when comparing animals of different mature size.

Figure 2.b.6. shows the changes in muscle:fat ratio from about 20% mature up to maturity in large and small mature size Merino rams. The two strains closely follow the same trend in which the ratio changes from around 4:1 to around 1:1. On this basis of proportions of mature liveweight the two strains were obviously following a similar path, however, when the same sheep are compared on the basis of equal liveweight, the small sheep tend to have a lower muscle to fat ratio as shown in Figure 2.b.7. and comparisons on this basis may be more useful for the meat industry.

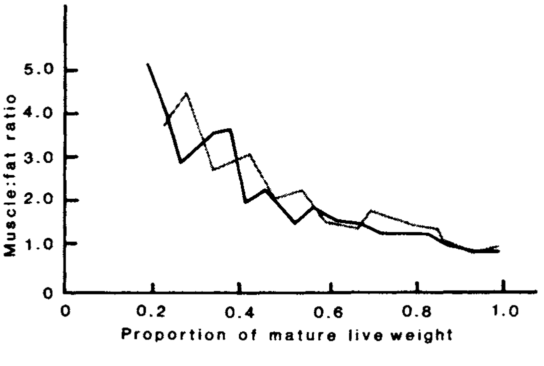


Figure 2.b.6.
Muscle:fat ratio of large and small strains of Merino rams during progress to mature fleece-free full liveweight.

As with muscle:bone ratio it is to be expected that any differences in the growth of muscle relative to fat will be displayed most effectively by plotting one on the basis of the other and so in Figure 2.b.8. is shown fat weight relative to muscle weight, and the tendency for the smaller strain to have more fat relative to muscle is apparent at higher weights although the difference is less apparent at the lower weights.

The continuing downward trend on similar patterns towards similar mature values means that comparisons at equal maturity will show no difference between large and small sheep whereas they will be different at similar weights. Commercial comparisons at similar live or carcase weights will favour the larger sheep in markets seeking higher yields of muscle.

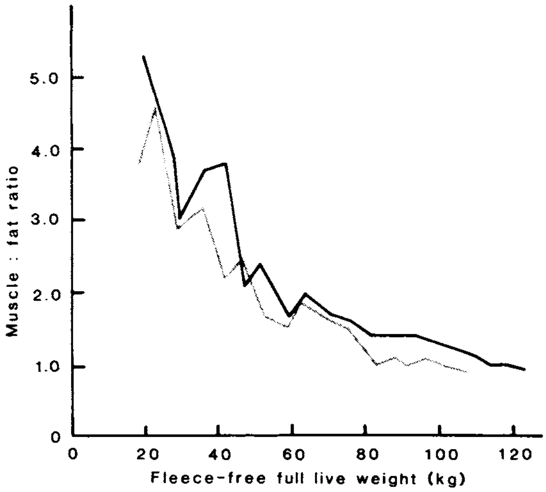


Figure 2.b.7.
Muscle:fat ratio of large and small strains of Merino rams at equal fleece-free full liveweight.

c. THE INFLUENCE OF MATURE SIZE ON GROWTH WITHIN THE MUSCULATURE

Most of the comparisons which have been made of muscle-weight distribution have been at approximately the same weight, or level of fatness, although multiples of birth weight have been used by Lohse (1971) and Lohse *et al.* (1971) in sheep and by Pirchner (1984) in a recent cattle study. As muscles have different maturing patterns from each other, breed comparisons reflect genetic differences of muscle-weight distribution only if carried out at the same degree of maturity of the total musculature. Wolf (1982) suggested that differences in muscle-weight distribution of six breeds which he studied would be reduced, although not eliminated, when adjusted to equal stage of maturity. Taylor (1968) drew attention to the need to consider the stage of maturity in such comparisons. Although several authors have stated that observed differences in muscle-weight distribution *probably* reflect differences in stage of maturity, it was not until 1980 that Taylor, Mason and McClelland took account of mature size of the animals in a comparison of muscle-weight distribution of breeds of sheep of diverse size. However, they did not have data on mature total muscle weight to enable them to demonstrate precisely the influence of stage of maturity of the musculature. By comparisons of muscle-weight distribution in two strains of Merino rams Taylor's assertions were experimentally demonstrated by Butterfield *et al.* in 1983(b).

The optimum study of the relationship between mature total muscle weight and muscle-weight distribution would be to have sheep which were genetically "identical" in all other characteristics except total muscle weight in which they would ideally be very diverse. It would then be necessary to define the composition of the total musculature at maturity, and this can be achieved by the dissection of individual muscles and the recording of their weights.

By definition, the musculature of a mature animal will itself be mature. However, there may be some special problems associated with the musculature in that the dissected units will contain a proportion of intramuscular fat and it was shown by Butterfield (1963) that muscle-weight distribution was influenced by the level of fatness of animals. Johnson, Pryor and Butterfield (1973), in a study of the relationship between muscle-weight distribution and carcase fatness, showed that there are factors involved which are still not understood. They agreed with Butterfield (1963) that changes in total fatness are associated with changes in muscle-weight distribution in cattle but showed that these changes were not explainable by differences in intramuscular fat content of the muscles. It seems, therefore, that it is necessary to minimise any effect on muscle-weight distribution in mature animals due to different levels of fatness and that this may be partly achieved by ensuring that all mature animals are sacrificed as soon as

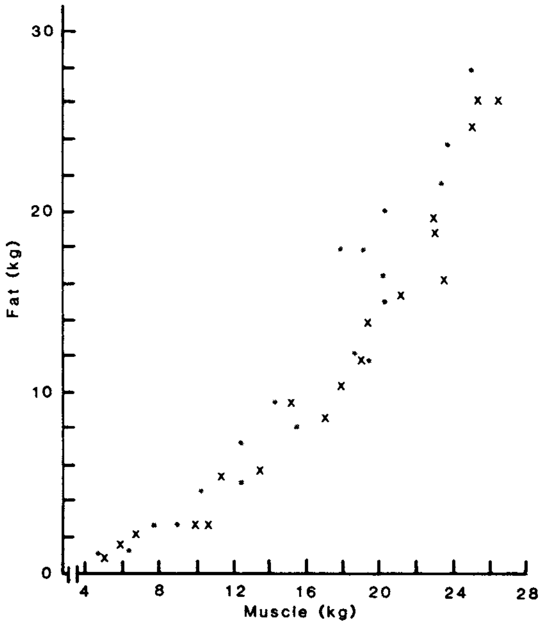


Figure 2.b.8.
Fat weight relative to muscle weight in large and small mature size Merino rams.

possible after reaching the defined mature state rather than being allowed to accumulate more fat. Alternatively the intramuscular fat content may be accepted as an intrinisic part of the dissected muscles just as is intramuscular water and if different animals have different levels of intramuscular fat in mature muscle that this be accepted as an inherent difference.

Unlike the total weights of carcase tissues which were studied on the basis of liveweight changes, the progress to maturity of individual muscles and groups is best studied on the basis of changing total muscle weight. This is clearly in line with the thinking of Wallace (1948) when he expressed doubts about comparisons involving units within systems on the basis of the total animal or carcase.

There is the possibility that muscle weight may be distributed differently in accordance with genetic size in order to locate a higher proportion of total muscle weight in the limbs. Berg and Butterfield (1976) showed, using unpublished data of Ledger, that the proportion of muscle weight around the spinal column of game animals was smallest in the larger species, but failed to attach any significance to the differences in the proportion of muscle weight in the limbs. They also showed that across the species they had dissected there was a "size index" to the proportion of muscle weight in the region surrounding the spinal column. This is shown in Table 2.c.1. where the values given are related to that of cattle = 100.

Berg and Butterfield were more inclined to relate the degree of development of limb muscles to agility and this ties in with the suggestion of Fowler (1980b) that much of the adaptation to increased size appears to be a relative slowing down of motion, which he illustrated with the suggestion that "An elephant moving its legs at the same speed as a running hare would travel at about 500 km/h!"

Fowler warned of the risk of relying too heavily on relative size as an indication of functional importance as the force a muscle can exert may be greatly influenced by the length of the lever on which it acts and so it is unwise to become too excited about across-species differences as an indication of functional differences where the skeletal structure varies greatly. What appears to be a contradiction of this line of thought is that whereas the Water Buffalo has considerably shorter dorsal lumbar spines than cattle (Butterfield, 1964c) it also has lighter muscles around the spinal column. There are, of course, other variables in this consideration. It may well be that size is no indication of functional strength of the muscles involved, as the buffalo may have a more complex pennate structure (although that is unlikely) within the muscles resulting in increased strength from more muscle fibres within the the smaller bulk of muscle. There is also the consideration that different species do involve themselves in different activities and therefore any comparison across species must be a very approximate process.

The composition of the musculature in mature rams of different mature total muscle weight is shown in Tables 2.c.2. and 2.c.3., and in more detail in Appendix 5 Table 2. These data, along with those collected from animals slaughtered throughout progress to maturity, can be used to determine the maturing patterns of all the muscles, which are indicated by the maturity coefficients "q" also in Appendix 5 Table 2.

The first conclusion which can be drawn from this information is that there is a general similarity between the muscle-weight distribution of the large and small mature size rams at maturity.

Maturing patterns of the muscles in the majority of cases are similar for the two groups of rams. From a total of 93 muscles only 15 have significantly different 'q' values for the strains. Most of these 15 are very small muscles and they total less than

Table 2.c.1 The proportion of muscle weight surrounding the spinal column relative to the value for cattle = 100. From Berg and Butterfield (1976)

Species	Index
Water buffalo	79
Moose	96
Cattle	100
Bison	102
Banteng	103
Deer	122
Sheep	139
Pig	141

Table 2.c.2. The weight of "Standard Muscle Groups" of mature large and small Merino rams. Detail of individual muscles will be found in Appendix 5 Table 2. (adapted from Butterfield 1983b)

"Standard Muscle Groups"	Weight (g) Large	Small
1. Proximal hind limb	3301	2516
2. Distal hind limb	578	436
3. Spinal	1999	1571
4. Abdominal wall	1338	1112
5. Proximal forelimb	1403	1114
6. Distal forelimb	352	293
7. Thorax to forelimb	1111	890
8. Neck to forelimb	983	794
9. Neck and thorax	1587	1340
Scrap muscle not included in a Standard Muscle Group	311	272
Total Half-carcase Muscle Weight	12963	10338

Table 2.c.3 The percentage of total muscle weight in each "Standard Muscle Group" of mature large and small Merino rams. Detail of individual muscles will be found in Appendix 5 Table 2. (adapted from Butterfield *et al.*, 1983b)

"Standard Muscle Groups"	% of total muscle weight Large	Small
1. Proximal hind limb	25.5	24.3
2. Distal hind limb	4.5	4.2
3. Spinal	15.4	15.2
4. Abdominal wall	10.3	10.8
5. Proximal forelimb	10.8	10.7
6. Distal forelimb	2.7	2.8
7. Thorax to forelimb	8.6	8.6
8. Neck to forelimb	7.6	7.7
9. Neck and thorax	12.2	13.0
Scrap muscle not included in a Standard Muscle Group	2.4	2.6
Total Half-carcase Muscle Weight	100.0	100.0

Table 2.c.4 The maturity coefficient ('q') and growth impetus of the "Standard Muscle Groups" in large and small Merino rams from approximately 20% mature to maturity (adapted from Butterfield *et al.*, 1983b)

"Standard Muscle Groups"	'q'			Growth impetus
	Large	Small	Pooled	
1. Proximal hind limb	1.22	1.24	1.23	Low
2. Distal hind limb	1.25	1.33	1.30	Low
3. Spinal	1.25	1.05	1.15	Low
4. Abdominal wall	1.02	0.81	0.92	Average
5. Proximal forelimb	1.12	1.09	1.10	Low
6. Distal forelimb	1.13	1.09	1.11	Low
7. Thorax to forelimb	0.86	0.83	0.85	High
8. Neck to forelimb	0.49	0.73	–	High
9. Neck and thorax	0.53	0.75	0.64	High
Expensive (1+3+5)	1.21	1.15	1.18	Low

10% of the total muscle weight. In addition, 'q' values calculated for each "Standard Muscle Group" in each strain are shown in Table 2.c.4. With the exception of only one group the 'q' values for the strains are not significantly different so that pooled values can be derived.

This similarity of maturing patterns in individual muscles and groups of muscles in animals of different size indicates that the growth of the musculature is a regimented procedure in which not only the final relative weight of each muscle, but also the pattern on which it proceeds to that weight, shows minimal variation associated with size. From this information it can be concluded that, even though these strains differed markedly in total muscle weight at maturity, their muscles proceeded to their particular individual mature muscle weights on similar patterns irrespective of the magnitude of the mature weight of the total musculature or that of its intrinsic units in each strain. This, therefore, allows comparisons to be made of composition of the musculature at any chosen point in the maturing process with confidence that the differences revealed will be mirrored in the differences at any other point during the maturing process. It also means that comparisons of the composition of the musculature of animals of different mature total muscle weight, made at the same total muscle weight, will give misleading results in a genetic sense.

Many individual muscles are proceeding on their own particular patterns which are different from that of the total musculature resulting in comparisons at equal total muscle weight reflecting a combined influence of the mature composition of the musculature and the stage of maturity.

Using the muscles grouped in "Standard Muscle Groups" two comparisons are made of the muscle-weight distribution of two groups of rams, and these are shown in Table 2.c.5.

Table 2.c.5. Predicted means for weights of muscle groups as percentages of total muscle weight for large and small mature size rams after adjustment to (i) the mean total muscle weight (8.2 kg), and (ii) the mean proportion of mature muscle weight (0.7) of the available data (Based on Butterfield *et al.*, 1983b)

	At the same total muscle weight				At the same proportion of maturity			
	Large mature	Small mature	Difference	Significance	Large mature	Small mature	Difference	Significance
1. Proximal hind limb	27.63	25.48	2.14	***	27.15	25.95	1.21	**
2. Distal hind limb	4.93	4.47	0.46	***	4.83	4.57	0.25	***
3. Spinal	16.49	15.93	0.56	NS	16.30	16.12	0.18	NS
4. Abdominal wall	10.01	10.58	0.56	*	10.08	10.50	0.42	NS
5. Proximal forelimb	11.24	11.01	0.23	NS	11.15	11.10	0.05	NS
6. Distal forelimb	2.82	2.90	0.08	NS	2.80	2.92	0.12	*
7. Thorax to forelimb	8.10	8.34	0.24	NS	8.20	8.24	0.03	NS
8. Neck to forelimb	6.19	7.27	1.07	***	6.50	7.10	0.60	*
9. Neck and thorax	10.46	11.78	1.32	***	10.81	11.41	0.60	NS
Sum of differences	–	–	6.66	–	–	–	3.46	–
Expensive muscles Groups 1 + 3 + 5	55.36	52.42	2.94		54.6	53.17	1.43	

Perhaps the simplest assessment of the two different comparisons can be achieved by examining the sum of the differences, ignoring sign, for all groups in the two strains. Whereas this was approximately 6.7% in comparison at equal weight, it was only approximately 3.5% in comparison at the same proportion of maturity. Because the maturing patterns of the groups are different from that of the total musculature, and because the muscle-weight distribution is more similar at maturity than at mean total muscle weight of the animals, the difference between the strains in every muscle group except one was less when compared at equal maturity than at equal weight.

It is interesting, in light of the many comparisons which have been made of muscle-weight distribution on the basis of equal total muscle weight, to look at the more commercially important aspects of the difference shown in this comparison. Whereas the "expensive group" (Butterfield and Berg, 1966c) (i.e. Groups 1, 3 and 5 combined) differed by 2.94% when compared at the same total muscle weight, this was reduced at the same degree of maturity to only 1.43%. This 50% reduction highlights the inadequacy of comparisons at the same total muscle weight as indicators of genetic difference in muscle-weight distribution in animals of different mature muscle weight. Figure 2.c.1. shows how the difference in muscle-weight distribution is reduced at the same proportion of mature total muscle weight.

The muscles surrounding the spinal column which attract much attention because of their commercial value and because they can be seen in cross-section in the quartered carcase; although not significantly different in either comparison, vary by only 0.18% at the same level of maturity as against 0.56% at the same total muscle weight. The declining growth impetus of this group along with the greater part of the "expensive" musculature, certainly makes comparisons at equal muscle weight poor indicators of genetic differences in distribution of expensive muscle weight in animals of different mature muscle weight.

It seems that for Merino rams, irrespective of size, maturing patterns such as are presented in Table 2.c.6. could be appropriately used in the adjustment of muscle-weight distribution data. The pathways to maturity demonstrated in this Table show the need to consider just where the muscle weights being compared are sited on their maturing patterns. In the overall thinking of the advantages and disadvantages of large and small mature size, consideration might be given to the advan-

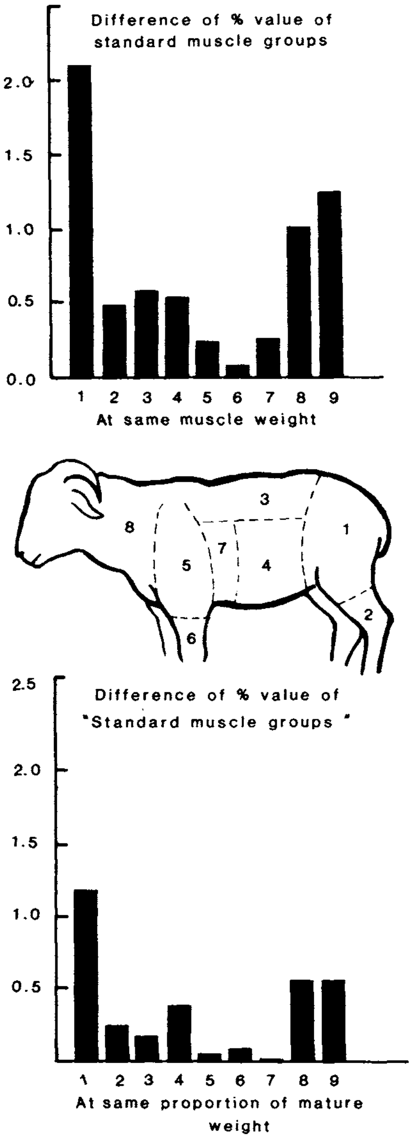


Figure 2.c.1.
Comparison of difference (ignoring sign) in muscle-weight distribution of large and small mature size Merino rams.

Table 2.c.6. The progress to maturity of muscle groups of large and small mature size Merino rams relative to the progress to maturity of total muscle weight

Standard muscle group				Percentage maturity						Mature Weight Grams Large	Small
Total muscle weight	20	30	40	50	60	70	80	90	100 =	12963	10338
1. Proximal hind limb	24+	35	46	56	66	75	84	92	100 =	3301	2516
2. Distal hind limb	25	36	47	57	67	76	85	93	100 =	578	436
3. Spinal	22	33	44	54	64	73	82	91	100 =	2025	1597
4. Abdominal wall	19	28	38	48	58	68	79	89	100 =	1338	1112
5. Proximal forelimb	22	32	42	53	62	72	82	91	100 =	1403	1115
6. Distal forelimb	22	32	43	53	63	72	82	91	100 =	352	293
7. Thorax to forelimb	18	27	36	46	56	67	78	89	100 =	1111	890
8. Neck to forelimb											
L†	12	19	28	37	48	59	72	85	100 =	983	–
S	16	24	34	43	54	64	76	88	100 =	–	794
9. Neck and thorax	14	22	31	41	51	62	74	87	100 =	1561	1314

* Calculated using pooled maturity coefficients, with the exception of group 8 where separate maturity coefficients for each strain were used.
† L, large mature size.
S, small mature size.

Table 2.c.7. Percentage of muscle in each joint grouped by sire breeds of cattle of very different mature size
Data from Berg *et al.* (1978b)

Joint	Chianina	Hereford	Difference Chianina minus Hereford	Probable 'q'
Hind shank	4.4	4.1	+ 0.3	Greater than 1
Round	26.0	23.5	+ 2.5	Greater than 1
Loin + rib	16.8	16.6	+ 0.2	Greater than 1
Flank	4.1	4.6	− 0.5	Less than 1
Brisket	16.5	18.7	− 2.2	Less than 1
Foreshank	2.5	2.3	+ 0.2	Greater than 1
Shoulder	14.9	13.9	+ 1.0	Greater than 1
Fore rib	6.5	7.0	− 0.5	Less than 1
Neck	8.1	9.2	− 1.1	Less than 1
Sum of groups:				
(i) with 'q' greater than 1	64.6	60.4	+ 4.2	
(ii) with 'q' less than 1	35.2	39.5	− 4.3	
Pistol	47.2	44.2	+ 3.0	Greater than 1
Hindquarter	44.8	42.0	+ 2.8	Greater than 1
Forequarter	55.2	58.0	− 2.8	Less than 1

tage of large over small genotypes which results from knowledge that at any weight the musculature of the genetically large animals will be less mature and therefore of more desirable distribution.

An illustration of the apparent influence of the stage of maturity in bulls is shown in two extreme-size breeds in the paper by Berg *et al.* (1978b). Comparison of the muscle-weight distribution of the inherently-large Chianina bulls with the inherently-much-smaller Hereford bulls was made at a total side muscle weight of 87.5 kg which was the arithmetic mean of a large number of bulls of a wide variety of breeding. The data in Table 2.c.7. is extracted from the report of that study, and even though the influence of the two breeds is through only the sires, the demonstration is striking.

Berg *et al.* pointed out that dissection of mature animals could clarify some of the problems in interpretation of muscle-weight distribution studies, and the data in Table 2.c.7. certainly suggests this, as the differences shown could be very largely, if not entirely, absent in comparison at the same proportion of mature muscle weight. The Hereford musculature is much closer to its mature weight than that of the Chianina and so all the early developing (i.e. low impetus) muscle groups form a lower proportion of total muscle weight in the Herefords and the late developing (i.e. high impetus) groups a higher proportion. Acceptance of these figures as an indication of comparative inherent muscle-weight distribution could prove to be totally misleading.

The foregoing concentration on comparisons of muscle-weight distribution for genetic purposes should not detract from the importance of comparisons for meat trade purposes. The meat man has no interest in genetic implications of comparisons but is concerned at the proportions of various muscle groups within the carcase at a preferred weight or at a preferred level of fatness. Clearly, if the proportion of "expensive" muscles is higher in some cases than in others at the desired slaughter weight or degree of finish, this is of commercial interest.

As it is now clear that beyond about 20% of mature weight the proportion of "expensive" muscle weight is slowly falling it would be an advantage in muscle-weight distribution to slaughter as soon as possible beyond this point.

To achieve the same total muscle weight the smaller animals must proceed further towards maturity and hence will have the least desirable muscle-weight distribution. This appears to be the opposite finding to that which would be expected from the early work of Hammond and the reason for this has been well expressed by Pomeroy (1978) when he explained "certain defects" in the Cambridge dissection technique, which resulted in the loin muscles being described as "late developing". Fortunately the decline in the proportion of "expensive" muscle weight is very small as the maturity coefficient for the expensive muscles ('q' = 1.18), differs from total muscle by so little and it is therefore of little economic importance, particularly in castrates and females, where, as will be shown in later chapters, the differential muscle growth associated with the maturing process is minimal. In addition, as the decline in the proportion of "expensive" muscles occurs concurrently with an increase in muscle:bone ratio the total economic effect is small.

The changes of individual muscle weights and proportions between birth and maturity and the maturing patterns associated with those changes are shown in Appendix 5 Table 1.

It is important to note that the information presented in this section deals with only the period from about 20% mature up to maturity. As shown in Chapter 1 the phase of greatest variety of growth impetus of muscles was immediately postnatal. Consequently it would be expected that any attempts to compare inherent muscle-weight distribution during the phase from birth (about 4% mature in rams and 5-6% mature in ewes) up to 20 % maturity would be much more confounded by developmental changes than has been demonstrated for those made during the later stages of progress to maturity.

Table 2.c.8. Summary of impetus grouping of individual muscles from 20% mature to maturity of large and small mature size Merino rams (For detail see Appendix 5 Table 3)

	Large rams	Small rams
Muscles with 'q' < 1.0		
Number	25	22
% of total muscle weight	30.57	28.38
Mean 'q'	0.64	0.65
Muscles with 'q' = 1.0		
Number	30	35
% of total muscle	22.11	25.47
Mean 'q'	0.99	0.99
Muscles with 'q' > 1.0		
Number	38	36
% of total muscle	44.66	43.24
Mean 'q'	1.28	1.26
Total Muscle		
Number	93	93
% of total muscle	100	100
'q'	1.00	1.00

IMPETUS GROUPING:

It is instructive as a measure of "anatomical harmony" to group muscles into impetus groups and compare different types of animals. In Table 2.c.8. is shown a summary of such a comparison in large and small Merino rams. The detail showing the individual muscles is in Appendix 5 Table 3.

The very high degree of similarity of maturing patterns throughout the musculature of large and small sheep adds further support to the suggestion of Fowler (1980) that the main adaptation to increasing size is probably a decrease in the speed of movement.

d. THE INFLUENCE OF MATURE SIZE ON GROWTH WITHIN THE SKELETON

Callow (1962) showed that the weight of the major limb bones comprised a greater percentage of total bone weight in the heaviest of three breeds of cattle when compared at around 1200 lb liveweight. He noted that "there is no such effect on the pelvis or scapula". Callow suggested that this difference may have been in some way related to the function of weight support which he attributed to the former group of bones. It now appears that this difference observed by Callow is explainable, at least in part, on the basis of the maturing patterns of the various bones as Butterfield *et al.* (1983d) concluded that animals of different total bone weight, but of genetically similar bone-weight distribution, will, if compared at different proportions of their mature weight, have different bone-weight distribution.

The major limb bones listed by Callow; radius—ulna, humerus, femur and tibio-fibula; were all shown by Butterfield *et al.*, to develop early relative to total bone in sheep (i.e., all had 'q' values greater than 1.0). Therefore, if animals are compared at the same total bone weight and providing the maturing pattern of each bone is similar in the animals being compared, it is axiomatic that these bones will comprise a larger proportion of total bone weight in animals of larger mature bone weight, even though they comprise the same proportion of total bone weight at maturity.

Sheep studies have also shown that the pelvis which Callow identified as being not different in his three breeds of cattle of different size, has a maturing pattern which is very similar to that of total bone ('q' = 1.03) and therefore its proportion of total bone will remain virtually unchanged throughout the maturing process. The scapula with a 'q' of 0.73 comprises an increasing proportion of total bone weight and therefore in Callow's comparison was relatively lighter in the heaviest breed.

The differences observed by Callow may have been, in part, true breed differences as data are not available to allow us precisely to compare his animals at equal maturity, but on the other hand the data he presented could approximate the results expected purely on the basis of relative maturing patterns.

Of the major limb bones shown by Callow to be proportionately heavier in his heavy breed of cattle, it is the radius-ulna which is least different and it is also the bone in which the maturing pattern differs least from that of the total skeleton in sheep. It is, therefore, not surprising that Callow found the weight of this bone to be the best index of the weight of total bone when used on his mix of breeds.

Table 2.d.1. shows the weights of the individual bones of the mature skeleton of two strains of Merino rams and Table 2.d.2. shows these data as proportions of the weight of the mature skeletons.

As the skeletons differ by about 700 g the individual bone weights differ accordingly and comprise, in general, similar proportions of total bone weight. However, the four major weight-carrying long bones which Callow had shown to be proportionately heavier in his large breed of cattle were all marginally proportionately heavier in the heavier sheep skeletons and in total comprised 27.6% vs 25.9% and so the relationship between overall animal size and individual bone-weight distribution may be an additional factor to maturity patterns in determining part:whole relationships within the skeleton.

Kempster (1978) gave several examples from the literature and from M.L.C. data of larger cattle having a greater proportion of their bone weight in the limb bones when comparisons were made at similar total bone weight. However, he also pointed out that in cattle there is evidence that throughout the normal commercial slaughter weight range there is little difference in the rate of growth of individual bones. Kempster questioned if differences observed could be "due entirely to mature size or whether other factors are involved". A striking example which does not support this idea of disproportionately larger limb bones in larger animals comes from Davies and Henning (1985) who worked with the extremes of the Göttingen miniature pig and the German Landrace. They concluded that the larger pigs (approximately six times larger) "support their weight without need of a disproportionate development of supporting structures . . ."

Maturity coefficients for large and small Merino rams are shown in Table 2.d.3. and these, in general, are similar for both strains. Only the tarsus and the cervical vertebrae had significantly different 'q' values, and these are both aggregates of small bones of little importance in the overall picture and pooled values are given for all bones.

In Table 2.d.4. can be seen the progress to its mature weight of each bone relative to the progress of total bone; so that, for example, when total bone is 50% mature, then the femur is 59%, the scapula 43% and the axial skeleton 47% mature. It is, of course, possible from the use of such information along with the mature weights given in the table, to establish the actual weights of any bone at any stage of maturity of total bone weight.

Using the mature weights of bones and their maturing patterns it is possible to calculate the weight of any bone at the mean total bone weight of all available animals and also at the

Table 2.d.1. Weights of individual bones in the half carcase of mature rams from large and small Merino strains (Data from Butterfield *et al.*, 1983d)

Individual bones	Weight (g) Large	Weight (g) Small
Hindlimb		
Femur	261	189
Patella	16	11
Tibia	228	165
Tarsus	80	54
Axial Skeleton		
Pelvis + sacrum	314	232
Lumbar vertebra	278	221
Thoracic vertebra + ribs	858	699
Cervical vertebra	405	313
Sternum	172	153
Forelimb		
Scapula	163	126
Humerus	213	151
Radius/ulna	179	128
Carpus	33	22
Total bone	3200	2464
Liveweight (kg)	116.5	90.9

Table 2.d.2. Weights of individual bones as percentages of total bone weight in the half carcase of mature rams from large and small Merino strains

	Percent of total bone Large	Percent of total bone Small
Hindlimb		
Femur	8.2	7.7
Patella	0.5	0.5
Tibia	7.1	6.8
Tarsus	2.5	2.2
Axial Skeleton		
Pelvis + sacrum	9.8	9.4
Lumbar vertebrae	8.6	8.9
Thoracic vertebrae + ribs	26.8	28.3
Cervical vertebrae	12.7	12.6
Sternum	5.4	6.2
Forelimb		
Scapula	5.1	5.1
Humerus	6.7	6.2
Radius/ulna	5.6	5.2
Carpus	1.0	0.9
Total bone	100	100

Table 2.d.3. Maturity coefficients 'q' for weights of carcase bones relative to weight of total bone of large and small mature size Merino rams

	Pooled 'q'
Hindlimb	
Femur	1.37
Patella	1.48
Tibia	1.32
Tarsus	1.42
Whole limb	1.36
Axial Skeleton	
Pelvis + sacrum	1.03
Lumbar vertebrae	0.88
Thoracic vertebrae + ribs	0.83
Cervical vertebrae	0.74
Sternum	1.16
Whole axis	0.88
Forelimb	
Scapula	0.73
Humerus	1.23
Radius and Ulna	1.18
Carpus	1.26
Whole limb	1.07

Table 2.d.4. The progress to maturity of bone weights of large and small mature size Merino rams relative to the progress to maturity of total bone weight

	Percentage maturity									Mature Weight Grams (½ carcase)	
										Large	Small
Total bone	20	30	40	50	60	70	80	90	100 =	3200	2464
Hind limb											
Femur	26	38	49	59	69	78	86	93	100 =	261	189
Patella	28	40	52	62	72	80	88	94	100 =	16	11
Tibia	25	37	48	58	68	77	85	93	100 =	228	165
Tarsus	27	39	50	61	70	79	87	94	100 =	80	54
Whole limb	26	38	49	59	69	78	86	93	100 =	585	419
Axial Skeleton											
Pelvis + sacrum	20	31	41	51	61	71	80	90	100 =	314	232
Lumbar vertebrae	18	27	37	47	57	67	78	89	100 =	278	221
Thoracic vertebrae and ribs	17	26	36	46	56	66	77	88	100 =	858	699
Cervical vertebrae	16	25	34	44	54	65	76	88	100 =	405	313
Sternum	23	33	44	54	64	73	83	91	100 =	172	153
Whole axis	18	27	37	47	57	67	78	89	100 =	2027	1618
Forelimb											
Scapula	16	24	34	43	54	64	76	88	100 =	163	126
Humerus	24	35	46	56	66	75	84	92	100 =	213	151
Radius/Ulna	23	34	44	55	64	74	83	92	100 =	179	128
Carpus	24	35	46	57	66	75	84	92	100 =	33	22
Whole limb	21	31	42	52	62	71	81	91	100 =	588	427

same proportion of mature total bone weight and this is shown in Table 2.d.5. There are differences on both bases of comparison, and, although they are reduced in the majority of cases at equal maturity, Kempster's doubt regarding stage of maturity being the only factor in observed differences is well supported by the differences which remain at equal maturity.

Despite the finding of Davies and Henning (1985) in pigs, it seems that mature weight of the animal and the mature weight of the skeleton may be separate factors in the relative growth of bones in sheep and possibly cattle. The mature weight of each bone predetermines the weight which it will be at any stage of the maturing process of the skeleton. The mature weight of the animal may determine genetically the proportion of the total skeleton weight which is distributed into each bone.

Table 2.d.5. The weights of individual bones as percentages of total bone weight for large and small mature size Merino rams after adjustment to (i) the same total bone weight (2.0 kg), and (ii) the same proportion of mature total bone weight (0.73) of the available data

Bones	At same total bone weight			At same proportion of mature total bone weight		
	Large	Small	Diff.	Large	Small	Diff.
Hind limb						
Femur	9.4	8.2	1.2	9.1	8.6	0.5
Patella	0.6	0.5	0.1	0.6	0.5	0.1
Tibia	8.2	7.2	1.0	7.9	7.4	0.5
Tarsus	2.8	2.5	0.3	2.7	2.6	0.1
Axial Skeleton						
Pelvis and sacrum	10.3	9.6	0.7	10.2	9.8	0.4
Lumbar vertebraee	8.4	8.8	0.4	8.5	8.7	0.2
Thoracic vertebrae and ribs	26.4	28.2	1.8	26.5	28.1	1.6
Cervical vertebrae	13.4	11.8	1.6	13.2	11.2	2.0
Sternum	5.9	6.5	0.6	5.8	6.7	0.9
Forelimb						
Scapula	4.9	5.0	0.1	5.0	5.0	–
Humerus	7.5	6.5	1.0	7.3	6.7	0.6
Radius and ulna	6.2	5.5	0.7	6.0	5.6	0.4
Carpus	1.2	1.0	0.2	1.1	1.0	0.1
TOTAL DIFF.	–	–	9.7	–	–	7.4

It seems that large mature size sheep may have a greater proportion of skeletal weight in limb bones than small mature size sheep. However, the progress of each bone to its mature weight is likely to be along the same path for that bone irrespective of the magnitude of that mature weight relative to the mature weight of the whole skeleton. Therefore, the weight of any limb bone at a particular skeleton weight may be a function of (a) the mature weight of the animal; (b) the mature weight of the skeleton; (c) the stage of maturity of the bone.

e. THE INFLUENCE OF MATURE SIZE ON GROWTH WITHIN THE BODY FAT

Wood (1982) stated that the partitioning of fat was not influenced by mature size but rather by breed itself and further that: "There is no difference in fat partitioning of mature animals of different breeds which can be related to their mature size. However, if the mature sizes of breeds are different, this will have an effect on the fat partitioning of animals killed at the same body weight or the same weight of fat because fat depots grow at characteristic rates. Thus intermuscular fat would form a higher proportion of total fat in a late maturing breed (large body size) and subcutaneous fat would form a higher proportion in an early maturing breed.

If different breeds are compared at the same stage of maturity of body fat, and differences in fat partitioning are found, then a true breed effect exists. However, subcutaneous fat alone cannot be used to describe stage of maturity of fat since it may itself be contributing to the difference in fat partitioning." (Wood, Personal communication, 1985.)

This section aims at throwing some light on two of the variables which could influence fat partitioning, namely the difference in weight of the total fat stores when the animal reaches maturity, and the maturing patterns of the various partitions. This is in line with Fitzhugh and Taylor's (1971) concept of dividing any measurement of size into the two components; mature size and proportion of mature size achieved as explained by the quote which heads this chapter.

In order that a decision can be made on the genetic validity of comparisons of fat partitioning of animals of different mature fat weight, it is necessary to know the maturing pattern of each fat partition relative to the maturing pattern of total fat. If a partition has a similar maturing pattern to total fat (i.e. 'q' NSD from 1.0) then comparisons of the proportion in this partition in two animals at equal fat weight will give a similar answer to comparison at equal maturity of total fat weight. However, if a fat partition has a maturing pattern which differs significantly from that of total fat ('q' is greater or less than 1.0) then it is only from comparison at the same degree of maturity that useful genetic conclusions can be drawn. Butterfield *et al.* (1983d) and Thompson (1983) presented maturing patterns of fat partitions of Merino rams under high plane nutrition. In both studies, although the mature total fat weights were different proportions (38 vs 30%) of total body weight, the partitioning of fat in the mature animals of all strains was remarkably similar at maturity.

Table 2.e.1. shows the mature weights of the various fat partitions and Table 2.e.2. shows the same values as percentages of total fat weight in the two strains of Butterfield *et al.* and these data reveal a general similarity of fat-partitioning in the two strains.

Using the data from mature rams (Table 2.e.1.) and that from immature rams, the maturity coefficients for the fat partitions were calculated and are shown in Table 2.e.3. and are, with only one small exception, not different from 1.0. It

Table 2.e.1. Weight of partitions of fat in mature large and small Merino rams (Butterfield *et al.*, 1983d)

Fat Partition	Weight (kg) Large	Small	Large:Small
Carcase	27.37	21.08	1.3
Kidney plus channel	4.20	3.91	1.1
Omental	7.20	5.18	1.4
Mesenteric	3.20	2.98	1.1
Scrotal	0.80	1.17	0.7
Total body	42.77	34.32	1.3

Table 2.e.2 Fat partitions as percentages of total body fat weight in mature large and small Merino rams (Data from Butterfield *et al.*, 1983d)

Fat Partition	Percent of total fat Large	Small
Carcase	64	61
Kidney plus channel	10	12
Omental	17	15
Mesenteric	7	9
Scrotal	2	3
Total body	100	100

Table 2.e.3. Maturity coefficients of fat partitions of large and small Merino rams relative to progress to maturity of total body fat (adapted from Butterfield *et al.*, 1983d)

Fat partition	'q'			Relative to
	Large Rams	Small Rams	Pooled	1.0
Carcase	1.01	1.08	1.04	N.S.D.
Kidney plus channel	0.80	0.73	0.77	N.S.D.
Omental	1.10	1.10	1.10	N.S.D.
Mesenteric	1.06	0.95	1.01	N.S.D.
Scrotal	0.50	0.23	0.38	Sig. diff.

Table 2.e.4. Maturity coefficients of fat partitions of large, medium and small Merino rams relative to progress to maturity of total body fat (adapted from Thompson 1983)

Depot	'q'				Relative
	Large	Medium	Small	Pooled	to 1.0
Subcutaneous	1.1	1.3	1.8	–	NSD
Intermuscular	1.2	1.3	1.3	1.3	Greater
Carcase	1.2	1.3	1.1	1.2	NSD
Kidney	0.9	0.5	0.9	0.8	NSD
Omental	0.5	0.5	0.8	0.6	Less
Mesenteric	0.9	0.8	1.3	–	NSD
Scrotal	1.4	1.0	1.3	1.2	Greater

was unfortunate that in this study of Butterfield *et al.*, carcase fat was not divided into subcutaneous and intermuscular depots. However, in Thompson's study this separation was made and maturity coefficients from his rams are set out in Table 2.e.4.

The most important findings by Thompson were that there were significant differences between strains in 'q' values for subcutaneous and mesenteric fat in his rams of different size and that three partitions had 'q' values different from 1.0 (intermuscular, omental and scrotal). Surprisingly the scrotal partition was markedly early developing ('q' = 1.4) indicating low impetus growth, whereas Butterfield *et al.* had found a 'q' of only 0.4, indicating late development or high impetus growth. However, this scrotal partition is very small and the unresolved question of its maturity pattern should not be allowed to cloud the general picture.

Set out in Table 2.e.5. are the approximate maturing patterns of the various fat partitions in large and small rams based on the work of Thompson (1983).

Table 2.e.5. Maturing patterns of fat partitions in large and small Merino rams (adapted from Thompson 1983)

Depot	Mature size	Proportion of mature weight									Mature weight (kg)
Total body fat	Large Small	20	30	40	50	60	70	80	90	100	= 23.44 = 17.25
Subcutaneous	Large	22	32	42	53	62	72	82	91	100	= L 6.69
	Small	17	26	35	45	55	66	77	88	100	= S 5.35
Intermuscular		25	36	47	58	67	76	85	93	100	= L 7.47 S 4.85
Total carcase fat		23	34	45	55	65	74	83	92	100	= L 14.16 S 10.20
Kidney		17	26	35	45	55	66	77	88	100	= L 2.37 S 2.20
Omental		14	22	30	40	50	62	74	86	100	= L 4.55 S 3.00
Mesenteric	Large	18	28	38	48	58	68	78	89	100	= L 1.70
	Small	25	36	47	58	67	76	85	93	100	= S 1.30
Scrotal		23	34	45	55	65	74	83	92	100	= L 0.66 S 0.55

Because of the similarity of all the maturing patterns of the various partitions of fat in Butterfield *et al.*'s study, it seemed that stage of maturity was unlikely to be of importance in comparisons of fat partitioning and their comparisons at equal weight and equal stage of maturity yielded similar results. However, the work of Thompson (1983) showed "small strain differences" in maturing patterns of the partitions and indicated that it is necessary to know the patterns in the particular animals under consideration. This is supported by the work of Butler-Hogg (1984) working with Clun and Southdown sheep who showed that there was "a pattern of development of individual fat depots which is related to the total fatness of the animal and therefore its stage of maturity." (Butler-Hogg was using the term "depots" in this context to refer to partitions.)

Butler-Hogg suggested that the ranking of the non-significant differences in maturing patterns of fat partitions by Butterfield *et al.* was similar to his and this is so. However, his assumption that subcutaneous fat is necessarily "late maturing" relative to total body fat was not supported by the subsequent study in Merino rams by Thompson (1983) although it tended to be so in Dorset Horn rams and wethers of Butterfield *et al.* (1985c).

All of these minor disagreements highlight that we are probably, when discussing fat growth, dealing with many unknown variables associated with nutritional and genetic difference.

Much more information is still required to meet Kempster's (1980) requirements to be able to make accurate predictions "of fat development in practical circumstances . . ."

f. THE INFLUENCE OF MATURE SIZE ON THE GROWTH OF BODY ORGANS

It is important to determine the maturing patterns of body organs if we are to understand the anatomical and physiological changes in animals during growth. It is also important that genetic comparisons of proportions within the viscera and proportions of non-carcase relative to carcase structures be made in full knowledge of the effect of any changing proportions in body structures. In this section we are concerned with the relationship between the mature weights of sheep and of their component organs and the patterns on which these component organs proceed to their mature weight relative to the progress to maturity of total body weight. Knowing this we can predict the likely weight of any body organ throughout the maturing process.

Set out in Table 2.f.1. are the mature weights and the percentages which they comprise of liveweight at maturity of the body organs of large and small mature size rams. These data show a generally similar proportion of live-weight represented by each of the body organs at maturity in the two strains of sheep. The maturity coefficients are shown in Table 2.f.2. where it is seen that with 'q' values significantly greater than 1.0, almost all organs are early developing, but that the degree of early development is extremely variable with 'q' values ranging from 1.2 to 5.7. The maturing patterns are set out in Table 2.f.3. and show the wide diversity of progress associated with the 'q' values. For example, when the animal has achieved 50% of its mature weight, the small intestine has achieved 168%, the liver 87%, the heart 71%, the brain 90% and the hide 54%, of their mature weights.

The biological significance of the maturing patterns of the various organs is of considerable interest and was discussed in Chapter 1.f. Suffice that here we note the general pattern of early development of organs and non-carcase structures, and highlight the significance of this differential growth in com-

Table 2.f.1. Weights of individual organs and organ contents and their percentage of liveweight of mature Merino rams of large and small mature size (From Butterfield *et. al.*, 1983c)

	Weight (kg)		Percent of SFLW†	
	Large n = 3	Small n = 3	Large n = 3	Small n = 3
Alimentary tract				
Oesophagus	0.10	0.07	0.08	0.07
Ruminoreticulum	1.13	0.86	0.94	0.89
Omasum	0.13	0.08	0.11	0.09
Abomasum	0.27	0.21	0.23	0.22
Small intestine	0.66	0.38	0.56	0.39
Large intestine	0.58	0.47	0.49	0.49
Total	2.87	2.08	2.41	2.15
Alimentary tract contents				
Ruminoreticulum contents	5.02	4.23	4.17	4.31
Omasum contents	0.15	0.16	0.13	0.16
Abomasum contents	0.34	0.37	0.28	0.39
Small intestine contents	0.77	0.50	0.64	0.51
Large intestine contents	1.06	0.70	0.89	0.73
Total	7.33	5.95	6.11	6.10
Other major internal organs				
Liver	1.26	0.95	1.05	0.97
Kidneys	0.21	0.20	0.18	0.20
Spleen	0.14	0.10	0.11	0.11
Heart	0.35	0.28	0.29	0.29
Trachea	0.08	0.06	0.07	0.06
Lungs	0.53	0.48	0.45	0.49
Thyroid	0.02	0.02	0.02	0.02
Pancreas	0.07	0.06	0.06	0.06
Total	2.66	2.15	2.23	2.20
Central nervous system				
Brain	0.11	0.11	0.09	0.11
Eyes	0.03	0.03	0.03	0.03
Total	0.14	0.14	0.12	0.14
Miscellaneous components Blood				
Blood	4.50	2.99	3.77	3.07
Head	6.84	6.55	5.72	6.74
Penis + bladder	0.11	0.08	0.09	0.08
Hide	9.86	9.36	8.17	9.79
Distal limbs	1.65	1.54	1.38	1.59
Total	22.95	20.52	19.13	21.27
Shorn empty liveweight	112.32	91.17	93.89	93.90
Shorn full liveweight	119.66	97.12	100.00	100.00

* rounding of numbers may lead to differences between sum of components and figure for total
+ SFLW = Shorn full live weight

Table 2.f.2 Maturity coefficients of body organs and organ contents of large (n = 19) and small (n = 16) mature size Merino rams, relative to the progress to maturity of shorn full liveweight (from Butterfield *et al.* 1983c)

	'q'	s.e.
Alimentary tract		
Oesophagus	1.82a*	0.10
Ruminoreticulum	2.32a	0.19
Omasum	L 2.76a	0.21
	S 3.96a	0.42
Abomasum	2.13a	0.19
Small intestine	5.72a	0.36
Large intestine	3.23a	0.23
Total	3.20a	0.16
Alimentary tract contents		
Ruminoreticulum contents	2.14a	0.22
Omasum contents	2.88a	0.24
Abomasum contents	1.74a	0.31
Small intestine contents	4.35a	0.30
Large intestine contents	3.43a	0.32
Total	2.50a	0.19
Other major internal organs		
Liver	2.47a	0.17
Kidneys	1.96a	0.10
Spleen	1.40a	0.09
Heart	1.83a	0.05
Trachea	2.51a	0.13
Lungs	2.33a	0.14
Thyroid	L 3.55a	0.94
	S 0.86	0.38
Pancreas	2.07a	0.12
Total	2.24a	0.12
Central Nervous system		
Brain	'b'† = 0.25	0.02
Eyes	'b' = 0.40	0.03
Total	'b' = 0.29	0.02
Miscellaneous components		
Blood	1.56a	0.07
Head	L 1.40a	0.06
	S 1.16a	0.08
Penis + bladder	1.17	0.10
Hide	1.15	0.13
Distal limbs	1.86a	0.08
Total	1.32a	0.06
Shorn empty liveweight	0.90b	0.01

* a, b : 'q' is greater and less than 1 respectively ($P < 0.05$)
† 'b' The values given under 'q' for eyes and brain are not 'q' values as quadratic regressions were unsuitable to represent the maturing patterns of these organs. The linear regression $y = a + bx$ (constrained to pass through (1, 1)) was used to calculate the progress to maturity of these organs.

parisons of animals, of different inherent size. All body organs shown having 'q' values of more than 1.0 therefore have declining weight increments as the maturing process proceeds.

Once the mature size of breeds and the maturing patterns of the organs are more accurately known, then comparisons can become meaningful between breeds and strains of different size. The information currently available should be regarded as merely the beginning.

The need for this work is shown in the comparison of organ weights from large and small strains set out in Table 2.f.4. Here it is seen that there is little relationship between the results of comparison at equal weight and those at equal maturity. Some differences which were large and highly significant at equal weight, became small and non-significant at equal proportion of mature weight, e.g. heart and large intestine; whereas some differences which were small and non-significant at equal weight, became large and highly significant at equal proportion of mature weight, e.g. distal limbs and omasum contents. Nevertheless, a greater number of the structures are more similar than dissimilar at the same stage of maturity as would be expected from the likeness of the mature composition of the two strains and the similarity of maturing patterns in the strains, but this need not always be so if strains or breeds are compared which are different in composition at maturity or in which organs have different maturing patterns.

Table 2.f.3. Maturing patterns from 20% mature to maturity of body organs and organ contents of large and small mature size Merino rams, relative to the progress to maturity of shorn full liveweight

											Mature weight (kg)	
					Percentage maturity						Large	Small
Shorn full liveweight		20	30	40	50	60	70	80	90	100 =	119.66	97.12
Alimentary tract												
Oesophagus		33	47	60	70	80	87	93	97	100 =	0.10	0.07
Ruminoreticulum		41	58	72	83	92	98	101	102	100 =	1.13	0.86
Omasum	L	48	67	82	94	102	107	108	106	100 =	0.13	–
	S	67	92	111	124	131	132	127	117	100 =	–	0.08
Abomasum		38	54	67	78	87	94	98	100	100 =	0.27	0.21
Small intestine		96	129	153	168	173	169	156	132	100 =	0.66	0.38
Large intestine		56	77	94	106	114	117	116	110	100 =	0.58	0.47
Total		55	76	93	105	113	116	115	110	100 =	2.87	2.08
Alimentary tract contents												
Ruminoreticulum contents		38	54	67	78	87	94	98	100	100 =	5.02	4.23
Omasum contents		50	69	85	97	105	109	110	107	100 =	0.15	0.16
Abomasum contents		32	46	58	68	78	86	92	97	100 =	0.34	0.37
Small intestine contents		74	100	120	134	140	140	134	120	100 =	0.77	0.50
Large intestine contents		59	81	98	111	118	121	119	112	100 =	1.06	0.70
Total		44	61	76	87	96	101	104	103	100 =	7.33	5.95
Other major internal organs												
Liver		44	61	75	87	95	101	104	103	100 =	1.26	0.95
Kidneys		35	50	63	74	83	90	95	99	100 =	0.21	0.20
Spleen		26	38	50	60	70	78	86	94	100 =	0.14	0.10
Heart		33	47	60	71	80	87	93	97	100 =	0.35	0.28
Trachea		44	62	76	88	96	102	104	104	100 =	0.08	0.06
Lungs		41	58	72	83	92	98	101	102	100 =	0.53	0.48
Thyroid	L	61	84	101	114	121	124	121	113	100 =	0.02	–
	S	18	27	37	46	57	67	78	89	100 =	–	0.02
Pancreas		37	52	66	77	86	92	97	100	100 =	0.07	0.06
Total		40	56	70	81	90	96	100	101	100 =	2.66	2.15
Central nervous system												
Brain		80	82	85	87	90	92	95	97	100 =	0.11	0.11
Eyes		68	72	76	80	84	88	92	96	100 =	0.03	0.03
Total		77	80	83	85	88	91	94	97	100 =	0.14	0.14
Miscellaneous components												
Blood		29	42	53	64	73	82	89	95	100 =	4.50	2.99
Head	L	26	38	50	60	70	78	86	94	100 =	6.84	–
	S	23	33	44	54	64	73	83	91	100 =	–	6.55
Penis + bladder		23	34	44	54	64	74	83	92	100 =	0.11	0.08
Hide		22	33	44	54	64	73	82	91	100 =	9.86	9.36
Distal limbs		34	48	61	71	81	88	94	98	100 =	1.65	1.54
Total		25	37	48	58	68	77	85	93	100 =	22.94	20.52
Shorn empty liveweight		18	28	38	47	58	68	78	89	100 =	112.32	91.17

L,S. = Large and small rams respectively

A recent example of the limitations to genetic interpretation of comparisons made at some specific objective measure is seen in the study of Jones, Rompala, Wilton and Watson (1984), who, for commercial purposes, compared dressing percentage and proportions of body organs of large and small breeds of cattle at equal fat thickness. Their conclusion was that: "Large animals had a greater proportion of warm carcase weight and hind feet and a lower proportion of head, hide, liver, kidneys, omasum and small intestine." Ignoring the hind feet, all these differences could be explained by different stage of maturity. Accepting the risk of using information derived from sheep the carcase weight is late developing ($q < 1.0$) and all the other organs mentioned are early developing ($q > 1.0$) therefore the results achieved by Jones *et al.* are as would be expected if the large and small breeds had the same composition at maturity and were slaughtered when the large ones were more mature. On the other hand, the same thickness of fat may be, in many cases, a close approximation to equal stage of maturity in animals of different genetic size and the differences in proportions of organs are really genetic. However, it must be borne in mind that a large breed and a small breed are not expected to have the same *thickness* of subcutaneous fat at the same stage of progress to maturity of this fat depot. The problem is that, without more information on maturing patterns in cattle, it is

Table 2.f.4. The weights of body organs and organ contents as percentages of shorn full liveweight for large and small mature size Merino rams after adjustment to (1) the same shorn full liveweight (68 kg) and (2) the same proportion of mature shorn full liveweight (0.62)

	At the same shorn full liveweight			At the same proportion of maturity		
Organ/organ content	Large mature size	Small mature size	Significance size	Large mature size	Small mature	Significance
Alimentary tract						
Oesophagus	0.11	0.09	***	0.11	0.10	*
Ruminoreticulum	1.49	1.25	*	1.42	1.34	NS
Omasum	0.19	0.16	*	0.18	0.18	NS
Abomasum	0.34	0.30	NS	0.32	0.31	NS
Small intestine	1.69	0.95	***	1.54	1.09	***
Large intestine	0.95	0.81	**	0.90	0.90	NS
Total	4.70	3.58	***	4.40	3.93	*
Alimentary tract contents						
Ruminoreticulum contents	6.27	5.86	NS	6.00	6.23	NS
Omasum contents	0.23	0.25	NS	0.22	0.27	**
Abomasum contents	0.38	0.47	NS	0.37	0.49	*
Small intestine contents	1.57	1.03	***	1.45	1.16	**
Large intestine contents	1.82	1.25	***	1.70	1.39	*
Total	10.12	8.92	NS	9.61	9.61	NS
Other major internal organs						
Liver	1.72	1.41	**	1.63	1.52	NS
Kidneys	0.25	0.26	NS	0.25	0.28	**
Spleen	0.13	0.12	**	0.13	0.12	NS
Heart	0.40	0.36	***	0.39	0.38	NS
Trachea	0.11	0.09	***	0.11	0.10	*
Lungs	0.70	0.69	NS	0.67	0.74	NS
Thyroid	0.03	0.02	NS	0.03	0.02	NS
Pancreas	0.09	0.09	NS	0.09	0.09	NS
Total	3.43	3.06	*	3.27	3.26	NS
Miscellaneous components						
Blood	4.67	3.60	***	4.55	3.73	***
Head	6.70	7.07	NS	6.58	7.15	*
Penis + bladder	0.10	0.09	*	0.10	0.09	*
Hide	8.78	10.08	*	8.71	10.19	*
Distal limbs	1.89	2.00	NS	1.82	2.11	***
Total	22.44	23.65	NS	22.08	24.17	**
Shorn empty liveweight	89.79	91.02	*	90.32	90.32	NS

not possible to apportion the difference between the stage of maturity and the mature composition and therefore no conclusion can be drawn about the genetic composition of these cattle. This is in no way critical of the study by Jones *et al.* which was carried out for a specific purpose unrelated to genetic comparison.

Butterfield *et al.* (1983c) concluded that "... in genetic comparisons of animals of different mature size, the most appropriate basis of comparison of relative organ weight will be at the same proportion of mature liveweight." However, a great deal more information is needed on mature sizes and maturing patterns achieved under various conditions before confidence can be placed on any comparison except those made under nutritional conditions which are similar to those from which mature weight and maturing patterns are derived.

It is also desirable that the knowledge of maturing patterns be extended back to birth and also antenatally. Some structures, such as the small intestine, will possess quite different patterns in the early post-natal period to those demonstrated here and consequently comparisons of proportions in animals of different mature size during this period will embrace different problems.

g. CONCLUSIONS

(a) *Composition*

The differences in structure and in composition of mature sheep which can be directly related to size appear to be few. The information available shows little if any real difference in the proportions of carcase tissues relative to liveweight, in muscleweight distribution, or in fat partitioning. There does appear to be an effect of size on bone weight in that it is greater as a proportion of liveweight in larger animals (Fig. 2.b.1.); and on the distribution of bone weight, in that the major limb bones are proportionately heavier in larger animals, however, these differences are not of major degree and is not supported by evidence from widely diverse mature size pig breeds.

(b) *Maturing Patterns*

In order that the general similarity of composition of mature animals be reflected throughout the growth process, it is necessary that each tissue and individual structure should have the same maturing patterns irrespective of size. This is essentially what occurs. Very few structures and tissues differ in their maturing patterns because of size. In Butterfield *et al.*'s studies, muscle, bone and carcase fat each share the same maturity coefficients in large and small rams; 78 of the 93 individual muscles share common maturing patterns; eight out of nine "Standard Muscle Groups" share common patterns; as do all five fat partitions and 11 out of 13 skeletal components. Even body organs maintain the record with only three of the 26 structures exhibiting different maturity coefficients and one of these is the head where the horns obviously play a part.

It is apparent, therefore, that there is a general similarity of composition of animals as they proceed to maturity which is not generally affected by the inherent size of those animals. So why do we need to concern ourselves with mature size?

If we are interested in the composition of animals only in reference to some meat trade or other non-genetic requirement, then there might seem to be no need to concern ourselves with the problems related to different mature size. However, if the need is to discover the inherent differences and similarities of the composition of animals, it is essential that we understand that comparisons at other than equal proportion of maturity may give very misleading results because many tissues do not grow at the same rate as the total animal. Hence, at any specific point selected for a particular comparison which is at other than equal stage of maturity, there will be a confusion of the differences due to the stage of maturity and those due to inherent structure.

MAJOR REFERENCES FOR CHAPTER 2

Butterfield *et al.* (1983a, b, c, d) "Changes in body composition relative to weight and maturity in large and small strains of Australian Merino rams"

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Thompson (1983) "Feed intake, growth and body composition in flocks of Merino sheep selected for high and low weaning weight"

Thompson *et al.* (1985/6) "Food intake growth and body composition in Australian Merino sheep selected for high and low weaning weight"

Thonney *et al.* (1986) "Breed and sex differences in muscle distribution of equally mature sheep and goats"

Wood (1982) "Factors controlling fat deposition in meat animals"

CHAPTER 3

THE INFLUENCE OF CASTRATION ON THE GROWTH OF SHEEP

a. INTRODUCTION

The practice of castration of meat animals has a variable acceptance throughout the world and across the species, although it is of very ancient origin, in that it was widespread in the time of Aristotle in 350 BC (Short, 1980). Whereas the castration of pigs for slaughter is mandatory in Canada, it has been largely abandoned in Australia. Yet castration of cattle is almost universal in Australia but is regarded as an act of stupidity in Italy. In sheep, castration of lambs due for slaughter as lambs, is currently being questioned in many countries, not only because of its alleged undesirable effect on body composition, but also in light of growth efficiency, humanitarian considerations and the doubtful commonsense of surgically interfering with lambs almost on the eve of slaughter. As long ago as 1951 Walker demonstrated the main advantages to be gained from rearing ram lambs in New Zealand and suggested that, if two-thirds of New Zealand's male lambs were to be left uncastrated, this would add 1,000 tons of meat annually to New Zealand production.

The various reasons for, and effects of, castration have been given as "to reduce restlessness and spontaneous activity" (Hoskins, 1925) "to depress growth and mature size, to facilitate fattening, to increase palatability of meat, and to increase dressing percentage" (Brody, 1945). Within this assortment of reasons and alleged affects there is scope for considerable critical assessment. Does a castrated lamb, prior to its early slaughter, burn up less energy in frivolous activity than a ram lamb? Does the present-day consumer prefer the meat of the castrate? Does castration depress mature size? Is a high dressing percentage a desirable characteristic if its achievement is linked with increased fatness? Can the pain of castration be justified in lambs destined for early slaughter?

We do not set out to answer all of these questions but rather attempt to provide a little of the scientific basis from which at least some of the questions can be approached. Although it is generally known that castration modifies body composition, the detail of how the various modifications are effected throughout the growth span need to be further explored as modifications of body composition may not be uniform throughout the growth process. Is the expression of the genetic factor for mature weight, A, of Taylor (1982) for each body structure, modified immediately by castration so that relative growth impetus of tissues is changed, or does the growth of some tissues and structures merely cease earlier, or continue longer, in the castrate than in the entire male animal? In other words, are the patterns by which tissues proceed to maturity modified by castration, or do the tissues merely proceed at the same rates relative to their modified mature size? It is important that we establish the answers to these fundamental questions if we are to be able to derive the most useful basis for comparisons of castrated sheep with those of other sex status.

b. THE INFLUENCE OF CASTRATION ON THE GROWTH OF CARCASE TISSUES

As discussed in Chapter 1.b. the preferred method of study of growth of carcase tissues is by the derivation of maturing patterns based on full liveweight expressed as proportions of mature full liveweight with each carcase tissue weight expressed as a proportion of its own mature weight.

The first step in determining maturing patterns of the carcase tissues is to obtain the mature weights of rams and wethers and their tissues. Data set out in Table 3.b.1. show that, even though the weights of mature rams and wethers are similar and that the total weight of carcase tissues are almost identical, the contribution of each carcase tissue is different. This is shown more clearly in Table 3.b.2. where the proportional contribution of the tissues to liveweight is shown. A further comparison is shown in Table 3.b.3 where the influence of head and testes is removed. The difference in assessment of proportionate composition with and without head and testes can be seen in Figure 3.b.1. where it is clear that their exclusion reduces the differences between rams and wethers in so far as fat and carcase weight are concerned but increases the differences in muscle and bone.

Table 3.b.1. Live weight and weights of carcase tissues in Mature Dorset Horn rams and wethers. (Adapted from Butterfield *et al.*, 1984a)

	kg Rams N = 5	 Wethers N = 7	 Effect of Castration
Shorn full liveweight	99.7	95.9	−3.8
Liveweight minus head and testes	93.1	92.5	−0.6
Whole carcase tissues			
Muscle	24.7	21.9	−2.8
Bone	4.7	4.0	−0.7
Fat	24.7	28.8	+4.1
Carcase	54.1	54.7	+0.6

Table 3.b.2. Weights of carcase tissues expressed as percentages of shorn full liveweight in mature Dorset Horn rams and wethers (Adapted from Butterfield *et al.*, 1984a)

	% of shorn full liveweight Rams N = 5	 Wethers N = 7	 Effect of castration
Liveweight minus head and testes	93.4	96.5	+3.1
Whole carcase tissues			
Muscle	24.8	22.9	−1.9
Bone	4.7	4.2	−0.5
Fat	24.8	30.0	+5.2
Carcase	54.3	57.1	+2.8

Table 3.b.3. Weights of carcase tissues as percentages of shorn liveweight minus head and testes of mature Dorset Horn rams and wethers

	% of shorn liveweight less head and testes Rams N = 5	 Wethers N = 7	 Effect of Castration
Whole carcase tissues			
Muscle	26.5	23.7	−2.8
Bone	5.1	4.3	−0.8
Fat	26.5	31.1	+4.6
Carcase	58.1	59.1	+1.0

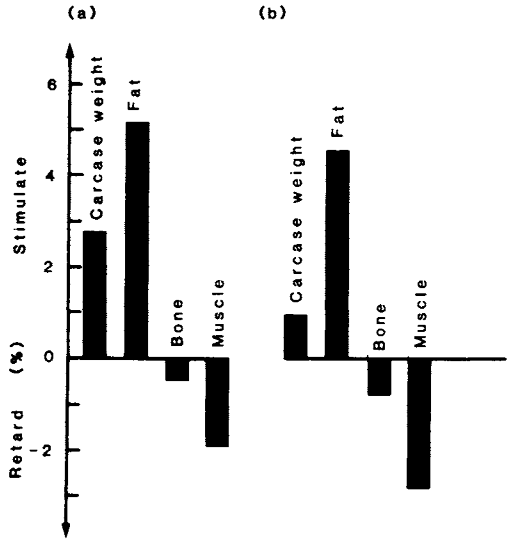


Figure 3.b.1.
The effect of castration on the proportionate composition of Dorset Horn rams and wethers compared at (a) proportions of fleece-free full liveweight; and (b) proportions of fleece-free full liveweight minus head and testes. Values are percentage units of liveweight.

Short (1980) suggested that the difference in size between male and female cattle or sheep must be androgen-dependent because the weights of castrated animals were less than those of entire males. More recent work suggests that there is little difference in the mature weights of entire and castrated male pigs (Walstra, 1980) or sheep (Butterfield *et al.*, 1984a). However, there is a depression of the non-fat carcase tissues by castration which is compensated by fat growth, and is accompanied by smaller appetites and slower growth in the castrates. Therefore, if mature weight is defined by the technique of Taylor (1982) which fixes the level of fatness, the wethers would be lighter at maturity than the rams. This approach is NOT adopted in this book; however, implications of such a procedure are particularly apparent in the comparison of males and castrates as the size scaling would be based on very different composition in each method.

By the use of the mature values in Table 3.b.1. and data from immature animals, maturing patterns can be derived and these are shown by maturity coefficients in Table 3.b.4.

Castration apparently does not significantly alter the maturing patterns of muscle, bone or fat and hence common 'q' values can be used to define the maturing patterns of these three major carcase tissues of rams and wethers. An example of patterns derived for Dorset Horn rams and wethers is shown in Figure 3.b.2. which shows similar patterns to those of Merino rams (Table 2.b.3.).

With knowledge of the above patterns and of the mature weights of the tissues and of the animals, the increments of muscle, bone and fat can be determined for any segment of liveweight gain expressed as units of mature liveweight (Figure 3.b.3.).

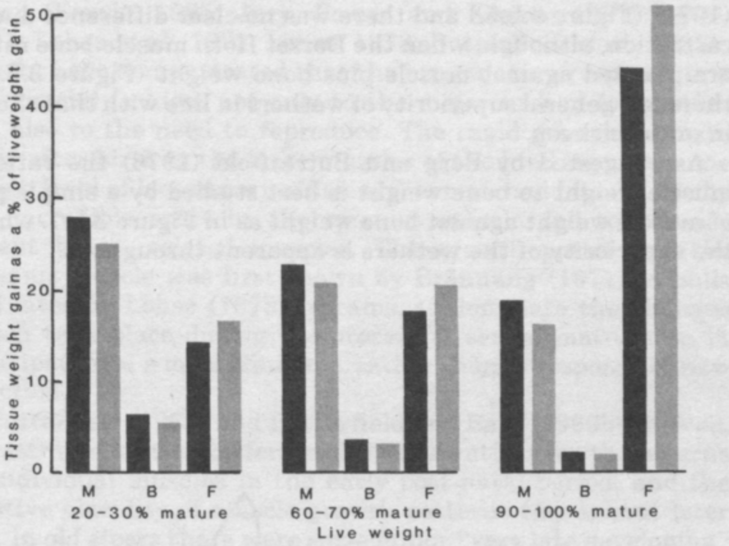


Figure 3.b.3.
The composition of carcase gain during progressive increments of liveweight gain in rams and wethers. (Based on Butterfield *et al.*, 1984a.)

As castration did not alter the maturing patterns of muscle, bone and fat in the study of Butterfield *et al.* 1984a, it is likely that their study commenced after puberty in the ram lambs. It is probable that some difference in the maturing patterns of wethers would occur if the whole patterns are considered using data from birth. However, little is known about the influence of testes on prepubertal growth in sheep, although there may be some influence as Comstock and Winters (1944) decided that testes accelerated prepubertal gain in pigs. It is clear that the effect of castration on carcase composition is expressed from at least 20% mature up to maturity as Kirton, Clarke and Hickey (1982) in New Zealand showed that in lambs of around 15 kg carcase weight wethers are already fatter than rams. Their rams had 3.2% (of carcase weight) less chemical fat than their wethers, and 1.2% (of carcase weight) more protein.

Admitting that a considerable range of interpretations is possible according to the definition of maturity used, it appears that the mature weight of rams and wethers is more similar than previously suggested by Brody (1945) and that the yield of carcase weight from rams and wethers appears to be very similar (Table 3.b.1.), although castration increases the proportion of fat in that carcase weight. Earlier comparisons of rams and wethers at equal carcase weight (Palsson, 1955; Bradford and Spurlock, 1964; Seebeck, 1966b) were probably made at approximately the same degree of maturity. Of these studies those of Palsson, and of Bradford and Spurlock, gave results

Table 3.b.4. Maturity coefficients for carcase tissues relative to liveweight of Dorset Horn rams and wethers

Carcase tissue	'q' Rams	 Wethers	 Pooled*†
Muscle	1.21	1.33	1.27
Bone	1.63	1.87	1.72
Fat	0.05	0.22	0.15
Total carcase	0.72	0.79	0.75

* Values for rams and wethers did not differ significantly in the study of Butterfield *et al.* 1984a.

† All 'q' values different from 1.0

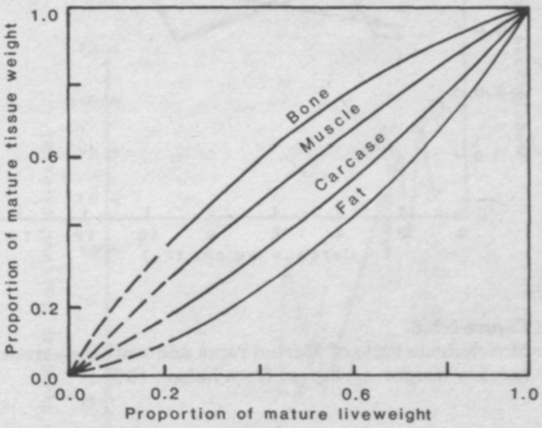


Figure 3.b.2.
Maturing patterns of muscle, bone, fat and carcase weight of Dorset Horn rams and wethers. Muscle: 'q' = 1.27, Bone: 'q' = 1.72, Carcase: 'q' = 0.75, Fat: 'q' = 0.15.

which would be expected if this were so, whereas that of Seebeck did not. It is presumed that the failure of Seebeck's sheep to show any significant difference in carcase composition of rams and wethers was due to the poor growth rates achieved which did not allow the expression of sex differences.

Muscle:Bone Ratio

Using the weights of muscle and bone from Table 3.b.1., muscle:bone ratios of 5.28 and 5.43 can be calculated for mature rams and wethers respectively. Figure 3.b.4. shows the plot of muscle:bone ratio for Dorset Horn rams and wethers from about 20% mature up to maturity. The same general upwards trend can be seen in both Dorset Horn rams and wethers and Merino rams and wethers in the study of Lohse (1971) (Figure 3.b.5.) and there was no clear difference due to castration, although, when the Dorset Horn muscle:bone ratios are plottted against muscle plus bone weight (Figure 3.b.6.), there is a general superiority of wethers in line with that shown in mature sheep.

As suggested by Berg and Butterfield (1976) the ratio of muscle weight to bone weight is best studied by a simple plot of muscle weight against bone weight as in Figure 3.b.7. where the superiority of the wethers is apparent throughout.

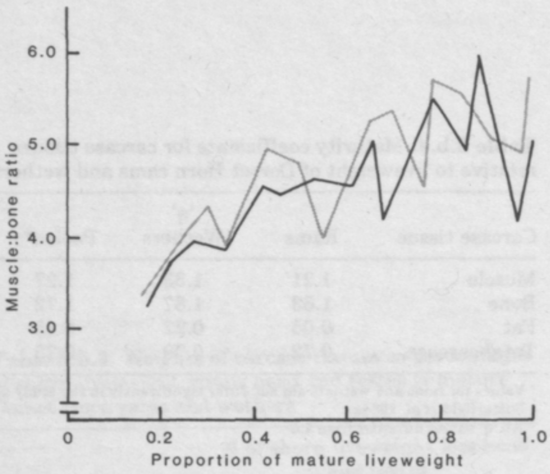


Figure 3.b.4.
Muscle:bone ratio of Dorset Horn rams and wethers versus proportion of mature liveweight. (Butterfield, unpublished.)

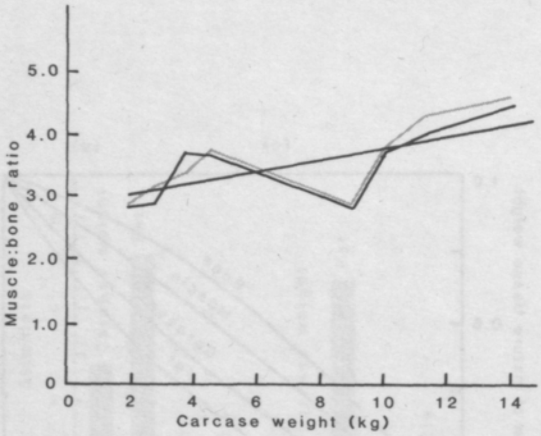


Figure 3.b.5.
Muscle:bone ratio of Merino rams and wethers versus carcase weight. (Adapted from Lohse, 1971.)

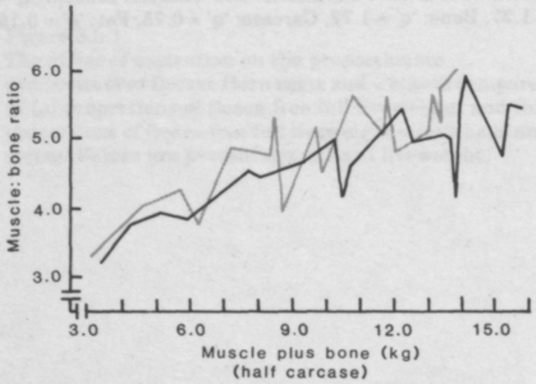


Figure 3.b.6.
Muscle:bone ratio versus muscle plus bone weight of Dorset Horn rams and wethers. (Adapted from Butterfield *et al.*, 1984a.)

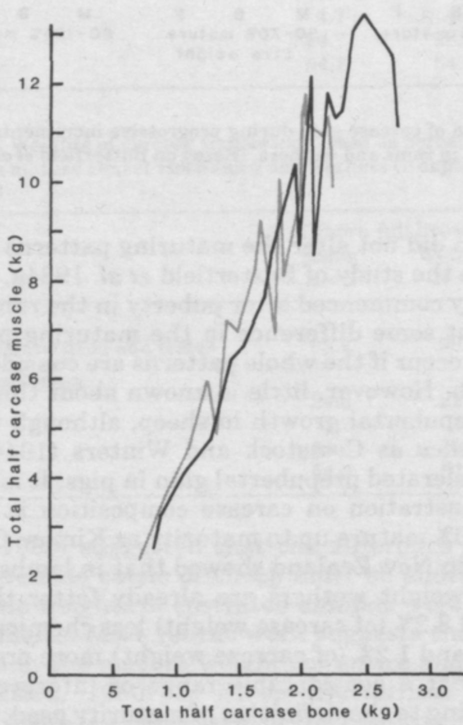


Figure 3.b.7.
Muscle weight relative to bone weight in Dorset Horn rams and wethers. (Adapted from Butterfield *et al.*, 1984a.)

Muscle:Fat Ratio

Castration clearly reduces the muscle to fat ratio. Data from Dorset Horn rams and wethers presented in Figure 3.b.8. as a ratio and in Figure 3.b.9. with the two tissues plotted against each other, indicate the very definite effect of castration. Wethers have a lower muscle:fat ratio throughout growth from about 20 kg liveweight. The only available data is from sheep reared under rather poor pastoral conditions up to weaning and so there is need for information on young lambs which have been reared on maximum nutrition.

c. THE INFLUENCE OF CASTRATION ON GROWTH WITHIN THE MUSCULATURE

Studies of growth and development of the musculature of sheep (Fourie, 1965; Jury, Fourie and Kirton, 1977; Lohse, 1971; Lohse *et al.*, 1971; Lohse, 1973; Butterfield *et al.*, 1983b, 1984b) have demonstrated that the musculature responds in a differential fashion, not only to the major task of locomotion but also to the need to reproduce. The rapid growth immediately after birth in the large muscles of the hind leg to assume a high level of locomotory efficiency, is matched later in life by the incredible spurt by the splenius muscle and to a lesser extent by its related muscles. The growth pattern of the splenius muscle was first shown by Brännäng (1971) in bulls and later by Lohse (1973) in rams, to dominate the changes which take place during the process of sexual maturation in anticipation of a masculine role, rather than in response to new function.

Butterfield (1963) and Butterfield and Berg (1966b) showed, in castrated cattle, the ferment of differential growth patterns of individual muscles in the early post-natal period, and the relative placidity of muscle growth patterns throughout later life. In old steers there were some minor "very late developing" changes in the musculature of the neck (Butterfield, 1963). It is in the growth of the musculature following puberty when the differential effects due to male hormones occur and hence it is in this period; from about 20% mature to maturity, that most interest in the effects of castration on relative muscle growth lies.

In attempting to understand maturing patterns within the musculature as a basis for comparison of entire and castrated animals, there are four major possible effects of castration which might be considered.

1. Does castration alter the mature weight of the total musculature?
2. Does castration alter the maturing pattern of the total musculature relative to the whole animal?
3. Does castration differentially alter the mature weights of individual muscles?
4. Does castration alter the maturing patterns of the individual muscles?

Table 3.c.1. shows that in Dorset Horn sheep the mature weight of the musculature is depressed by castration. Even though the mature liveweight of wethers was shown to be not significantly different at about 96% of that of rams and the carcase weight was not different at 101% of that of rams, muscle weight of the wethers was depressed by about 3 kg relative to the rams, so that the muscle weight of the wethers was only about 89% of that of the rams.

An important aspect of this depression of muscle weight in the wethers is that, even though we may be comparing rams and wethers of the same liveweight, it is unlikely that they will be of similar total muscle weight. Therefore, although it may be possible to make simple comparisons of the total tissue

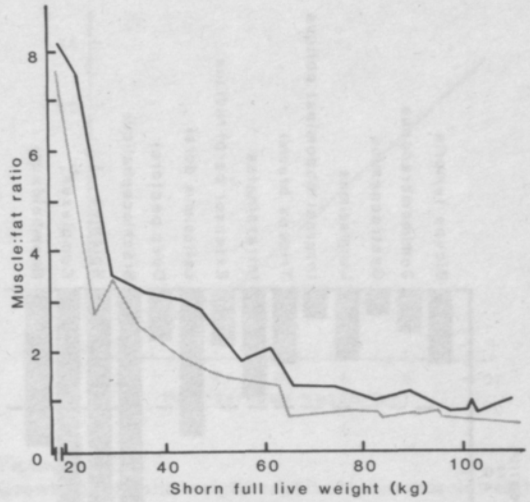


Figure 3.b.8.
Muscle:fat ratio versus liveweight of Dorset Horn rams and wethers. (Adapted from Butterfield *et al.*, 1984a.)

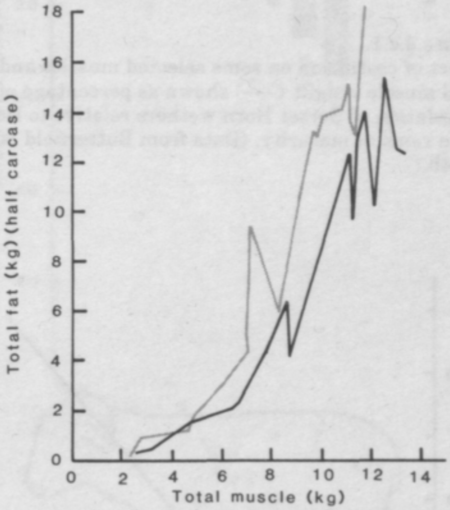


Figure 3.b.9.
Fat weight relative to muscle weight of Dorset Horn rams and wethers. (Adapted from Butterfield *et al.*, 1984a.)

Table 3.c.1. The weight of the total musculature and liveweight of mature Dorset Horn rams and wethers (from Butterfield *et al.* 1984a)

	Rams (kg)	Wethers (kg)	Wethers as % of rams
Muscle weight	24.65	21.87	88.7
Shorn full liveweight	99.72	95.89	96.2
Shorn full liveweight less head and testes	93.15	92.53	99.3

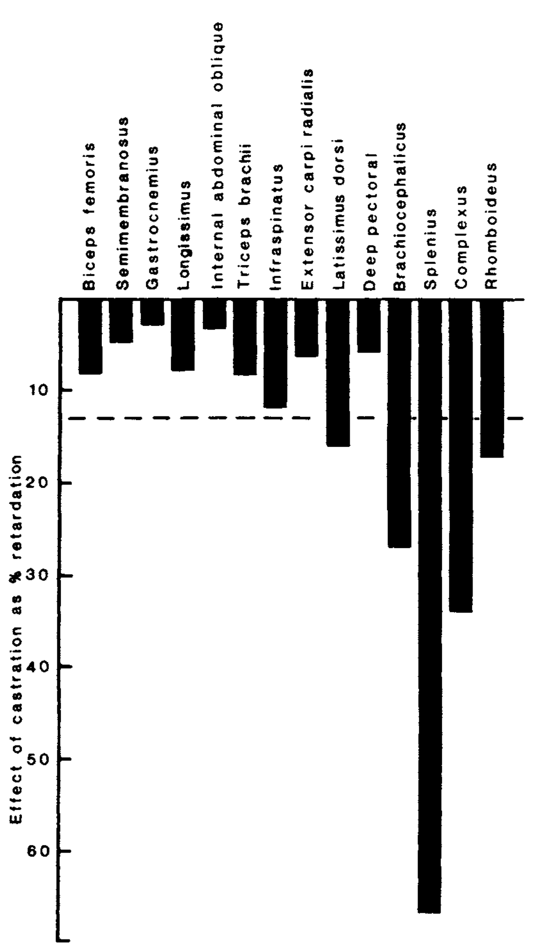


Figure 3.c.1.
Effect of castration on some selected muscles and on total muscle weight (---) shown as percentage of retardation of Dorset Horn wethers relative to Dorset Horn rams at maturity. (Data from Butterfield *et al.*, 1984b.)

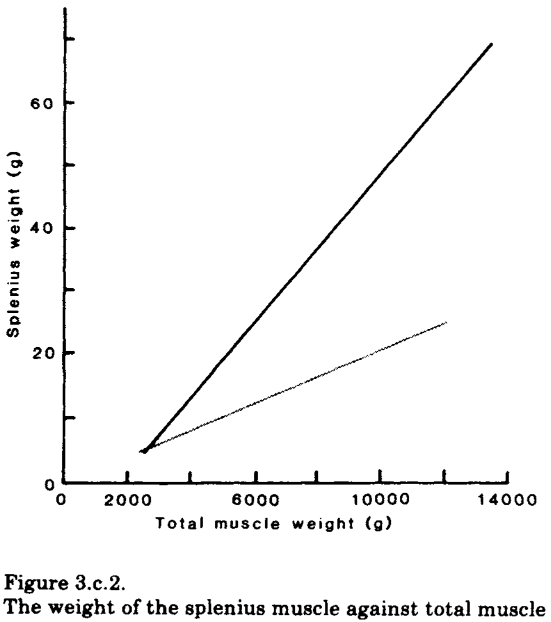


Figure 3.c.2.
The weight of the splenius muscle against total muscle weight in Dorset Horn rams and wethers. (Butterfield, unpublished.)

weights as percentages of liveweight at the same liveweights, it may not be appropriate for within-tissue comparisons to be made at the same liveweights, unless care is taken to account for differences in the weight of each tissue.

The second question has already been answered in Section 3.b. where it was shown that castration had no effect on the maturing pattern of total muscle weight relative to liveweight.

The third question relates to mature weights of individual muscles. Appendix 5 Table 4 shows that all muscles in wethers are, in fact, lighter than the corresponding muscles in the rams. However, the degree of depression resulting from castration is by no means uniform and Figure 3.c.1. shows the relative retardation of a few selected muscles.

The muscle which is retarded to the maximum degree by castration is obviously the splenius and this is also the case in cattle (Brännäng, 1971). There is still much to be learned about the histological structure of the splenius and about the unique process by which the splenius apparently responds to male gonadal sex hormones. Tan (1981), in an important study of Jersey cattle, has shown significant differences in the number of muscle fibres in the splenius muscle of male and female calves in that the bull calf at birth, and throughout life, has twice the number of fibres of the heifer. This suggests an interesting field of investigation of the effects of the castration process. Tan showed that the neck muscles closely related to the splenius also had a greater number of fibres in male calves and this probably explains their tendency to react similarly, although a little less dramatically, to testicular hormones.

Similarly in sheep, the other muscles which are retarded a great deal more than average by castration, are all found in close anatomical relationship with the splenius. In the ram these muscles support the major growth achievement of the splenius but lack the full potential to achieve the same degree of differential enlargement. The purpose of this "crest" development in the neck is unclear but Berg *et al.* (1978b) suggested that it is "probably an evolutionary response to selection related to male dominance—a combination of fighting superiority and 'bluff profile' display." In Figure 3.c.2. the weight of the splenius muscles is plotted against the weight of total muscle for Dorset Horn rams and wethers. From the start of the study at about 2 kg side muscle weight, the influence of male sex hormone was being exerted in the rams. Each "sex" was clearly established on the path which it was to follow to maturity and this is reflected in the maturing patterns to be discussed later. Lohse (1973) showed that the growth of the splenius muscle in Merino rams relative to the growth of half carcase muscle weight had a breakpoint from low to high impetus growth at about 2 kg of side muscle weight (Figure 3.c.3.). It seems, therefore, that the onset of the response of the splenius to androgens may occur at about the same stage of muscle growth in Dorset Horn and Merino rams. Of course, this is more likely to be causally related to testicular activity than to muscle weight and, as will be discussed in Chapter 5, the degree of response may be different in different breeds.

It is perhaps more instructive in terms of the whole animal and the total musculature to look at the effects of castration on the "Standard Muscle Groups" and as shown in Figure 3.c.4. castration has a marked differential effect. Compared with the retardation of the total musculature of about 13% of the weight of the ram musculature, the economically important muscle group of the proximal hind limb is retarded only 7 to 8%, whereas the intrinsic muscles of the thorax and neck are retarded by almost 28%. It is tempting to try to relate this pattern of retardation to maturing patterns and this will be taken up later.

For the present we can conclude that entire males display greater relative development of muscles in the cranial end of the trunk, which results in proportionately less muscle weight in the caudal end (Lohse, 1973; Butterfield *et al.*, 1984b). Those muscle groups in the middle of the animal (i.e., around the spinal column and in the abdominal wall) are unaffected and surprisingly perhaps the muscles of the thoracic limb are slightly proportionately heavier in wethers. As these data are based on quite small numbers, a high level of confidence should not be placed on the detailed findings, although the overall picture seems to be clear. The muscle-weight distribution of mature rams and wethers is set out in Appendix 5 Table 4 in detail and that of the same animals using only "Standard Muscle Groups" in Table 3.c.2. where actual weights are shown and in Table 3.c.3. where percentage distribution is shown.

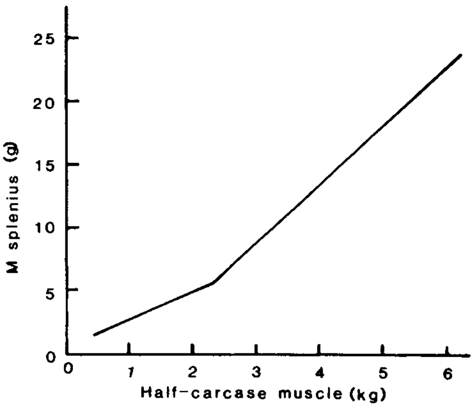


Figure 3.c.3.
Growth of splenius weight relative to side muscle weight in Merino rams. (Lohse, 1973.)

Table 3.c.2. Muscle weights of half carcase of mature Dorset Horn rams and wethers (Butterfield *et al.*, 1984b)

Standard Muscle Groups	Weights (kg) Rams	Weights (kg) Wethers
1. Proximal hind limb	3.17	2.94
2. Distal hind limb	0.50	0.46
3. Spinal	1.88	1.66
4. Abdominal wall	1.71	1.52
5. Proximal forelimb	1.28	1.16
6. Distal forelimb	0.29	0.26
7. Thorax to forelimb	1.22	1.05
8. Neck to forelimb	0.87	0.67
9. Neck and thorax	1.20	0.87
Expensive muscles (Groups 1+3+5)	6.33	5.76
Scrap Muscle	0.21	0.14
Total half-carcase muscle weight	12.33	10.73

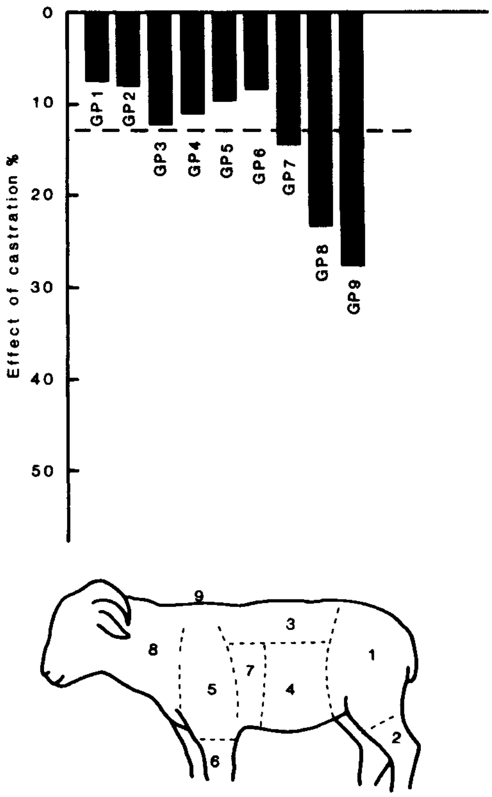


Figure 3.c.4.
Effect of castration on weight of total muscle (----) and "Standard Muscle Groups" shown as percentage of retardation of Dorset Horn wethers relative to rams at maturity. (Data from Butterfield *et al.*, 1984b.)

Table 3.c.3. Muscle-weight distribution of mature Dorset Horn rams and wethers (From Butterfield *et al.*, 1984b.)

Standard Muscle Groups	Percentages of total muscle weight Rams	Percentages of total muscle weight Wethers	Wethers relative to rams
1. Proximal hind limb	25.73	27.44	+
2. Distal hind limb	4.06	4.29	+
3. Spinal	15.25	15.42	+
4. Abdominal wall	13.82	14.22	+
5. Proximal forelimb	10.38	10.81	+
6. Distal forelimb	2.33	2.45	+
7. Thorax to forelimb	9.91	9.77	−
8. Neck to forelimb	7.10	6.27	−
9. Neck and thorax	9.72	8.08	−
Expensive muscles (Groups 1+3+5)	51.36	53.67	+
Scrap muscle	1.70	1.25	
Total muscle weight	100.00	100.00	

Having established the muscle-weight distribution of mature animals from knowledge of the mature weights of all individual muscles, the next step to answer our fourth question is to assess if the muscles achieve their final status by following the same or different maturing patterns in the 'sexes'.The maturity coefficients of the individual muscles are set out in Appendix 5 Tables 4 and 5. In those few muscles where the 'q' values were different they are given for both the rams and wethers. A pooled value is presented when values do not differ significantly. The relationship of 'q' to 1.0 is also shown. Similar values are shown for the "Standard Muscle Groups" in Table 3.c.4.

Table 3.c.4. The maturity coefficients 'q' of "Standard Muscle Groups" of Dorset Horn rams and wethers

Muscle group	Rams	'q' Wethers	Pooled	Relative to 1.0
1. Proximal hind limb	1.17	1.16	1.16	Greater
2. Distal hind limb	1.22	1.17	1.19	Greater
3. Spinal	1.13	1.19	1.16	Greater
4. Abdominal	0.53	0.50	0.52	Smaller
5. Proximal forelimb	1.23	1.09	1.16	Greater
6. Distal forelimb	1.26	1.17	1.22	Greater
7. Thorax to forelimb	0.64	0.66	0.65	Smaller
8. Neck to forelimb	0.85	0.93	0.89	N.S.D.
9. Neck and thorax	0.97	1.10	1.03	N.S.D.
Expensive	1.17	1.15	1.16	Greater

The most significant and surprising feature of the maturing patterns of individual muscles is that castration has little if any effect. Only twelve very small muscles out of a total of 93 have significantly different maturing patterns between rams and wethers and it is notable that a similar number of small muscles had different 'q' values between large and small strains of Merino rams in Chapter 2 (p. 48). None of the "Standard Muscle Groups" differ in their maturing patterns between the rams and wethers. This similarity of maturing patterns seems to indicate that each muscle has an intrinsic maturing pattern which defies alteration by castration despite the broad differential effect of castration on the final target weights of the individual muscles.

Although the splenius muscle was regarded as having a common maturing pattern in the rams and wethers ('q' = 1.02) by Butterfield *et al.* (1983b) with mature weights of 62 vs 21 g, there was a tendency for the rams to be later developing as the 'q' for the rams was 0.76 ± 0.19 and for the wethers 1.27 ± 0.25. The splenius of the two sexes were set on their paths to very different final weights from as early as 20% of mature weight. It would perhaps have been expected that the maturing pattern of the splenius muscle would have been more extreme in the Dorset Horn rams than occurred in this study and this is discussed in Chapter 5 (p. 107).

The only large muscle in which the maturing patterns differed in the sexes is the complexus muscle, a close anatomical relation of the splenius. The maturing pattern of the complexus indicated later development in the rams resulting from higher impetus growth in late life than in the wethers.

Studies of Merinos and Dorset Horns have produced different results. The muscle group which includes the intrinsic muscles of the neck and thorax has a 'q' of only 0.64 in Merino rams, which indicates a marked difference from the pattern of total musculature. In the Dorset Horn rams it is 0.97 which is not different from the total muscle.

It seems in retrospect that the choice of the Dorset Horn breed to study effects of castration was unfortunate in so far as the musculature is concerned, as the muscular manifestations of masculinity are less extreme in this breed where the splenius muscle achieves only 0.51% of total muscle weight compared with 0.62% in Merino rams. As shown in Figure 3.c.5., the Group 9 muscles in Dorset Horn rams and wethers followed different pathways in their progress to different mature weights when plotted as simple percentage values of total muscle weight. However, when converted to maturity coefficients, these values were not significantly different from 1.0 or from each other. It is likely that, had this type of comparison been carried out using Merino rams and wethers, the influence of castration may have been much more apparent.

From the 'q' values of individual muscles and groups the maturing patterns can be tabulated and those of the "Standard Muscle Groups" are shown in Table 3.c.5. The complexities of comparisons of muscle-weight distribution can be highlighted by comparison at any chosen degree of maturity of total muscle weight, e.g., when the total muscle weight is 50% mature the groups range from 41% to 56% mature. Comparisons of muscle-weight distribution which attempt to describe the differences produced by castration need to be made in the knowledge of the influences of the four factors which have been considered if they are to be really meaningful in other than the precise conditions of the comparison.

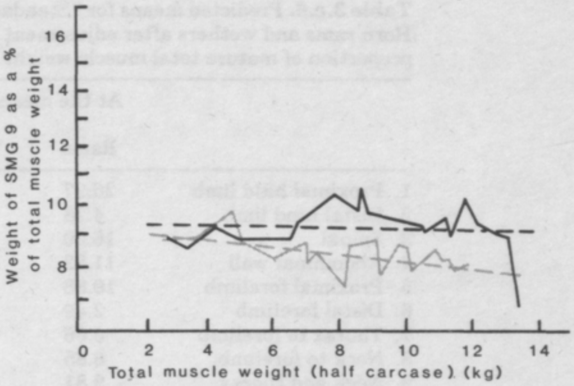


Figure 3.c.5.
Weight of "Standard Muscle Group 9" expressed as a percentage of total muscle versus half carcase total muscle weight of Dorset Horn rams and wethers. (Data from Butterfield *et al.*, (1984b).)

Table 3.c.5. The progress to maturity of "Standard Muscle Groups" of Dorset Horn rams and wethers relative to the progress to maturity of total muscle weight

Standard Muscle Group	Percentage Maturity									Mature weight Grams	
										Rams	Wethers
Total muscle weight	20	30	40	50	60	70	80	90	100 =	12,326	10,716
1. Proximal hind limb	23	33	44	54	64	73	83	91	100 =	3,169	2,938
2. Distal hind limb	23	34	45	55	65	74	83	92	100 =	499	459
3. Spinal	23	33	44	54	64	73	83	91	100 =	1,881	1,656
4. Abdominal wall	12	20	28	38	48	60	72	86	100 =	1,707	1,523
5. Proximal forelimb	23	33	44	54	64	73	83	91	100 =	1,279	1,157
6. Distal forelimb	24	35	45	56	65	75	84	92	100 =	287	263
7. Thorax to forelimb	14	23	32	41	52	63	74	87	100 =	1,222	1,048
8. Neck to forelimb	18	28	37	47	57	68	78	89	100 =	874	672
9. Neck and thorax	20	31	41	51	61	71	80	90	100 =	1,199	866

A comparison of muscle-weight distribution of castrated and entire male sheep which contain different weights of total muscle, will be most biologically meaningful if carried out at the same proportion of mature total muscle weight. Comparisons at the same total muscle weight will embrace components of stage of maturity, as well as components of compositional difference directly related to castration. This contention is supported by the data in Table 3.c.6. which shows that different conclusions could be drawn from comparisons at equal weight to those made from comparison at equal proportion of maturity. For example, it is seen that, whereas the intrinsic muscles of the forelimb (Groups 5 and 6) would be regarded as comprising a not significantly different proportion of the musculature at equal total muscle weight of rams and wethers, they are highly significantly different at equal proportion of mature total muscle weight, whereas in some other groups the magnitude of differences became smaller at similar maturity than they were at equal total muscle weight.

The conclusion is that castration alters the muscle-weight distribution of Dorset Horn sheep and that this is achieved in most instances without major alteration of the maturing patterns of the muscles from puberty to maturity. Therefore, as castration alters the mature weight to which each muscle aspires, the increments of weight by each muscle relative to the increments of weight of the total musculature are changed by castration throughout the entire post-pubertal growth period.

Table 3.c.6. Predicted means for "Standard Muscle Groups" as percentages of total muscle weight for Dorset Horn rams and wethers after adjustment to (i) the mean total muscle weight (8.6 kg) and (ii) the mean proportion of mature total muscle weight (0.75) of all animals dissected (From Butterfield *et al.*, 1984b)

	At the mean total muscle weight			At the same proportion of mature muscle weight		
	Rams	Wethers	Difference	Rams	Wethers	Difference
1. Proximal hind limb	26.97	28.29	1.32***	26.76	28.53	1.77***
2. Distal hind limb	4.28	4.45	0.17*	4.24	4.49	0.25**
3. Spinal	16.00	15.95	0.05	15.88	16.08	0.20
4. Abdominal wall	11.82	12.84	1.02**	12.16	12.47	0.31
5. Proximal forelimb	10.88	11.14	0.26	10.80	11.23	0.43**
6. Distal forelimb	2.49	2.56	0.07	2.46	2.59	0.13**
7. Thorax to forelimb	8.86	9.09	0.23	9.03	8.91	0.12
8. Neck to forelimb	6.85	6.13	0.72***	6.89	6.09	0.80***
9. Neck and thorax	9.81	8.13	1.68***	9.80	8.15	1.65***
Sum of difference	–	–	5.52			5.66
Expensive muscles						
Groups 1 + 3 + 5	53.85	55.38	1.53**	53.44	55.84	2.40***

This illustrates the modification by castration of the expression of the genetic size factor (Taylor, 1982) for each muscle in every stage of growth in the castrate to enable new target (mature) weights to be achieved in a manner not greatly different from that seen in the ram.

The temporal relationship of castration, puberty and the commencement of the study of maturing patterns of muscles will have an influence on the maturing patterns revealed. If prepubertal testes exert no influence, the muscles of rams and wethers castrated soon after birth may be expected to share common paths up to puberty; paths from which the rams then depart in those muscles which are androgen responsive. However, if there is a prepubertal influence of testes and castration is carried out near birth then different patterns of growth may emerge. This requires further study.

Impetus Grouping

As in the comparison of sheep of different size it is useful to remove the confounding effects on maturing patterns brought about by the inclusion of muscles of different impetus patterns within anatomical groups. Accordingly, in Table 3.c.7. in summary, and in Appendix 5 Table 5, in detail are shown the groupings of muscles in impetus groups. The general similarity of maturing patterns for muscles of rams and wethers is confirmed with little difference in the overall 'q' value for each impetus group in the rams and wethers.

The effect of castration is shown to be a reduction in the proportion of the musculature which has a high post-pubertal growth impetus ('q' < 1) and an increase in the proportion of the musculature which has a low post-pubertal growth impetus ('q' > 1). That portion of the musculature with an average post-pubertal growth impetus ('q' = 1) remains unaltered by castration as a proportion of total muscle weight.

The important principle gained from the study of maturing patterns, based on proportions of mature weight, is that it is not the maturing pattern of the muscles which is altered by castration, but the final target weights at which the muscles are aiming. Hence, the relative proportion of total muscle weight of the same group compared between rams and wethers will always be ranked in the same order at any stage of maturity, although the magnitudes of the differences will depend on the stage of maturity and degree by which each maturing pattern differs from that of total muscle weight. This is supported by the comparisons of muscle-weight distribution at maturity in Table 3.c.3. and at 0.75 mature in Table 3.c.6.

Table 3.c.7. Summary of impetus grouping of individual muscles of Dorset Horn rams and wethers from 20% mature to maturity. (For detail see Appendix 5 Table 5)

Impetus Groups	Rams	Wethers
Muscles with 'q' < 1.0		
Number	16	13
% of total muscle weight	25.0	21.8
Mean 'q'	0.5	0.5
Muscles with 'q' = 1.0		
Number	34	36
% of total muscle weight	35.2	35.7
Mean 'q'	1.0	1.0
Muscles with 'q' > 1.0		
Number	43	44
% of total muscle weight	38.0	43.8
Mean 'q'	1.3	1.3
Total Muscle		
Number	93	93
% of total muscle	100	100
Mean 'q'	1.00	1.00

d. THE INFLUENCE OF CASTRATION ON THE GROWTH WITHIN THE SKELETON

Castration in man produces dramatic changes in the length of certain long bones (Short, 1980). Brännäng (1966) showed that castration in cattle also influenced bone length so that steers were of greater height but less length than bulls. Robertson, Paver and Wilson (1970) also showed that steers were higher at the withers and the sacrum than their entire controls.

Little work has been done in sheep or in other meat animals on relative weights or lengths of bones and also it is not clear if the effects of castration are confined to certain bones or whether they are general. However, as the eunuchoidal condition of Klinefelter's syndrome in humans delays epiphyseal fusion differentially (Short, 1980), it is likely that castration in sheep produces a differential effect on bone length, although discussion following the paper of Davis, Hossner and Ohlson (1984) recorded in "Manipulation of Growth of Farm Animals" indicated a confused state of knowledge across species.

In our meat animals shorter limb bones have been associated with better "conformation" and so the entire animal may have an advantage in visually assessed merit if castration of sheep does indeed lead to longer bones.

Table 3.d.1. Weights of individual bones in the half carcase of mature Dorset Horn rams and wethers.

Individual bones	Weight (g) Rams	Weight (g) Wethers	Wethers as percentage of rams
Hind limb			
Femur	191	174	91
Patella	12	10	83
Tibia	146	138	95
Tarsus	53	52	98
TOTAL HIND LIMB	**402**	**374**	**93**
Axial Skeleton			
Pelvis + sacrum	227	187	82
Lumbar vertebrae	175	151	86
Thoracic vertebrae + ribs	679	522	77
Cervical vertebrae	272	190	70
Sternum	148	137	93
TOTAL AXIAL SKELETON	**1501**	**1187**	**79**
Forelimb			
Scapula	127	102	80
Humerus	153	137	90
Radius and ulna	129	116	90
Carpus	25	22	88
TOTAL FORELIMB	**434**	**377**	**87**
TOTAL BONE	2337	1938	83

Bone Weight

There is probably little commercial interest in the distribution of bone weight in sheep unless castration produces changes large enough to be reflected in variation of economic significance in the relative proportions of bone in the dearer and cheaper cuts. This could be more of a factor in sheep than in cattle as a higher proportion of bone is sold to the eventual consumer, although current trends in some countries toward the marketing of boneless sheep meat may alter this situation in the future.

In this section the relationship between the bones of rams and wethers is shown and any differences in the pathways traversed by each bone on its way to a mature weight are defined.

Table 3.d.1. shows the weights of bones at maturity in rams and wethers and Table 3.d.2. shows the percentages which each of these bones comprises of total bone weight at maturity. In these data is seen a retardation of total bone weight due to castration so that the weight of the total carcase skeleton of wethers weighed only 83% of that of rams. It seems that the limb bones are less retarded than the axial skeleton; the retardation of both limbs approximating 10% and that of the axial skeleton 20% (Table 3.d.1.) so that the final proportions of the skeleton of the wethers indicated a proportional increase in the limb bones and a proportional decrease in the axial skeleton (Table 3.d.2.). The overall effect is best seen in Figure 3.d.1.

In Table 3.d.3. are shown the maturity coefficients of the weights of the bones of rams and wethers, indicating that castration has no effect on the maturing patterns of the bones of wethers relative to those of rams, as the 'q' values are not significantly different for any of the bones.

In line with the patterns shown in Chapter 2 for Merino rams it is clear from Table 3.d.3 that the limb bones, with the exception of the scapula, have advanced further towards their mature weights earlier in life than have the remaining parts of the skeleton, irrespective of castration or not. As castration does not alter the pattern on which each individual bone progresses towards its ultimate mature weight and, as the mature weights of all the bones are altered by castration, the

Table 3.d.2. Weights of individual bones as percentages of half carcase bone weight of mature Dorset Horn rams and wethers

Individual bones	Percentage of total bone Rams	Percentage of total bone Wethers
Hind limb		
Femur	8.2	9.0
Patella	0.5	0.5
Tibia	6.2	7.1
Tarsus	2.3	2.7
TOTAL HIND LIMB	17.2	19.3
Axial Skeleton		
Pelvis + sacrum	9.7	9.6
Lumbar vertebra	7.5	7.8
Thoracic vertebra + ribs	29.1	26.9
Cervical vertebra	11.6	9.8
Sternum	6.3	7.1
TOTAL AXIAL SKELETON	64.2	61.2
Forelimb		
Scapula	5.4	5.3
Humerus	6.6	7.1
Radius and ulna	5.5	6.0
Carpus	1.1	1.1
TOTAL FORELIMB	18.6	19.5
TOTAL BONE	100.0	100.0

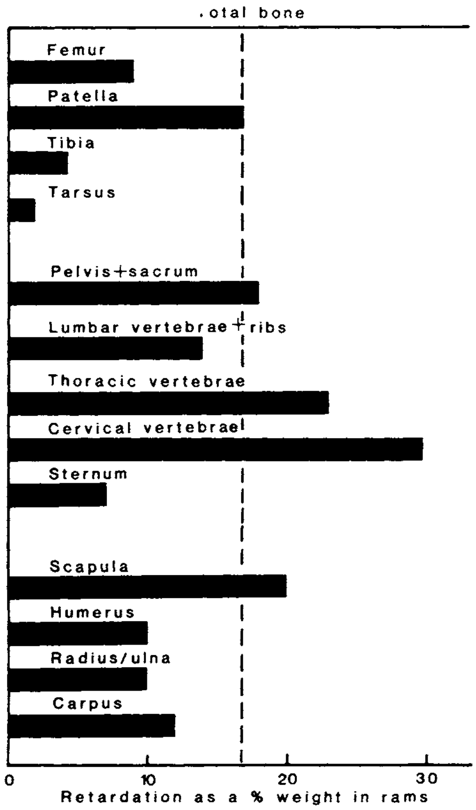


Figure 3.d.1.
Effect of castration on total bone (---) and individual bones shown as percentage retardation of Dorset Horn wethers relative to Dorset Horn rams at maturity. (Butterfield, unpublished.)

Table 3.d.4. Lengths of long bones of mature Dorset Horn rams (N = 5) and wethers (N = 8)

Individual bone	Rams (cm)	Wethers (cm)	Difference
Femur	17.42	17.66	+0.24
Tibia	19.26	19.80	+0.54
Scapula	14.72	14.39	−0.33
Humerus	14.56	14.50	−0.06
Radius	14.32	14.50	+0.18
Ulna	18.00	18.20	+0.20
Scapula width	11.70	11.47	−0.23
Radius width	3.84	3.83	−0.01

Table 3.d.3. Maturity coefficients ('q') for bone weight relative to total bone weight of Dorset Horn rams and wethers (Butterfield, unpublished)

	Maturity coefficients 'q' Rams N = 20	Wethers N = 20	Pooled	Relative to 1.0
Pelvis + sacrum	1.05	1.13	1.09	NSD
Femur	1.32	1.24	1.28	Greater
Patella	1.28	1.37	1.32	Greater
Tibia	1.23	1.15	1.20	Greater
Tarsus	1.53	1.40	1.47	Greater
Scapula	0.65	0.67	0.66	Less
Humerus	1.24	1.13	1.19	Greater
Radius and Ulna	1.06	0.89	0.98	NSD
Carpus	1.32	1.02	1.18	NSD
Cervical vertebra	1.04	1.24	1.13	NSD
Thoracic vertebra + ribs	0.69	0.79	0.73	Less
Lumbar vertebra	1.15	0.88	1.03	NSD
Sternum	1.19	1.00	1.11	NSD

increments of weight must be altered from the commencement of the study. As pointed out earlier, the animals used in the study by Butterfield *et al.* (1984a) must have been near or past puberty at the commencement of the study. It appears that the differential retardation of bones is linked with the same process in muscles. Those muscles which are most retarded by castration are those associated with the axial skeleton of the cranial end of the animal and the maximum retardation of bone occurred in the same region, namely in the cervical and thoracic vertebrae.

In meat animals it is sometimes desired to predict the total weight of bone in an animal or carcase from the weight of a single bone. This can be done with accuracy across the sexes only if there are no differences between the sexes in the relative weight of bones or unless any differences are understood.

Bone Length

Searle (pers. comm., 1985) studied the lengths of the major limb bones of the carcases of Dorset Horn rams and wethers from the study of Butterfield *et al.* (1984/5) on the bases of both age and empty body weight. His conclusions were that up to about 300 days the bones of the rams were longer than those of the wethers; however, at about 300 days the wethers caught up and there was little change in the lengths of the bones of either sex beyond this age. On the basis of empty body weight, there was no difference in the lengths at any weight and the bones made very little increase in length beyond 50 kg empty body weight.

It seems, therefore, that the growth in length of the bones was unaffected by castration other than in an indirect manner associated with growth rate. As the growth rate of the wethers was inhibited by castration so was the growth in bone length.

From the small amount of data available there appears to be no consistant change, due to castration, in the lengths of the long bones of the carcase in mature Dorset Horns (Table 3.d.4.). However, the maturing patterns do appear to be mildly affected as shown by simple plots of individual bone lengths (Figure 3.d.2.).

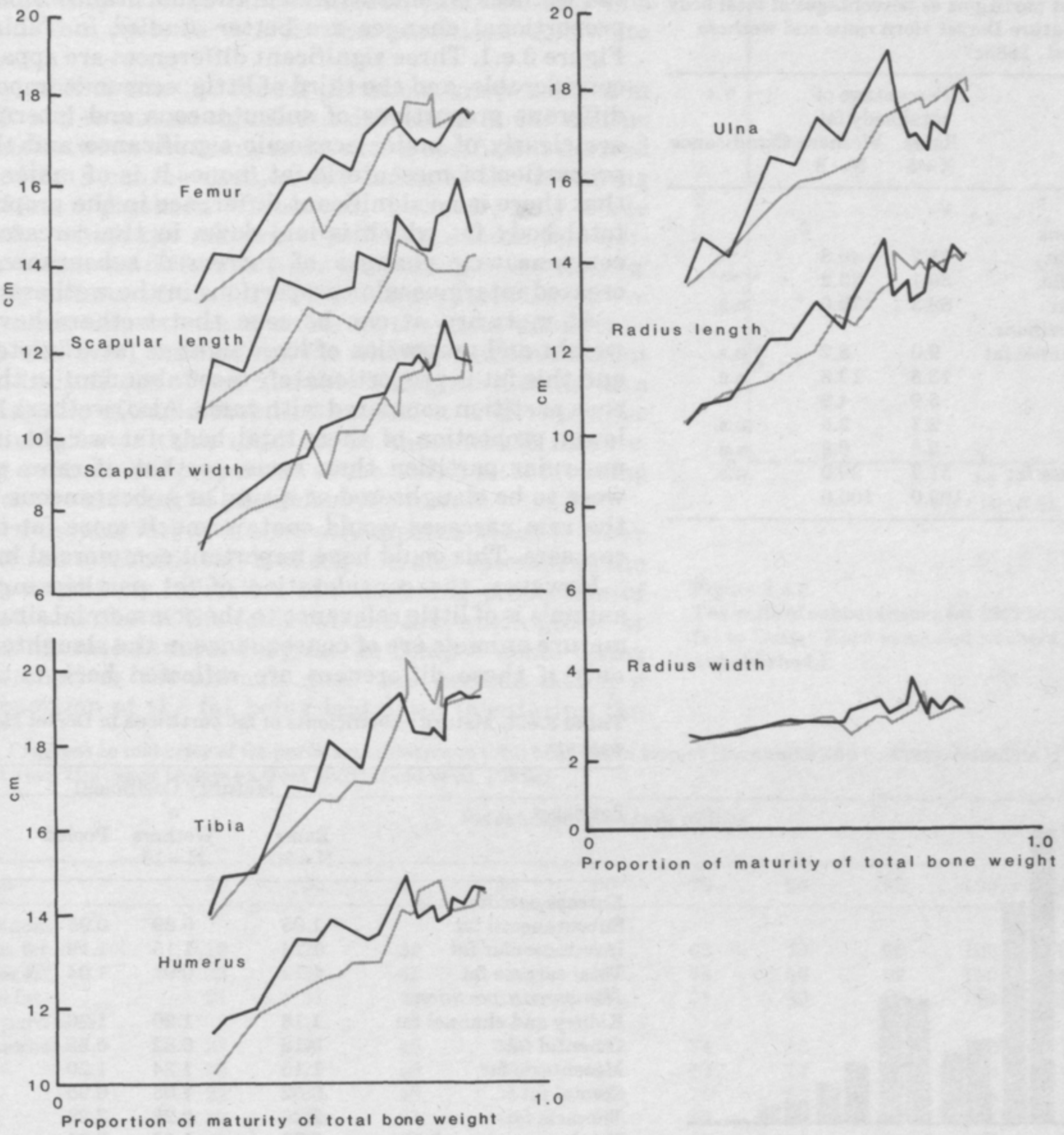


Figure 3.d.2.
Simple plots of bone lengths of Dorset Horn rams and wethers. (Butterfield, unpublished.)

e. THE INFLUENCE OF CASTRATION ON GROWTH WITHIN THE BODY FAT

In Section 3.b. (p. 60) it was shown that castration influences the total amount of fat within the body and, therefore, comparisons of rams and wethers at equal liveweight or equal proportion of mature liveweight are likely to take place at different total fat weights. If maturing patterns of fat partitions differ from that of the total body fat there will be problems of both different mature composition and of stage of maturity in any comparisons of fat partitioning made at equal liveweight. Such comparisons would be further complicated if the maturing patterns of any partition are different in the sexes. Therefore, as described in Section 1.e. (p. 24) the most appropriate basis for comparisons of fat partitioning to determine the effects of castration is equal maturity of total fat weight.

Fat partitioning in mature rams and wethers is shown in Table 3.e.1. and it is seen that almost all the additional fat in

Table 3.e.1. Weight of partitions of fat in mature Dorset Horn rams and wethers (Butterfield *et al.*, 1985c)

Fat depot	Weight (kg) Rams N = 5	 Wethers N = 8
Carcase partitions		
Subcutaneous fat	13.79	18.67
Intermuscular fat	10.89	9.28
Total carcase fat	24.68	27.95
Non-carcase partitions		
Kidney and channel fat	3.30	3.26
Omental fat	4.87	5.42
Mesenteric fat	2.16	1.96
Scrotal fat	0.99	1.03
Thoracic fat	0.29	0.31
Total non-carcase fat	11.60	11.98
Total body fat	36.29	40.03

Table 3.e.2. Fat partitions as percentages of total body fat weight in mature Dorset Horn rams and wethers (Butterfield *et al.*, 1985c)

Fat depot	Percentage of total body fat Rams N = 5	 Wethers N = 8	Significance
Carcase partitions			
Subcutaneous fat	38.2	46.8	**
Intermuscular fat	30.1	23.2	**
Total carcase fat	68.3	70.0	n.s.
Non-carcase partitions			
Kidney and channel fat	9.0	8.2	n.s.
Omental fat	13.3	13.6	n.s.
Mesenteric fat	5.9	4.9	**
Scrotal fat	2.7	2.6	n.s.
Thoracic fat	0.8	0.8	n.s.
Total non-carcase fat	31.7	30.0	n.s.
Total body fat	100.0	100.0	

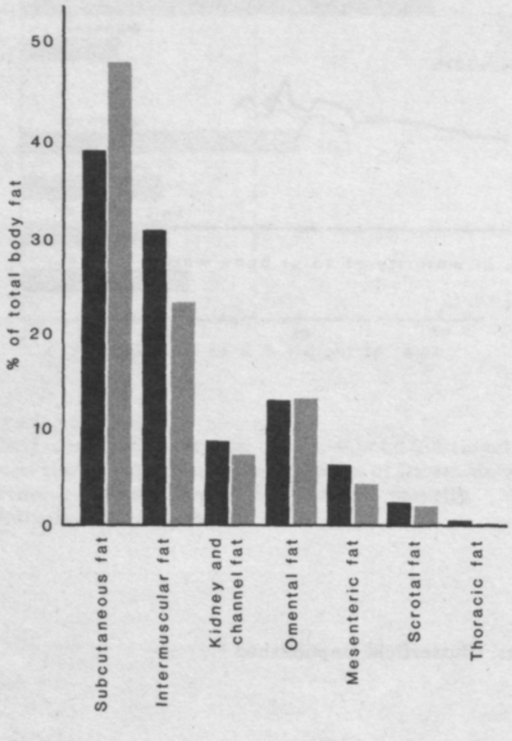


Figure 3.e.1.
Data from Table 3.e.2.

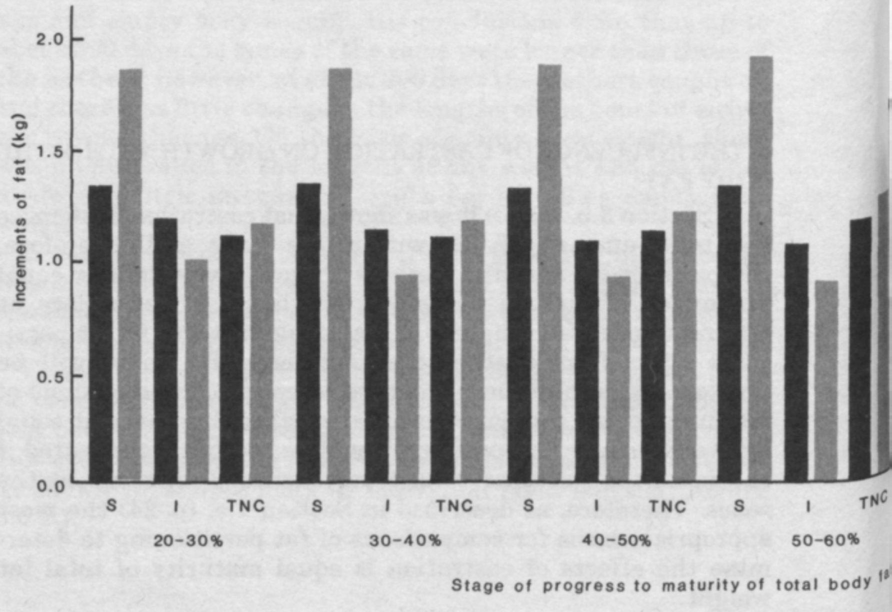
the wethers is concentrated in the subcutaneous partition. The proportional changes are better studied in Table 3.e.2. and Figure 3.e.1. Three significant differences are apparent. Two of considerable, and the third of little, economic importance. The different proportions of subcutaneous and intermuscular fat are clearly of major economic significance and the different proportion of mesenteric fat, none. It is of major importance that there is no significant difference in the proportion of the total body fat which is laid down in the carcase due to the compensating changes of increased subcutaneous and decreased intermuscular proportions in the wethers.

At maturity, it can be seen that wethers have a greater weight and proportion of liveweight as fat (Chapter 3.b. p. 60) and this fat is proportionately most abundant in the subcutaneous partition compared with rams. Also, wethers have a much lower proportion of their total body fat weight in the intermuscular partition than rams, so that, if rams and wethers were to be slaughtered at a similar subcutaneous fat content, the ram carcases would contain much more fat than wether carcases. This could have important commercial implications.

However, the consideration of fat partitioning in mature animals is of little relevance to the commercial situation as few mature animals are of consequence in the slaughter trade. It is only if these differences are reflected back onto immature

Table 3.e.3. Maturity coefficients of fat partitions in Dorset Horn rams and wethers

Fat depot	Maturity Coefficient 'q' Rams N = 20	 Wethers N = 19	 Pooled	Relative to 1.0
Carcase partitions				
Subcutaneous fat	1.03	0.89	0.95	NSD
Intermuscular fat	1.24	1.15	1.19	Greater
Total carcase fat	1.12	0.98	1.04	NSD
Non-carcase partitions				
Kidney and channel fat	1.18	1.20	1.20	NSD
Omental fat	0.16	0.82	0.52	Less
Mesenteric fat	1.15	1.24	1.20	NSD
Scrotal fat	0.82	1.05	0.95	NSD
Thoracic fat	2.26	2.26	2.26	Greater
Total non-carcase fat	0.75	1.05	0.91	NSD
Total body fat	1.00	1.00	1.00	



animals that they will be of commercial interest, and this depends on the patterns which the partitions follow to maturity.

Maturity coefficients ('q') for fat partitions are presented in Table 3.e.3. and reveal no significant difference in the maturing patterns between the sexes and hence a coefficient derived from pooled data can be used as the index of the maturing pattern of each partition. There are, however, only three partitions for which the maturity coefficients indicate a pattern of development different from that of total fat (i.e., 'q' significantly different from 1.0). Two of these partitions are of relatively minor importance in so far as the meat industry is concerned. However, the omental fat which constitutes about 5% of total body fat, is of considerable biological interest as a partition capable of rapid mobilisation and it is shown to be growing much faster than total fat as the animals mature, suggesting an increased proportion of the body's total fat being set aside for the meeting of physiological stresses.

The intermuscular fat, with a growth impetus which is lower than that of the total body fat, is of considerable interest as the low growth impetus is indicative of a declining proportion of the body fat, and also of the total carcase fat, which grows at about the same rate as total body fat. In compositional terms this means that, as the animals grow and become fatter, a smaller proportion of the fat being laid down is entering the

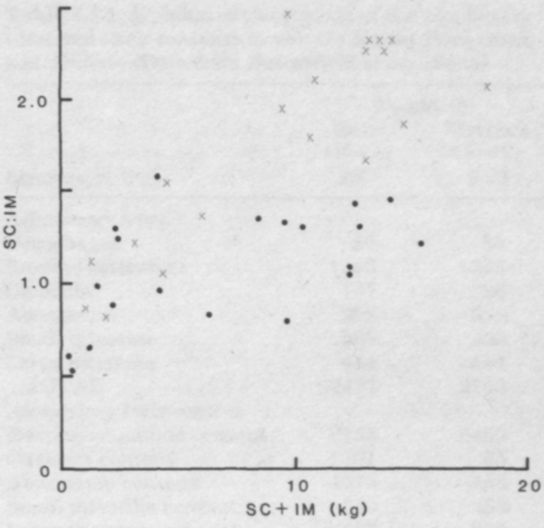


Figure 3.e.2.
The ratio of subcutaneous fat (SC) to intermuscular (IM) fat in Dorset Horn rams and wethers. (Butterfield, unpublished.)

Table 3.e.4. Progress to maturity of fat partitions relative to total body fat in Dorset Horn rams and wethers. Based on 'q' values which did not differ between the sexes (Adapted from Butterfield *et al.* 1985c)

	Percentage of mature weight									Ram (kg)	Wethers (kg)
Total body fat	20	30	40	50	60	70	80	90	100 =	36.29	40.03
Carcase partitions											
Subcutaneous fat	19	29	39	49	59	69	79	90	100 =	13.79	18.67
Intermuscular fat	23	34	45	55	65	74	83	92	100 =	10.89	9.28
Total carcase fat	21	31	41	51	61	71	80	90	100 =	24.68	27.95
Non-carcase partitions											
Kidney & channel fat	23	34	45	55	65	74	83	92	100 =	3.30	3.26
Omental fat	12	20	28	38	48	60	72	86	100 =	4.87	5.42
Mesenteric	23	34	45	55	65	74	83	92	100 =	2.16	1.96
Scrotal	19	29	39	49	59	69	79	90	100 =	0.99	1.03
Thoracic	40	56	70	82	90	96	100	101	100 =	0.29	0.31
Total non-carcase fat	19	28	38	48	58	68	79	89	100 =	11.60	11.98

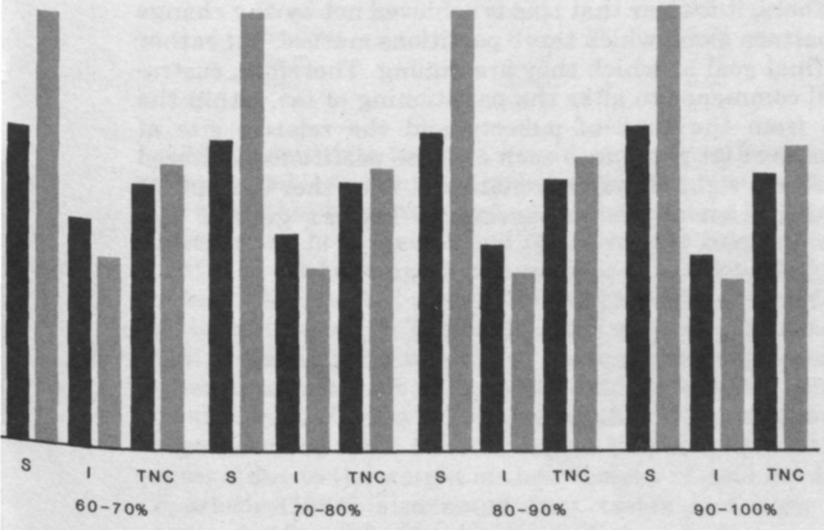


Figure 3.e.3.
The increments of fat in each partition during the progress to maturity. (S = Subcutaneous: I = Intermuscular: TNC = Total non-carcase) of Dorset Horn rams and wethers. (Butterfield, unpublished.)

intermuscular partition. If subcutaneous fat is remaining a constant proportion and intermuscular is a declining proportion, it means that the subcutaneous:intermuscular ratio must be progressively increasing, and as there is no difference in the maturing patterns of the sexes then this process will occur in both. Set out in Figure 3.e.2. is the ratio of subcutaneous to intermuscular fat in the rams and wethers.

Even if it is assumed that the non-significant differences from 1.0 in the maturity coefficients of the fat partitions are, in fact, real differences and a table such as Table 3.e.4. is developed, it is seen that at 50% maturity of total fat weight the major partitions vary very little from 50% mature. As the maturing patterns do not differ in the rams and castrates, the composition of the mature animals is a good indication of the relative proportions within the fat partitions of the rams and wethers throughout growth. However, the position regarding fat partitioning is far from clear as Butler-Hogg (1984) has demonstrated significantly different growth coefficients for fat partitions relative to total fat weight in Clun and Southdown wethers and ewes and Butler-Hogg and Johnsson (1986) have also demonstrated significant differences in Hampshire x Mule ewe lambs. It is increasingly apparent that a study of large numbers of animals is needed before the final story of fat partitioning in the sexes emerges.

Increments of fat weight in each partition during progress of rams and wethers to maturity are set out in Figure 3.e.3.

It is concluded that it would be unwise to rely on differences in maturity to explain differences in fat partitioning of rams and wethers revealed in any comparison, as it is necessary to know the maturing patterns of the partitions before confidence can be expressed in comparisons on any basis.

In summary, the total amount of fat as a proportion of liveweight is increased as a result of castration in sheep. However, as shown in Table 3.e.2. there is also a marked effect on the partitioning of fat within the carcase so that wethers have a greater proportion of total fat in the subcutaneous depot than rams, whereas rams have a greater proportion of their total fat in the intermuscular depot. These two differences balance one another so that the proportion of the total fat in the animal located in the carcase of rams and wethers is not significantly different. This, of course, means that the proportion of total fat in the non-carcase depots is also not different between rams and wethers.

Reverting to the marked difference between the proportion of fat in the subcutaneous and intermuscular partitions in rams and wethers, it is clear that this is achieved not by any change in the pattern along which these partitions mature, but rather by the final goal at which they are aiming. Therefore, castration will commence to alter the partitioning of fat within the carcase from the time of puberty and the relative size of increments of fat going into each of these partitions is altered from puberty right through to maturity. A further example of the modification of the expression of Taylor's genetic size factor!

f. THE INFLUENCE OF CASTRATION ON THE GROWTH OF BODY ORGANS

Castration produces quite dramatic changes in the external appearance of male animals which become increasingly apparent in older animals. Some of this different appearance is due to the structures which we will include under the general term of "body organs", a convenient grouping of all those structures which do not comprise part of the carcase or the fat partitions. Hence, in this section, as in Chapter 2.f., we deal with, for example, heads, hides and distal limbs as well as the internal body organs. The basis chosen for calculations of maturing patterns and comparisons of relative proportions of body organs is shorn full liveweight, as in Chapter 2.f.

Table 3.f.1. shows the actual weights of portions of the alimentary tract and their contents in mature rams and wethers and Table 3.f.2. shows the same information expressed as percentages of liveweight.

Due to the difficulties of accurate measurement, the small number of animals and the ephemeral nature of the contents of each section of the alimentary tract, it would be unwise to place too much reliance on the differences between rams and wethers for parts of the tract and contents. The overall similarity of the available data suggests that there is unlikely to be any difference in the weights of these characters relative to the weight of the animals in mature rams and wethers. As will be shown later, this similarity may not prevail throughout the whole of post-natal growth.

Table 3.f.3. shows the weights of major internal solid organs and Table 3.f.4. shows the same information expressed as percentages of liveweight. These data in Table 3.f.4. showed little difference between rams and wethers. There would seem to be little reason to expect differences due to castration and, indeed, these do not appear to occur. Similarly the brain, eyes and blood are not different.

Table 3.f.4. The weights of the "solid" body organs as percentages of liveweight of mature Dorset Horn rams and wethers

	Percentages	
	Rams (N = 5)	Wethers (N = 7)
Organs		
Liver	0.94	1.09
Kidneys	0.18	0.19
Spleen	0.09	0.09
Heart	0.30	0.29
Trachea and lungs	0.47	0.48
Thyroid	0.01	0.01
Pancreas	0.08	0.09
Brain	0.09	0.10
Eyes	0.03	0.03
TOTAL	2.19	2.37

As the only data for head weight comes from Dorset Horns it is not possible to comment on head weight *per se* as the massive horns of this breed dominate the head weight of rams. However, as the horn weight and testes weight contribute significantly to the liveweight in rams it is interesting to know the order of this contribution. The weights of the heads and the testes are set out in Table 3.f.5. It is necessary to consider the contribution of the weights of these structures to liveweight when discussing small proportionate differences within the total body as Turton (1969) stated that: "A small part of the superiority of rams for liveweight, particularly at the older ages, is due to the weight of their testes . . ." and Bradford and Spurlock (1964) also noted that testes and horn weights accounted for a large part of the difference in dressing percentage of rams and wethers. Also, the hide is almost 1 kg heavier in mature rams than in mature wethers (approximately 6 kg vs

Table 3.f.1. Weights of the regions of the alimentary tract and their contents in mature Dorset Horn rams and wethers (Data from Butterfield *et al.*, 1984a)

	Weight (g)	
	Rams (N = 5)	Wethers (N = 7)
Liveweight (kg)	99.7	95.9
Alimentary tract		
Oesophagus	86	83
Rumino-reticulum	1185	1385
Omasum	107	96
Abomasum	298	292
Small intestine	357	438
Large intestine	444	459
TOTAL	2477	2753
Alimentary tract content		
Rumino-reticulum content	6135	6450
Omasum content	101	65
Abomasum content	1375	858
Small intestine content	513	450
Large intestine content	866	990
TOTAL	8990	8813

Table 3.f.2. The weights of regions of the alimentary tract as percentages of liveweight in mature Dorset Horn rams and wethers (Data from Butterfield *et al.*, 1984a)

	Percentage	
	Rams (N = 5)	Wethers (N = 7)
Alimentary tract		
Oesophagus	0.1	0.1
Rumino-reticulum	1.2	1.4
Omasum	0.1	0.1
Abomasum	0.3	0.3
Small intestine	0.4	0.5
Large intestine	0.5	0.5
TOTAL	2.5	2.9
Alimentary tract content		
Rumino-reticulum content	6.1	6.7
Omasum content	0.1	0.1
Abomasum content	1.4	0.9
Small intestine content	0.5	0.5
Large intestine content	0.9	1.0
TOTAL	9.0	9.1

Table 3.f.3. Weights of the "solid" body organs of the mature Dorset Horn rams and wethers

	Weights (g)	
	Rams (N = 5)	Wethers (N = 7)
Liveweight (kg)	99.7	95.9
Organs		
Liver	940	1044
Kidneys	180	186
Spleen	91	86
Heart	296	274
Trachea and lungs	470	459
Thyroid	7	7
Pancreas	83	82
Brain	93	98
Eyes	31	31
TOTAL	2191	2267

Table 3.f.5. The weights of heads and testes in mature male Dorset Horn sheep

	Head (kg)	Testes (kg)	Head + testes (kg)
Rams (N = 5)	6.23	0.34	6.57
Wethers (N = 7)	3.36	–	3.36
Difference	2.87	0.34	3.21

Table 3.f.6. Maturity coefficients (q) for body organs relative to liveweight for Dorset Horn rams and wethers

Body organ	Maturity coefficient 'q' Rams	Wethers	Pooled
Alimentary Tract			
Oesophagus	1.63	1.53	1.58
Ruminoreticulum	2.12	1.07	*
Omasum	3.22	3.06	3.14
Abomasum	2.27	1.59	1.92
Small intestine	9.48	5.07	*
Large intestine	3.44	2.32	*
Total	3.47	2.11	*
Alimentary Tract Contents			
Ruminoreticulum contents	1.46	1.20	1.33
Omasum contents	3.22	6.51	*
Abomasum contents	0.14	0.82	0.49
Small intestine contents	6.83	4.90	*
Large intestine contents	3.34	2.63	2.98
Total	1.77	1.55	1.68
Other major internal organs			
Liver	4.43	2.78	*
Kidneys	3.11	2.06	*
Spleen	1.81	1.95	1.89
Heart	2.02	1.92	1.97
Trachea	2.32	2.18	2.25
Lungs	3.14	3.03	3.09
Thyroid	3.31	2.61	2.94
Pancreas	2.04	1.44	1.74
Total	3.44	2.51	*
Miscellaneous components			
Blood	1.76	1.94	1.86
Head	1.08	1.75	*
Hide	1.53	1.53	1.53
Distal limbs	1.84	1.70	1.77
Total	1.37	1.69	*
Penis + Bladder	1.68	1.81	1.74
Testes		–	
Central nervous system			
Brain			b† = 0.26
Eyes			b = 0.42
Total			b = 0.30
Shorn empty liveweight	0.92	0.94	0.93
Shorn full liveweight			1.00

* Significantly different in rams and wethers.
† 'b' as in y = a + bx constrained to pass through maturity.

5 kg) which translates to an approximate 1.0 per cent of liveweight.

Having established that, in general, body organs are not greatly influenced in their mature size by castration, it is interesting that the maturing patterns of several organs, particularly parts of the gastrointestinal tract, are markedly effected. The ruminoreticulum, the small intestine, the large intestine, the total gastrointestinal tract, the small intestinal contents, the liver and the kidneys, all have significantly larger 'q' values in the rams than in the wethers, whereas only the omasum has a higher 'q' in the wethers (Table 3.f.6.).

It seems that the act of castration either inhibits in some obscure way the latter part of the rapid growth of the gut which occurs in the early postnatal period (Widdowson, 1984), or, as a secondary effect to the depression of appetite by castration, the gut and associated organs such as the liver receive inadequate stimuli to grow to their maximum genetic potential in early life. Whatever the mechanism, the wethers do overcome this deficiency in later life so that the growth impetus is greater (i.e., 'q' is less) and the mature weights are similar.

Table 3.f.6. shows the 'q' values for all "body organs" relative to liveweight, except for brain and eyes, where a value "b" (from a linear regression y = a + bx constrained to pass through 1.0,1.0) is shown.

The several instances, mostly in the gastro-intestinal tract and liver, where castration has a dramatic effect on the maturing patterns, suggest that there is a spectrum of internal secondary sex characteristics, as well as the obvious differences in head and horns. However, these differences in rams and wethers could mostly, if not all, be accounted for as being secondary to differences in appetite and therefore become tertiary sex effects.

The difference between the patterns for the weight of the small intestine, as shown in Figure 3.f.1., may be somewhat less than the 'q' values indicate, but nevertheless the data points

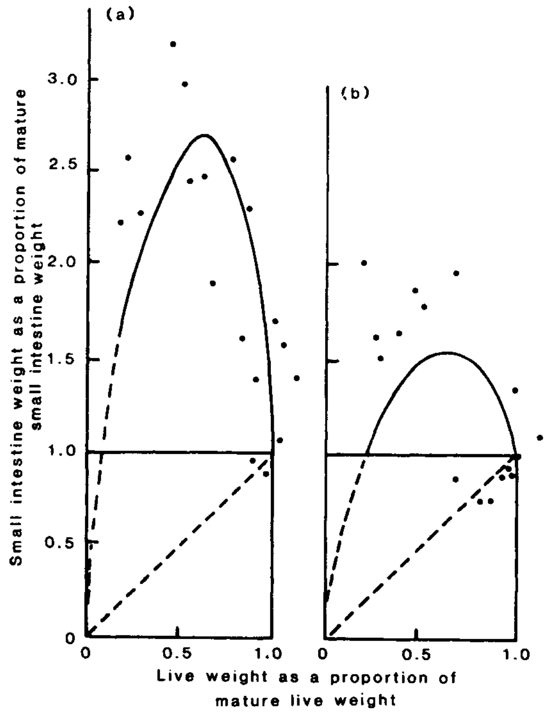


Figure 3.f.1.
Progress to maturity of the weight of the small intestine of Dorset Horn rams (a), and wethers (b), relative to progress of liveweight to maturity. (Butterfield *et al.*, 1984a.)

are clearly different for rams and wethers. Whereas the small intestine weight in the rams reaches about 2.5 times its mature weight when the animal is about 50% mature, in the wethers it reaches only about 1.5 times its mature weight.

The parallel effect is seen in the liver (Figure 3.f.2.) which reaches 1.4 times its mature weight in the rams and 1.02 times its mature weight in the wethers and confirms the relationship between gastrointestinal weight and liver weight (Ferrell and Jenkins, 1985). The individuality of liver weights relative to those of other organs is shown in Figure 3.f.3. where the stability of the heart weight is used as a control to the extremely variable weights of the liver once the animal passes about 40 kg liveweight.

In attempting to find a single suitable basis on which to make comparisons between rams and wethers of the proportions of liveweight comprised by body organs, we are confronted with somewhat different problems from those encountered elsewhere. It is helpful that rams and wethers seem to achieve similar mature liveweights, which allows comparison at equal liveweight to approximate comparison at the same proportion of mature liveweight. However, the several organs with different maturing patterns for rams and wethers make it clear that no general rule can be laid down for the comparison of the proportions of body organs in growing entire and castrate animals. Each of the many organs requires a special understanding of its individual growth characteristics. Figure 3.f.4. shows the different results which would be obtained in comparisons of the weight of the small intestine relative to liveweight at different stages of maturity of liveweight.

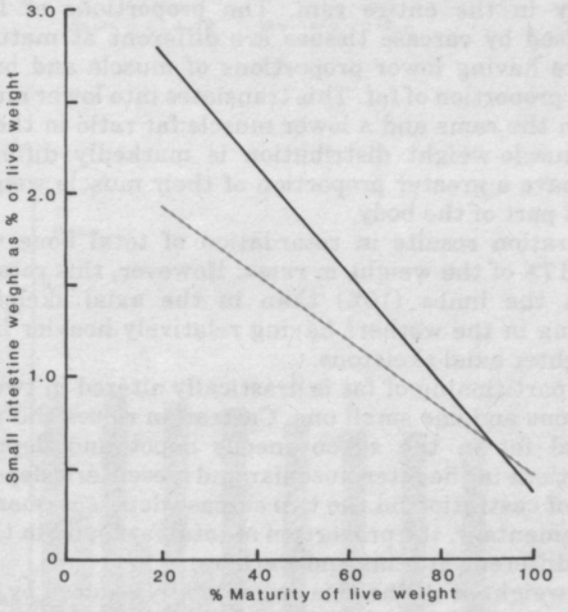


Figure 3.f.4.
Indicating the problem of comparing the small intestine weight as a proportion of liveweight in rams and wethers arising from their different maturing patterns.

The different maturing patterns of some organs result, of course, in different increments of organ weight at different stages of maturity of liveweight and this is shown for liver, head, small intestines, large intestines and M. rectus abdominus in Figure 3.f.5.

Jones *et al.* (1984) compared the weights and proportions of empty liveweight comprised by body organs in steers and bulls slaughtered at equal subcutaneous fat thickness; they concluded that steers had greater proportions of liver, spleen, heart, lungs, rumen, abomasum, large intestine and front feet

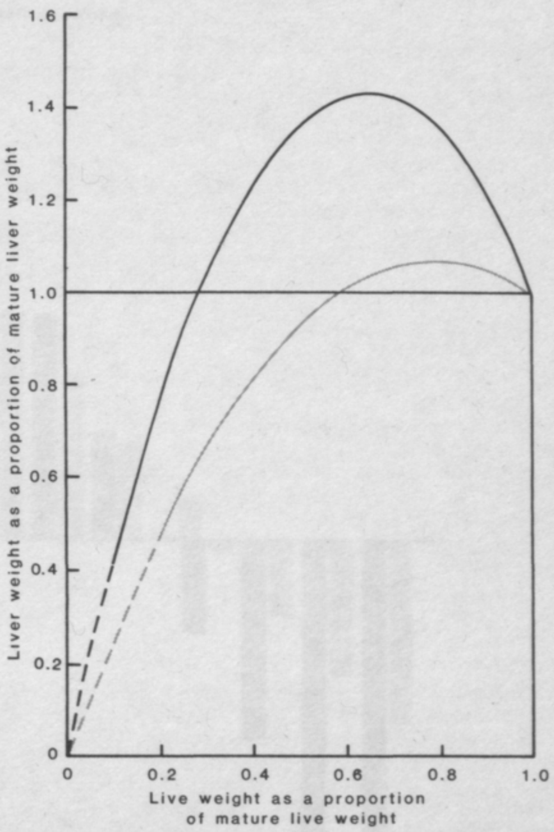


Figure 3.f.2.
The progress to maturity of the weight of the liver in Dorset Horn rams and wethers. (Butterfield, unpublished.)

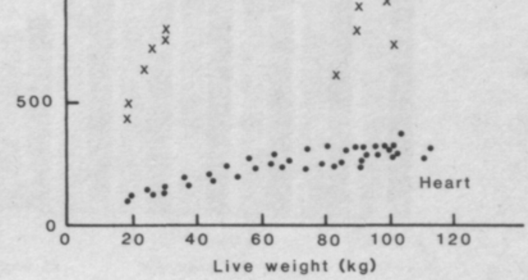


Figure 3.f.3.
Liver and heart weight of Dorset Horn rams and wethers relative to liveweight. (Butterfield, unpublished.)

relative to empty body weight than bulls. As they slaughtered at equal fat thickness the steers would have made less progress towards maturity than the bulls (See Chapter 3.e. p. 71), therefore their early developing organs would be a greater proportion of liveweight than in the bulls if they were to be of similar weight at maturity. It is fairly safe to presume that all the organs listed have 'q' values greater than 1.0 in cattle and therefore their results could be largely if not entirely due to stage of maturity rather than any intrinsic difference induced by castration. This is further supported by the fact that Jones *et al.*'s steers had a lower proportion of carcase to liveweight than their bulls as would be expected from the 'q' value of less than 1.0 which can be assumed for the carcase. It is not suggested that this is in any way a weakness in the Jones *et al.* study which was designed as a commercial comparison. Truscott (1980) demonstrated the same phenomenon in comparison of two breeds of cattle; when slaughtered at the same weight, the larger breed had a higher proportionate weight of internal organs, all of which had been shown by Truscott to be early developing components.

g. CONCLUSIONS

a. *Composition*

Rams and wethers differ markedly in some aspects of body composition and these differences become apparent soon after puberty in the entire ram. The proportions of liveweight comprised by carcase tissues are different at maturity with wethers having lower proportions of muscle and bone and a higher proportion of fat. This translates into lower muscle:bone ratio in the rams and a lower muscle:fat ratio in the wethers. The muscle-weight distribution is markedly different. The rams have a greater proportion of their muscle weight in the cranial part of the body.

Castration results in retardation of total bone weight by about 17% of the weight in rams. However, this retardation is less in the limbs (10%) than in the axial skeleton (20%) resulting in the wethers having relatively heavier limb bones and lighter axial skeletons.

The partitioning of fat is drastically altered in two large fat partitions and one small one. Castration raises the proportion of total fat in the subcutaneous depot and depresses the proportions in the intermuscular and mesenteric depots. As the effect of castration on the two carcase depots is quantitatively complementary, the proportion of total fat found in the carcase is not different in rams and wethers.

The weight of the head is dramatically reduced by castration due largely to the feminization of the horns and, of course, the testes and associated structures are non-existant in the wethers. However, most of the vital organs, such as the heart, remain a similar proportion of liveweight in the rams and wethers throughout growth. The mature weights of the alimentary tract and of its contents are not greatly altered although there is a trend for the gut and liver of the wethers to be heavier.

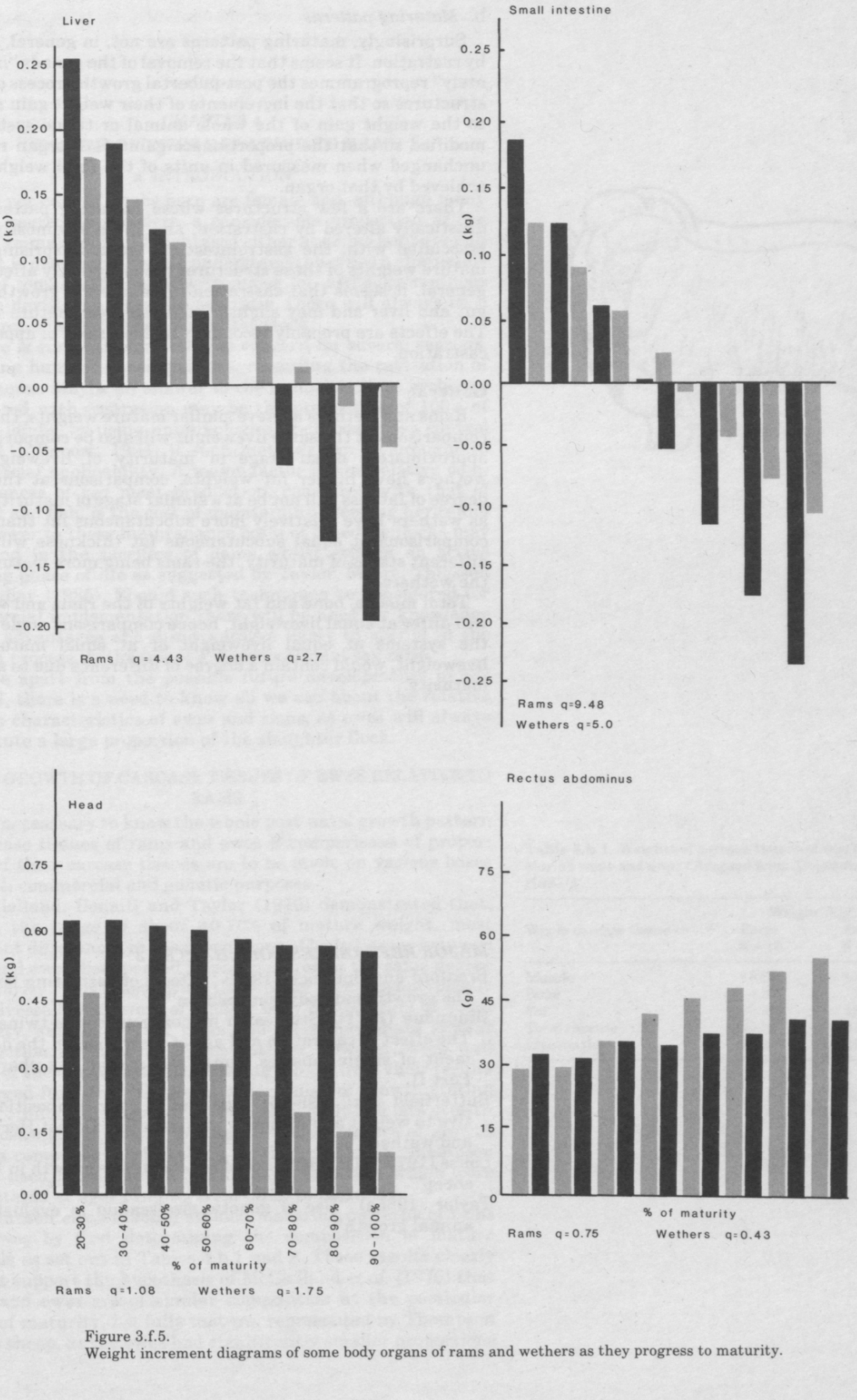


Figure 3.f.5.
Weight increment diagrams of some body organs of rams and wethers as they progress to maturity.

b. *Maturing patterns*

Surprisingly, maturing patterns are not, in general, altered by castration. It seems that the removal of the gonads "immediately" reprogrammes the post-pubertal growth process of many structures so that the increments of their weight gain relative to the weight gain of the whole animal or tissue system are modified so that the proportionate gain of an organ remains unchanged when measured in units of the final weight to be achieved by that organ.

There are a few structures whose maturing patterns are drastically altered by castration, and these are mostly in, or associated with, the gastrointestinal tract. Surprisingly the mature weights of these structures are not greatly affected. In general, it seems that castration inhibits early growth of the gut and liver and may slightly increase their mature weight. The effects are probably secondary to depression of appetite by castration.

General

Rams and wethers achieve similar mature weights, therefore comparisons at the same liveweight will also be comparisons at approximately equal stage of maturity of liveweight. As wethers have higher fat weights, comparisons at the same degree of fatness will not be at a similar stage of maturity. Also, as wethers have relatively more subcutaneous fat than rams, comparisons at equal subcutaneous fat thickness will be at different stages of maturity, the rams being more mature than the wethers.

Total muscle, bone and fat weights of the rams and wethers will differ at equal liveweight, hence comparisons made within the systems at equal liveweight or at equal maturity of liveweight, would contain a degree of difference due to stage of maturity.

MAJOR REFERENCES FOR CHAPTER 3

Bradford and Spurlock (1964) "Effects of castrating lambs on the growth and body composition"

Brännäng (1971) "Studies on monozygous cattle twins. XXII. The effect of castration and age of castration on the development of single muscles, bones and special sex characters. Part II."

Butterfield *et al.* (1984-5) "Changes in body composition relative to weight and maturity of Australian Dorset Horn rams and wethers."

Lohse (1973) "The influence of sex on muscle growth in Merino sheep"

Taylor (1985a) "Use of genetic size-scaling in evaluation of animal growth"

CHAPTER 4

GROWTH OF EWES RELATIVE TO RAMS

a. INTRODUCTION

Fifty per cent of lambs born are female and, although many will be reared as breeders, a considerable proportion of the female animals will be slaughtered either as prime lambs or cull ewes. It is necessary that we understand the growth characteristics of females compared with males for, although methods may be devised to alter the sex ratio, there will always be a large proportion of female slaughter stock.

There is currently considerable concern for several reasons, including humane considerations, regarding the castration of male lambs. Maybe an answer to the animal welfare problems associated with castration may be the production of 100% of female lambs, by using immunological methods of sex control (A.M.R.C. Report, 1984) if such methods can be brought to commercial applicability. A major factor in the relative competitiveness of red meat production, compared with that of poultry and fish, is the cost of maintaining breeding herds and the answer to these maintenance costs of breeding flocks may be found in the sacrifice of dams whilst still in an active growing phase of life as suggested by Taylor, Moore, Thiessen and Bailey (1985). Should such techniques be considered for commercial implementation there will be need for knowledge of the advantages and disadvantages likely to accrue in the growth process by the use of a disproportional sex ratio.

Quite apart from the possible future developments in sex control, there is a need to know all we can about the relative growth characteristics of ewes and rams, as ewes will always constitute a large proportion of the slaughter flock.

b. THE GROWTH OF CARCASE TISSUES OF EWES RELATIVE TO RAMS

It is necesasary to know the whole post-natal growth pattern of carcase tissues of rams and ewes if comparisons of proportions of their carcase tissues are to be made on various bases for both commercial and genetic purposes.

McClelland, Bonaiti and Taylor (1976) demonstrated that, within the range of about 40-70% of mature weight, most apparent differences in the proportions of body tissues between rams and ewes disappeared when compared at the same degree of maturity. This, along with their belief that phenotypically very diverse breeds were of similar body composition at equal maturity, suggested that rams and ewes may share similar composition at maturity. These authors, however, were well aware of the dangers of extrapolating too far from their results and urged further work over a wider range of growth stating that ". . .information on what happens in early and late growth being essential if we are to obtain a better picture of growth and its components." In taking up that challenge, Thompson (1983) used 140 ad lib-fed Merino rams and ewes which were slaughtered at ages ranging from birth to maturity.

Thompson *et al.* (1985b) studied maturing patterns of rams and ewes by first determining the composition of mature animals as set out in Tables 4.b.1 and 2. These results clearly did not support the hypothesis of McClelland *et al.* (1976) that rams and ewes are of similar composition at the particular stage of maturity, i.e. fully mature, represented by Thompson *et al.*'s sheep, as the ewes had significantly smaller proportions

Table 4.b.1. Weights of carcase tissues of mature Merino rams and ewes (Adapted from Thompson (1983))

Whole carcase tissue	Weight (kg) Rams N = 18	 Ewes N = 16
Muscle	18.53	11.76
Bone	4.37	2.74
Fat	20.47	18.77
Total carcase	43.37	33.27
Liveweight	69.4	49.0

Table 4.b.2. Weights of carcase tissues expressed as percentages of shorn full liveweight of mature Merino rams and ewes (Adapted from Thompson *et al.*, 1985b)

Whole carcase tissue	Percent of liveweight Rams N = 18	Ewes N = 16	Significance of difference	Ratio Ewes = 1 Rams =
Muscle	26.7	24.0	***	1.11
Bone	6.3	5.6	***	1.12
Fat	29.5	38.3	***	0.77
Total carcase	62.5	67.9		
Liveweight	100	100		

Table 4.b.3. The carcase tissues as percentages of mature full liveweight of a combined group of Romney, Southdown and Romney Southdown crosses (Data from Fourie *et al.* 1970)

Whole carcase tissue	Percent of liveweight Rams	Ewes	Ratio Ewes = 1 Rams =
Muscle	27.1	23.9	1.13
Bone	4.8	4.1	1.16
Fat	13.5	18.1	0.75

Table 4.b.4. Maturity coefficients for muscle, bone and fat relative to liveweight of Merino rams and ewes (Adapted from Thompson, 1983)

Carcase tissue	Maturity coefficient 'q' Rams (N = 18)	Ewes (N = 16)
Muscle	0.93	1.14
Bone	1.39	1.80
Fat	0.19	-0.09

Table 4.b.5 Growth coefficients of tissues of rams and ewes relative to starved body weight. Mean values from Southdowns, Romneys and their crosses. (Adapted from Fourie *et al.*, 1970)

Tissue	Growth coefficient ('b') Rams	Ewes
Body muscle*	0.97	1.00
Body bone	0.68	0.75
Body fat	1.62	1.50

* Body muscle = carcase muscle plus head muscle and waste.
Body bone = carcase bone plus skull, jaw and feet bones.
Body fat = carcase fat plus omental, cod or udder and internal fat.

of muscle and bone and a significantly higher proportion of fat. As few other comparisons of mature ewes and rams seem to be available, it seems that rams and ewes do differ considerably in the proportions of carcase tissues relative to liveweight at maturity at least when maturity is defined as by Thompson (1983). The data presented by Fourie *et al.* (1970) for "mature" rams and ewes came from flock animals of unknown nutritional history and, therefore, their relative weights and composition may be influenced by differences in nutrition. However, as shown in Table 4.b.3., the relative proportions of carcase tissues in their rams compared with ewes was very similar to the *ad lib* fed animals of Thompson *et al.* (1985a).

The next step in the understanding of the composition of ewes and rams was to develop the maturing patterns for the tissues relative to that of liveweight, and this was done by Thompson *et al.* (1985a). In Table 4.b.4. are shown the maturity coefficients for rams and ewes. These maturity coefficients for carcase tissues differ between the sexes, as did growth coefficients developed by Fourie *et al.* (1970) (Table 4.b.5.), and so it is readily apparent that conclusions drawn from comparisons made at any one degree of maturity may be quite different from those drawn at any other. Therefore, the results of McClelland *et al.* (1976), are unlikely to be relevant to stages of growth outside their field of study as indeed they suggested.

Whereas the 'q' for muscle was slightly less than 1.0 in rams, it was slightly greater than 1.0 in ewes in Thompson's (1983) study. This small difference of 0.21 around a coefficient of 1.0 would be associated with only minor differences in compositional change during growth. This is also seen in Fourie *et al.*'s (1970) data (Table 4.b.5.) where the 'b' values, although significantly different, vary by only 0.03 at 0.97 for rams and 1.00 for ewes, hence the trend for carcase muscle to have a lower impetus in ewes than rams is seen in the studies of both Thompson (1983) and Fourie *et al.* (1970).

The magnitude of the 'q' values for muscle in Thompson's (1983) study are somewhat lower than in several other studies, particularly for rams, which in both Merinos and Dorset Horns gave values of approximately 1.2 (Butterfield *et al.* 1983a, 1984a). No explanation of this is apparent. The 'q' value of 0.93 indicates a slightly increasing proportion of muscle relative to liveweight as the rams increase in weight, whereas the other studies show that muscle declines as a proportion of liveweight.

The coefficients for bone in rams and ewes not only differ significantly from 1.0 but also from each other and, therefore, comparisons of the contribution of bone to body composition at equal stage of maturity will be confused by different maturing patterns, unless adjusted according to those maturing patterns.

The maturing patterns for total body fat are represented by 'q' values which are clearly much less than 1.0 and differ significantly between rams (0.19) and ewes (-0.009). As pointed out by Thompson *et al.* (1985b) the negative value for fat in the ewes is a biological nonsense resulting from the inability of the quadratic function to fit the data from the very small lambs.

This was considered by Thompson *et al.* to be irrelevant as the curve fitted the major part of the data.

Figures 4.b.1, 2 and 3, derived from Thompson's (1983) study, indicate the changes in the proportion of the three tissues at different weights and throughout progress to maturity. They show how comparisons made when the animals are about half mature would suggest a close similarity between the sexes, whereas comparisons both considerably before and considerably after half maturity would indicate marked differences, but in different directions. The hazards of extrapolation from comparison of carcase composition made at any one body weight or narrow range of body weights, or any one stage of maturity, are therefore apparent. However, the important commercial consideration is that rams and ewes slaughtered at about half their mature weights will share similar carcase composition and, as pointed out by McClelland *et al.* (1976), lambs in the United Kingdom are slaughtered at about 50-60% of the weights of their dams. As rams are about 1.3 to 1.4 times the mature weight of ewes, this suggests the slaughter of rams at appropriately higher weights than ewes to achieve similar carcase composition. However, as the maturing patterns of the

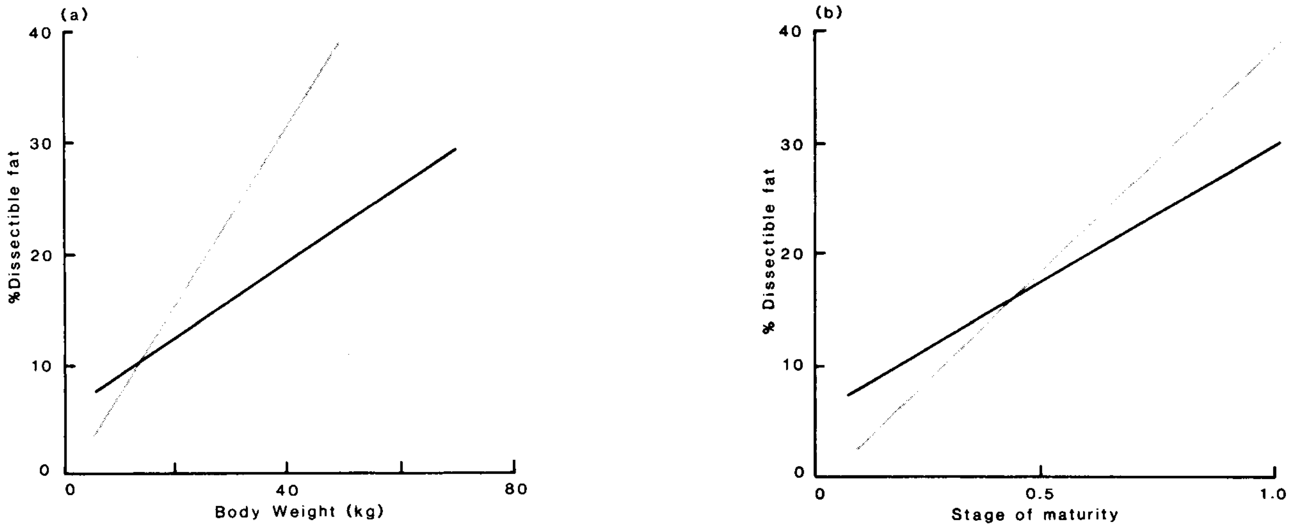


Figure 4.b.1.
Changes in the percentage of dissectible fat in the body of Merino rams and ewes relative to liveweight (a), and during progress to maturity (b). (From Thompson, 1983.)

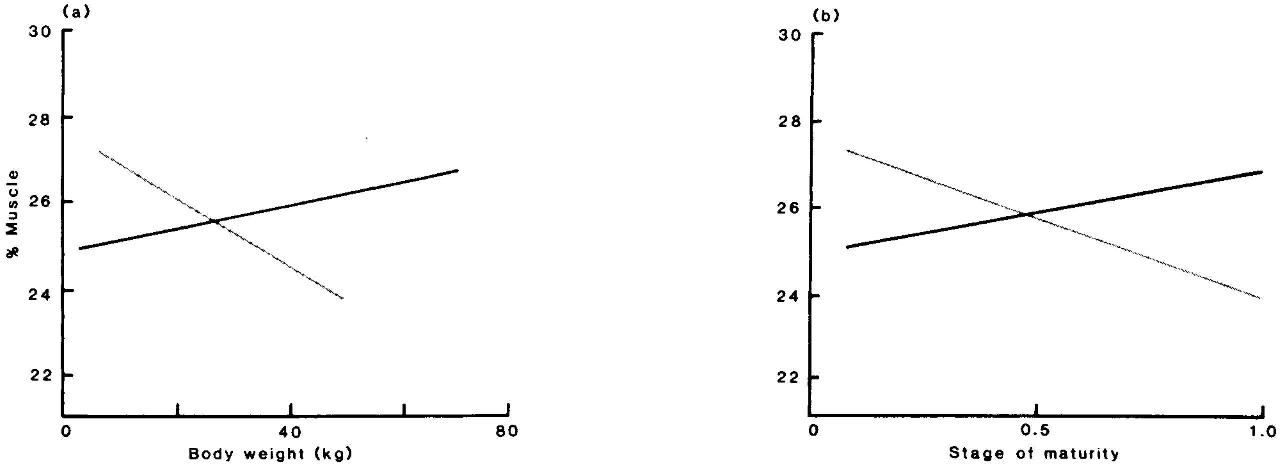


Figure 4.b.2.
Changes in the percentage of muscle in the body of Merino rams and ewes: (a) relative to liveweight, and (b) during progress to maturity. (From Thompson, 1983.)

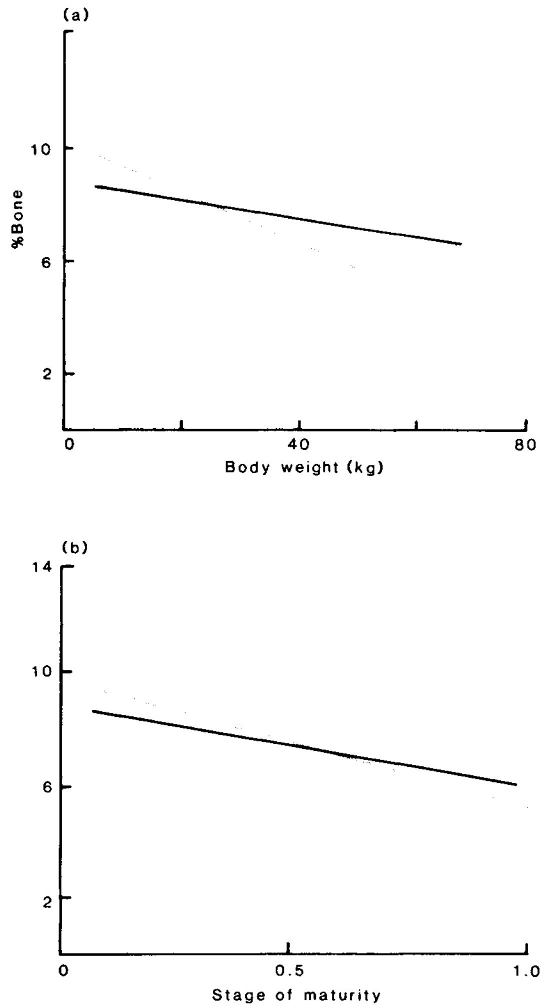


Figure 4.b.3.
Changes in the percentage of bone in the body of Merino rams and ewes: (a) relative to liveweight, and (b) during progress to maturity. (From Thompson, 1983.)

carcase tissues are different in the rams and ewes, the comparison is not quite the simple arithmetic problem suggested by their mature sizes.

From the difference in mature composition of rams and ewes and the difference in maturing patterns of the three major carcase tissues, it is apparent that the increments of tissue weight during growth must be different for rams and ewes.

Figure 4.b.4. shows the weight of carcase muscle, bone and fat gained in successive stages of progress to maturity, and Table 4.b.6. shows the progress to maturity of the carcase tissues of ewes and rams. From this can be derived the actual weights at any given weight or stage of maturity (Table 4.b.7.).

Fourie *et al.* (1970) presented the changes in *carcase* composition of rams and ewes over a range of 5-30 kg carcase weight. Both sexes showed regularly increasing proportions of fat and a corresponding decline in muscle and bone. Their estimated mean values for three breed groups are plotted in Figure 4.b.5. and show the ewe carcases to be fatter and to contain a lower proportion of muscle and bone at each weight.

Table 4.b.6 The progress to maturity of carcase tissues of Merino rams (R) and ewes (E) relative to progress to maturity of liveweight

	% maturity											Mature wt. (kg)
Liveweight	4	10	20	30	40	50	60	70	80	90	100 =	69.4 (R) 49.0 (E)
Muscle:												
Rams	4	9	19	29	38	48	58	69	79	89	100 =	18.53
Ewes	5	11	22	33	43	54	63	73	82	91	100 =	11.76
Bone:												
Rams	5	14	26	38	49	60	69	78	86	94	100 =	4.37
Ewes	7	17	33	47	59	70	79	87	93	97	100 =	2.74
Fat:												
Rams	1	3	7	13	21	30	41	53	67	83	100 =	20.47
Ewes	–	–	3	7	14	23	34	47	63	80	100 =	18.77

Table 4.b.7. Actual weights of carcase tissues (kg) of Merino rams and ewes as they progress to maturity relative to progress to maturity of liveweight

Liveweight as % of mature liveweight	4	10	20	30	40	50	60	70	80	90	kg 100 = 69.4 (R) = 49.0 (E) †
Muscle:											
Rams	0.69	1.74	3.50	5.29	7.10	8.94	10.81	12.70	14.62	16.56	18.53
Ewes	0.53	1.32	2.62	3.87	5.10	6.29	7.45	8.58	9.67	10.73	11.76
Bone:											
Rams	0.24	0.59	1.15	1.67	2.16	2.61	3.03	3.42	3.77	4.09	4.37
Ewes	0.19	0.47	0.90	1.28	1.62	1.92	2.17	2.38	2.54	2.66	2.74
Fat:											
Rams	0.18	0.55	1.44	2.66	4.21	6.09	8.30	10.85	13.72	16.93	20.47
Ewes	–	0.04	0.48	1.33	2.60	4.27	6.35	8.84	11.74	15.05	18.77

† (R) = rams; (E) = ewes.

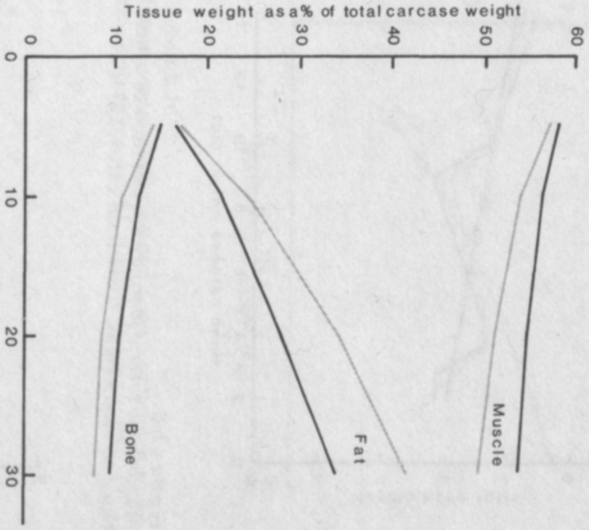


Figure 4.b.5.
Changes in tissue proportions of carcase weight at various carcase weights of rams and ewes. (Data from Fourie *et al.*, 1970.)

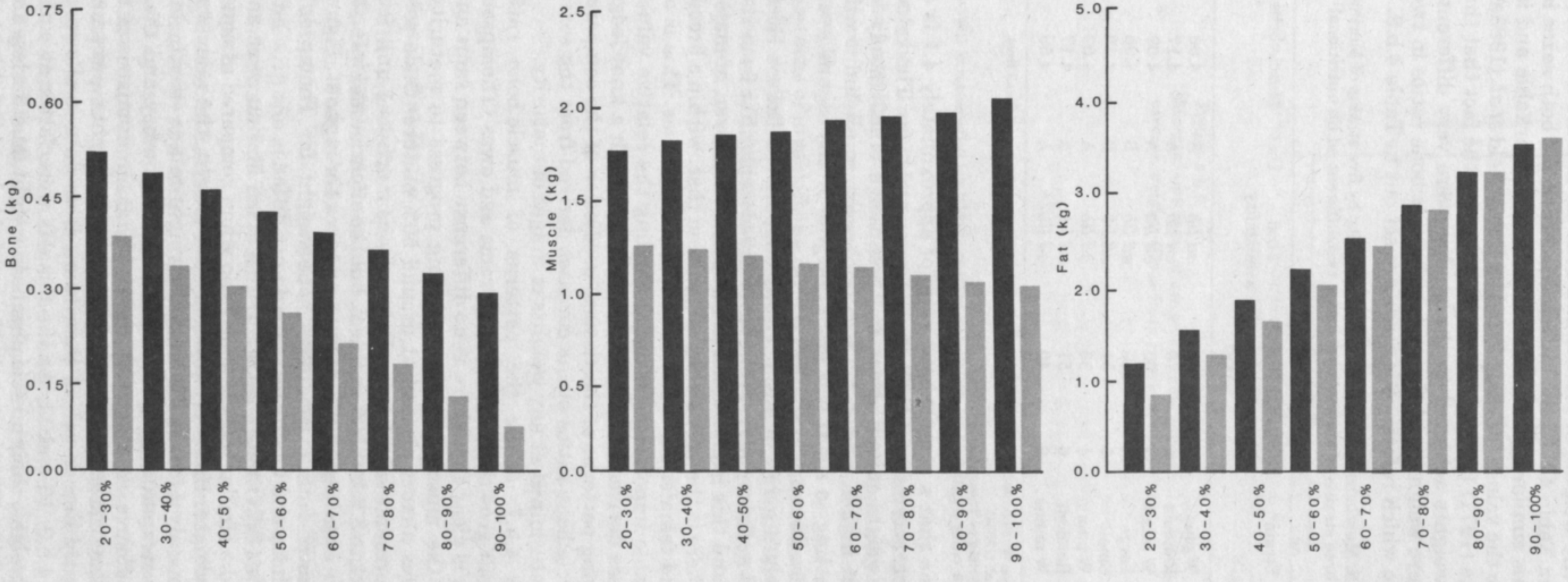


Figure 4.b.4.
The weight of carcase muscle, bone and fat gained in successive stages of progress to maturity of liveweight in Merino rams and ewes. (Adapted from Thompson, 1983.)

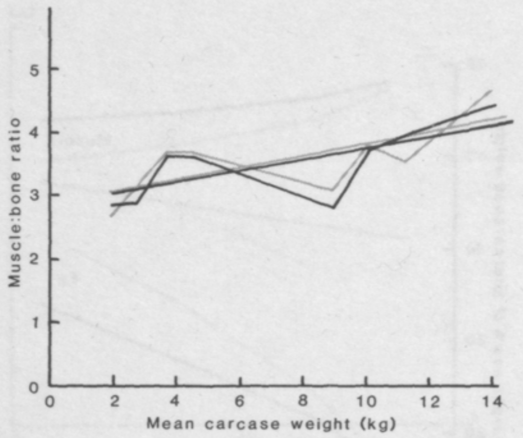


Figure 4.b.6.
Muscle:bone ratio of Merino ewes and rams compared at equal carcase weight. (Data from Lohse, 1971.)

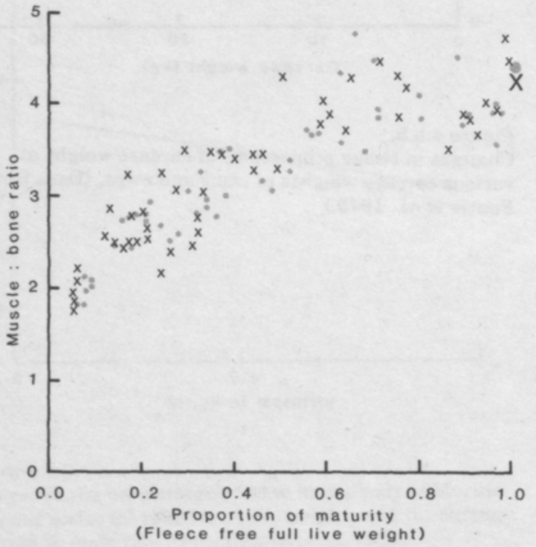


Figure 4.b.7.
Muscle:bone ratio of Merino ewes and rams relative to stage of maturity of liveweight. The large symbol "O" is the value (4.32) for 16 mature ewes and the large symbol "X" is the value (4.28) for 18 mature rams. (Data from Thompson, 1983.)

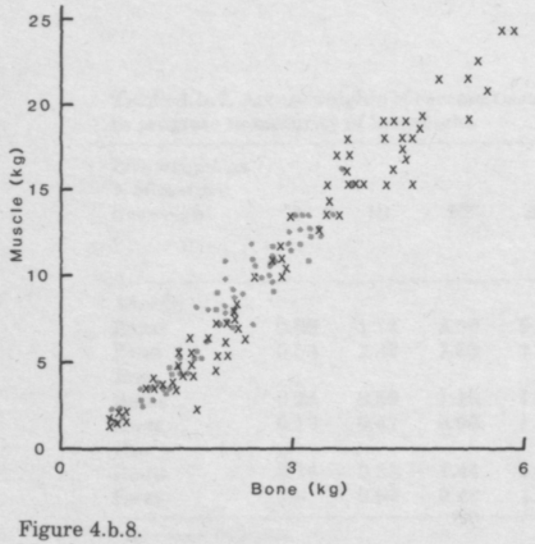


Figure 4.b.8.
Muscle versus bone weight of Merino rams and ewes. (Data from Thompson, 1983.)

Muscle:Bone Ratio

Using the weights of muscle and bone for mature rams and ewes from Table 4.b.1., the muscle:bone ratio for both sexes is 4.21 . This similarity for rams and ewes is remarkable and is similar to the values for rams found by Butterfield *et al.* (1983a) and Lohse (1971) (Figure 4.6.). This is despite the fact that the mature weights achieved in the studies were very different. The mature weights and the mature muscle:bone ratios in two studies to which reference is made are set out in Table 4.b.8.

Table 4.b.8. Muscle:bone ratio achieved at maturity by five strains of Merino rams and three strains of Merino ewes under two different ad lib nutritional regimes

Sex	Strain*	No.	Mature weight (kg)	Food availability	Diet†	Muscle:bone
Male	W plus	5	78	*ad lib*	A	4.06
Male	Random	6	70	*ad lib*	A	4.17
Male	W minus	7	60	*ad lib*	A	4.09
Male	Large	4	116	*ad lib*	B	4.05
Male	Small	6	91	*ad lib*	B	4.19
Female	W plus	4	56	*ad lib*	A	4.09
Female	Random	6	51	*ad lib*	A	4.17
Female	W minus	6	40	*ad lib*	A	4.59

* Strain: W plus, W minus and Random from Thompson *et al.* (1985a) and Large and Small from Butterfield *et al.* (1983a)
† Diet A—Described by Thompson *et al.* (1985a).
Diet B—'F 19' ration of CSIRO described by Graham and Searle (1972) and Butterfield *et al.* (1983a).

It seems that a muscle:bone ratio of approximately 4.1 is a robust characteristic of both Merino rams and ewes. The value for the "weight minus" ewes in Thompson's (1983) study is somewhat higher, however, the numbers are small and it will be interesting to see if this deviation was of any significance when more data are available.

The values given in the previous chapter for Dorset Horn rams and wethers suggest that other breeds will differ from the Merino, and this is addressed in Chapter 5. However, of major interest here is the very strong suggestion that, within a breed, males and females have similar muscle:bone ratios. This is of considerable importance in understanding the relative values of carcases derived from rams and ewes as, with a knowledge of maturing patterns of the tissues, prediction of the comparative muscle:bone ratios of the carcases derived from the sexes can be determined at any weights or stages of maturity.

Figure 4.b.7. shows the patterns of muscle:bone ratio throughout growth in Thompson's rams and ewes (Thompson, 1983). It is clear that there is no difference between rams and ewes in the muscle:bone ratio during progress to maturity. Both sexes almost plateau at around 50% mature. Once past 20% mature individual animals vary by as much as 1 unit (e.g from 2.5:1 to 3.5:1 at 30% mature), but the superior and inferior ratios are evenly spread over the two sexes throughout. Figure 4.b.8. shows muscle weight vs bone weight for Thompson's (1983) sheep and again the sexes do not differ.

Lohse's (1971) data also showed that his Merino ewes and rams had a similar muscle:bone ratio when compared at equal carcase weight. However, at his highest weight, the value was approximately 4.5 as in Thompson's weight-minus ewes.

Using composite data from Southdown, Romney and their crosses, Fourie *et al.* (1970) showed that, in comparison of muscle:bone ratio at four different carcase weights, ewes had consistently higher values than rams. This data is shown in Figures 4.b.9, 10 and 11. As the females were fatter at equal carcase weight, their muscle plus bone weight must be less and therefore we might expect that muscle plus bone weight would be less mature. Therefore, if the sexes had equal muscle:bone ratio at maturity, the ewes would be expected to have a lower muscle:bone ratio than the rams at the various carcase

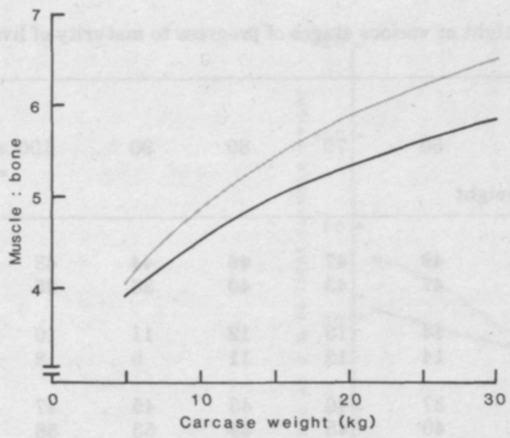


Figure 4.b.9.
Muscle:bone ratio of ewes and rams compared at equal carcase weight. (Data from Fourie *et al.*, 1970.)

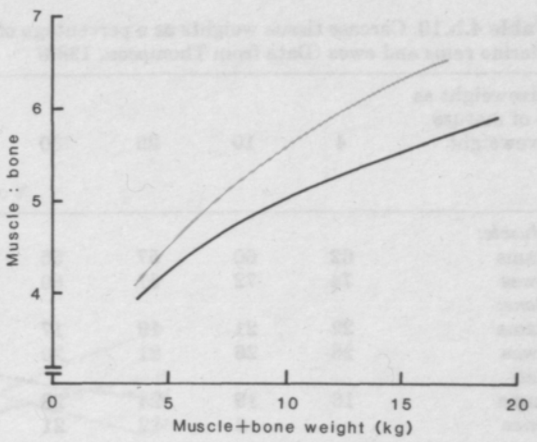


Figure 4.b.10.
Muscle:bone ratio of ewes and rams compared at equal muscle plus bone weight. (Data from Fourie *et al.*, 1970.)

weights. That this was not so could be an indication that either the ewes had a higher muscle:bone ratio at maturity than the rams; or the ewes were further advanced towards their mature muscle plus bone weights than the rams or the maturity patterns of muscle:bone ratio is different in the ewes. From the data available we must conclude that breeds differ in that, whereas sex seems to have no effect on muscle:bone ratio in Merinos, in some other breeds ewes are superior.

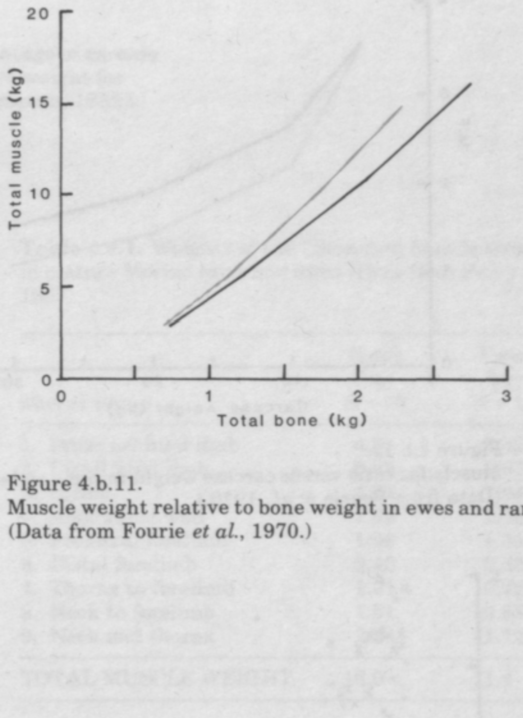


Figure 4.b.11.
Muscle weight relative to bone weight in ewes and rams. (Data from Fourie *et al.*, 1970.)

Muscle:Fat Ratio

The muscle:fat ratios of rams and ewes at maturity are clearly different. Ewes have a higher weight of fat per unit of muscle. This is seen in the data of Thompson *et al.* (1983) in Table 4.b.9. This ratio is of considerable commercial relevance and with the aid of the maturing patterns of fat and muscle as demonstrated in Table 4.b.10. can be ascertained throughout growth.

Table 4.b.9. Muscle:fat ratios of rams and ewes at maturity (Data from Thompson, 1983)

	Rams	Ewes
M:F ratio	1.5	1.1

Muscle:fat ratios of Fourie *et al.*'s (1970) rams and ewes are calculated and shown in Figure 4.b.12. over the range of 5-30 kg carcase weight. The rams excel over the ewes at each stage of the comparison and with the trend away from fat this must be viewed as an advantage for rams, particularly as this more than counteracts the slightly higher muscle:bone ratio of the ewes reported in the same comparison.

Figure 4.b.13. shows the muscle:fat ratios of Merino rams and ewes based on data from Thompson (1983). Although the mature values were significantly different (1.55 for rams and 1.08 for ewes), there was no clear difference appparent during earlier growth. This is of importance commercially if it is

Table 4.b.10. Carcase tissue weights as a percentage of total carcase weight at various stages of progress to maturity of liveweight of Merino rams and ewes (Data from Thompson, 1983)

Liveweight as % of mature liveweight	4	10	20	30	40	50	60	70	80	90	100 = 69.4 kg (R) = 49.0 kg (E)
	% of total carcase weight										
Muscle:											
Rams	62	60	57	55	53	51	49	47	46	44	43
Ewes	74	72	67	60	55	50	47	43	40	38	35
Bone:											
Rams	22	21	19	17	16	15	14	13	12	11	10
Ewes	26	26	21	20	17	15	14	12	11	9	8
Fat:											
Rams	16	19	24	28	31	35	37	40	43	45	47
Ewes	–	2	12	21	28	34	40	45	49	53	56
Total carcase weight (kg)											
Rams	1.1	2.9	6.1	9.6	13.5	17.6	22.1	27.0	32.1	37.6	43.3
Ewes	0.7	1.8	3.9	6.5	9.3	12.5	16.0	19.8	24.0	28.4	33.3

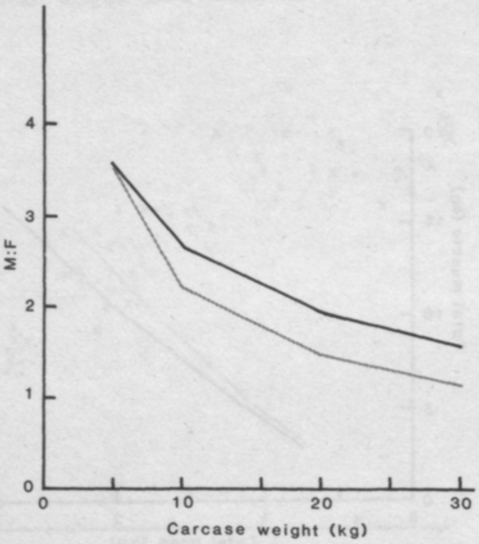


Figure 4.b.12.
Muscle:fat ratio versus carcase weight in rams and ewes. (Data from Fourie *et al.*, 1970.)

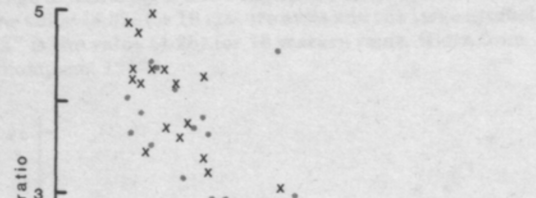


Figure 4.b.13.
Muscle:fat ratio during progress to maturity of Merino rams and ewes. The large symbol "O" is the value (1.08) for 16 mature ewes and the large symbol "X" is the value (1.55) for 18 mature rams. (Data from Thompson, 1983.)

suggested that prime ram lambs are leaner than ewes. This data from Thompson's (1983) study could be misleading in this regard as it is derived from sheep which were reared to weaning under pastoral conditions and therefore any data, particularly for fat, must be cautiously interpreted in relation to prime lamb growth. In Figure 4.b.14. the same data is used to express fat growth against muscle growth. From 3 kg to about 8 kg of muscle weight the rams and ewes had yet to diverge but from then on the ewes were obviously laying down more fat.

Turning from the study of the muscle:bone and muscle:fat ratio to simple proportions within carcases, it is clear from Figure 4.b.15. that Thompson's Merino rams had a higher proportion of muscle from about 50% of mature liveweight and that Fourie *et al.*'s rams were superior over the range 10-30 kg carcase weight (Figure 4.b.5.).

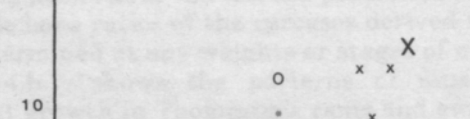


Figure 4.b.14.
Fat weight versus muscle weight (whole carcase) in Merino rams and ewes. The large symbol "O" represents 16 mature ewes and the large symbol "X" represents 18 mature rams. (Data from Thompson, 1983.)

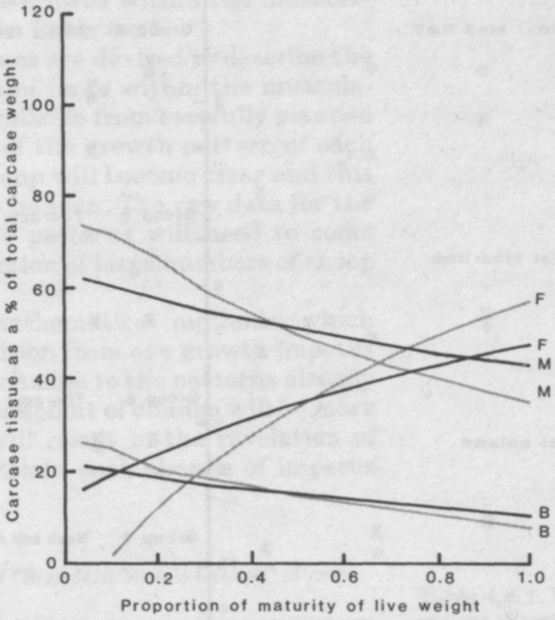


Figure 4.b.15
Muscle, fat and bone weights as a percentage of carcase weight at equal stages of maturity of live weight for Merino rams and ewes. (Data from Thompson, 1983.)

c. GROWTH WITHIN THE MUSCULATURE OF EWES RELATIVE TO RAMS

Jury *et al.* (1977) compared the muscle-weight distribution of rams and ewes from Romney, Southdown and their cross, over a range of total half-carcase muscle weight of 1 to 8 kg for rams and 1 to 6 kg for ewes. As seen in Figure 4.c.1. trends of change in distribution of muscle weight established up to 6kg total muscle weight in rams were continued up to 8 kg. Whereas the rams at the higher weights tended to develop a higher proportion of muscle weight in the muscles connecting the forelimb to the neck and the intrinsic muscles of the thorax and neck, this was offset by a decline in the proportion of the muscle weight in the proximal part of the hind limb. The ewes showed a tendency to develop their abdominal wall muscles earlier and hence these muscles reached 10.5% of total muscle weight at 4 kg total half-carcase muscle weight (ideal New Zealand lamb weight) whereas the rams did not achieve this same 10.5% until 6 kg total half carcase muscle weight.

A study of muscle-weight distribution of Merino rams and ewes was reported by Perry, Thompson and Butterfield (1987). This study was based on the "Standard Muscle Groups" and the composition of the musculature at maturity is shown in Table 4.c.1. and as proportions of total muscle weight in Table 4.c.2. The differences due to sex are clearly displayed. The ewes are significantly relatively heavier than the rams in all four limb groups (Groups 1, 2, 5 and 6) and significantly relatively lighter in the three groups associated with the cranial end of the trunk of the animal (Groups 7, 8 and 9). These compositional changes can be related in part to the post-weaning maturing patterns of the groups which appear in Table 4.c.3. The most extreme difference in 'q' values for the two sexes are in Group 9 and no doubt the proportional changes in this group have the major primary influence in the production of secondary compositional effects on the remainder of the musculature. The post-weaning values for Group 9 of 0.60 for rams and 1.14 for ewes are different from each other and significantly different from 1.0 in opposite directions. The difference in Group 8 is much less extreme and there is no difference in Group 7.

Table 4.c.1. Weights of the "Standard Muscle Groups" in mature Merino rams and ewes (Data from Perry *et al.* 1987)

Muscle group	Rams (kg) N = 19	Ewes (kg) N = 15
1. Proximal hind limb	4.91	3.43
2. Distal hind limb	0.83	0.57
3. Spinal	3.04	1.94
4. Abdominal wall	1.69	1.12
5. Proximal forelimb	1.98	1.31
6. Distal forelimb	0.49	0.33
7. Thorax to forelimb	1.21	0.72
8. Neck to forelimb	1.51	0.88
9. Neck and thorax	2.34	1.12
TOTAL MUSCLE WEIGHT	18.0	11.4

Table 4.c.2. Weights of "Standard Muscle Groups" as percentages of total muscle weight in mature Merino rams and ewes (Data from Perry *et al.* 1987)

Muscle group	Rams (n = 19)	Ewes (n = 15)	Sig. of Diff.
1. Proximal hind limb	27.3	30.1	***
2. Distal hind limb	4.6	5.0	**
3. Spinal	16.9	17.0	NS
4. Abdominal wall	9.4	9.8	NS
5. Proximal forelimb	11.0	11.5	**
6. Distal forelimb	2.7	2.9	**
7. Thorax to forelimb	6.7	6.3	*
8. Neck to forelimb	8.4	7.7	*
9. Neck and thorax	13.0	9.8	***
Total Muscle Weight (kg)	18.0	11.4	–

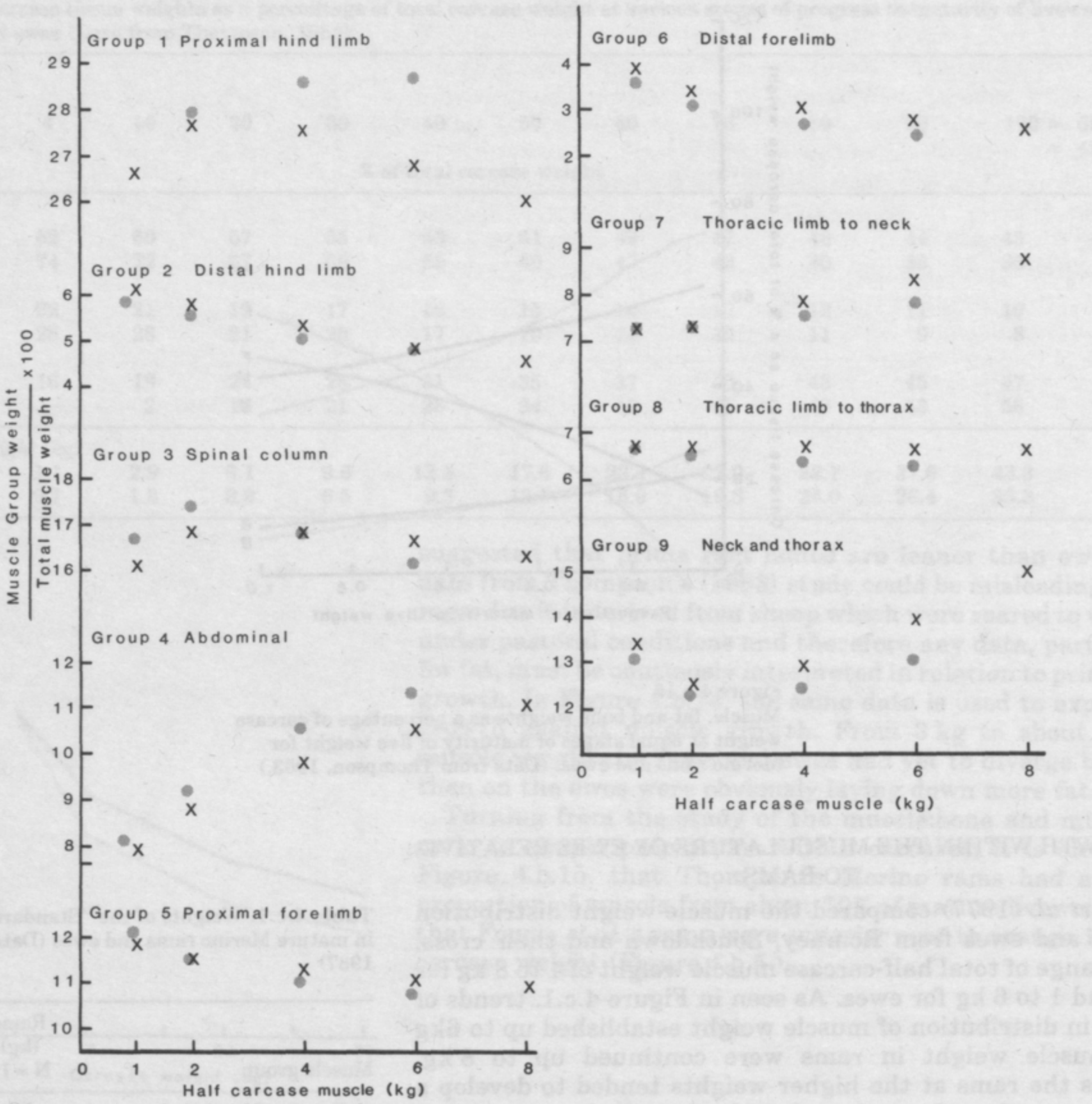


Figure 4.c.1.
Muscle-weight distribution comparison of rams and ewes. (Based on Jury *et al.*, 1977.)

Table 4.c.4. Maturing patterns of "Standard Muscle Groups" suggested from the data of Perry *et al.* (1987)

Muscle group	Growth impetus Rams Pre/post weaning	 Ewes Pre/post weaning
1. Proximal hind limb	Average/Low	High/Low
2. Distal hind limb	Low	Low
3. Spinal	High/Average	High/Average
4. Abdominal wall	High	High
5. Proximal forelimb	Low	Low/Average
6. Distal forelimb	Low	Low
7. Thorax to forelimb	Average	Average
8. Neck to forelimb	Low/High	Low/Average
9. Neck and Thorax	High	Low

Table 4.c.3. Maturity coefficients ('q') of "Standard Muscle Groups" relative to the weight of total muscle in Merino rams and ewes (Based on Perry *et al.* 1987)

Muscle Group	Rams Preweaning	 Postweaning	Ewes Preweaning	 Postweaning
1. Proximal hind limb	1.04	1.15[a]	0.88[b]	1.07[a]
2. Distal hind limb	1.50[a]	1.25[a]	1.50[a]	1.25[a]
3. Spinal	0.92[b]	0.97	0.92[b]	0.97
4. Abdominal wall	0.69[b]	0.90[b]	0.69[b]	0.64
5. Proximal forelimb	1.17[a]	1.11[a]	1.17[a]	1.02
6. Distal forelimb	1.67[a]	1.28[a]	1.67[a]	1.15[a]
7. Thorax to forelimb	0.97	0.94	0.97	0.94
8. Neck to forelimb	1.08[a]	0.84[b]	1.08[a]	0.96
9. Neck and thorax	0.79[b]	0.68[b]	0.99[a]	1.12[a]

a = significantly greater than 1.0
b = significantly less than 1.0

The maturing patterns of the rams and ewes based on the 'q' values of Perry *et al.* (1987) are shown in Table 4.c.4.

From the data from the 140 sheep slaughtered in the experiment of Perry *et al.* (1987), estimates of maturing patterns within the musculature can be derived. Using this information and that available from other studies (e.g., Lohse, 1971; Lohse *et al.*, 1971; Fourie, 1965; Jury *et al.*, 1977), the best estimate of the comparative growth within the musculature of rams and ewes is shown in Table 4.c.5.

As new mathematical techniques are devised to describe the changing impetus of the growth of units within the musculature and as more data become available from carefully planned studies, more precise definition of the growth pattern of each individual muscle and muscle group will become clear and this will allow fine sex differences to be seen. The raw data for the derivation of these more precise patterns will need to come from the individual muscle dissection of large numbers of sheep of known nutritional history.

It is not anticipated that mathematical methods, which attempt to fix the point of transition from one growth impetus to another, will result in drastic change to the patterns already obtained, but rather that the breakpoint of change will be more clearly defined. Whether this will result in the revelation of some physiological trigger to explain each change of impetus must remain to be shown.

Table 4.c.5. Growth impetus patterns of "Standard Muscle Groups" of rams and ewes (based on numerous studies)

Muscle group	Growth impetus Rams Phase 1/Phase 2	 Ewes Phase1/Phase 2
1. Proximal hind limb	High/Low	High/Low
2. Distal hind limb	Low	Low
3. Spinal	High/Low	High/Average
4. Abdominal wall	High/Average	High
5. Proximal forelimb	Low/Average	Low/Average
6. Distal forelimb	Low	Low
7. Thorax to forelimb	Average/High	Average
8. Neck to forelimb	Average/High	Average
9. Neck and thorax	Low/High	Average
"Expensive" (ie. 1+3+5)	High/Low	High/Average

* Phase 1 = up to 20 % of mature total muscle weight. Phase 2 = 20 to 100% of mature total muscle weight.

d. GROWTH OF BONES IN EWES RELATIVE TO RAMS

There appears not to be any data in the literature to form the basis of a discussion of relative bone growth of ewes and rams.

Little information has been published on the relative growth of bones in ewes and rams and I am indebted to Dr. J.M. Thompson for unpublished data from his study of Merino rams and ewes of three strains selected on weaning weight (Thompson, 1985a) For the purposes of this section, the data from Thompson's three strains have been combined within the sex groups.

Table 4.d.1. shows the mean mature weight of bones of rams and ewes from Thompson's three strains and Table 4.d.2. shows the same data expressed as percentages of total bone weight. All bones were heavier in the rams than in the ewes, and proportionately the rams had more bone in the axial skeleton and less in the limbs than the ewes. This difference is similar to that seen in rams and wethers (Table 3.d.2., p. 69).

The maturity coefficients for bones of rams and ewes shown in Table 4.d.3. show that there is difference in the maturing patterns of the hindlimb bones of rams and ewes in that the bones of the rams have relatively lower impetus than those of ewes. However, all of these hindlimb bones grow at lower relative rate than total bone in both sexes ($q > 1.0$). All the forelimb bones grow on similar patterns of lower impetus in the two sexes except the scapula which has a similar high impetus pattern in both sexes.

Within the axial skeleton, the pelvis plus sacrum and the thorax grow relatively fast whereas the lumbar vertebrae present different patterns of average impetus in the rams and low impetus in the ewes.

Table 4.d.1. Weights of individual bones in the half carcase of mature Merino rams and ewes (Data from Thompson, unpublished)

Individual bones	Weight (g) Rams (n = 18)	 Ewes (n = 16)	Ewes as proportion of rams
Hind limb			
Femur	172	122	0.71
Patella	11	8	0.73
Tibia	152	105	0.69
Tarsus	53	38	0.72
Total Hind Limb	**388**	**273**	**0.70**
Axial Skeleton			
Pelvis + sacrum	249	167	0.67
Lumbar vertebrae	170	84	0.49
Thoracic vertebrae + ribs	1000	588	0.59
Total Axial Skeleton	**1419**	**839**	**0.59**
Forelimb			
Scapula	99	65	0.66
Humerus	133	90	0.68
Radius and ulna	110	74	0.67
Total Forelimb	**342**	**229**	**0.67**
Total Bone	2149	1341	0.62

Table 4.d.2. Weights of individual bones as percentages of total bone weight of mature Merino rams and ewes (Data from Thompson, unpublished)

Individual bones	Percentage of total bone Rams (n = 18)	 Ewes (n = 16)
Hind limb		
Femur	8.0	9.1
Patella	0.5	0.6
Tibia	7.1	7.8
Tarsus	2.5	2.9
Total Hind Limb	**18.1**	**20.4**
Axial Skeleton		
Pelvis + sacrum	11.6	12.5
Lumbar vertebra	7.9	6.2
Thoracic vertebra + ribs	46.5	43.8
Total Axial Skeleton	**66.0**	**62.5**
Forelimb		
Scapula	4.6	4.8
Humerus	6.2	6.7
Radius and ulna	5.1	5.6
Total Forelimb	**15.9**	**17.1**
Total Bone	100.0	100.0

Table 4.d.3. Maturity coefficients ('q') for carcase bones relative to weight of total bone of Merino rams and ewes (Data from Thompson, unpublished)

	Maturity coefficients 'q'					
	Rams N = 73		Ewes N = 71		Pooled	Relative to 1.0
Hind limb						
Femur	1.34		1.14		–	Greater
Patella	1.52		1.21		–	Greater
Tibia	1.29		1.14		–	Greater
Tarsus	1.70		1.65		1.68	Greater
Total Hind Limb	**1.38**		**1.21**			
Axial Skeleton						
Pelvis + sacrum	0.95		0.78		0.87	Less
Lumbar vertebra	0.99	NSD	1.51	Greater	–	–
Thorax	0.81		0.85		0.83	Less
Total Axial Skeleton	**0.86**		**0.90**			
Forelimb						
Scapula	0.93		0.86		0.90	Less
Humerus	1.33		1.22		1.28	Greater
Radius and ulna	1.28		1.23		1.26	Greater
Total Forelimb	**1.20**		**1.12**		1.17	

Overall the weight relationships and relative growth of the components of the skeleton can be summed-up by saying that mature rams have heavier bones than mature ewes, the distribution of this weight is different with the ewes having proportionately heavier limb bones and lighter axial skeleton. The forelimb bones mature on a similar pattern in both sexes whereas the ewes have relatively lower impetus in the axial skeleton and higher impetus in the hindlimb.

Table 4.d.4. shows the progress to maturity of the bones relative to that of the total skeleton.

Table 4.d.4. The progress to maturity of bone weights of Merino rams and ewes relative to the progress to maturity of total bone weight (Data from Thompson, unpublished)

		Percentage maturity										Mature Weight Grams	
												Rams	Ewes
Total bone		10	20	30	40	50	60	70	80	90	100 =	2148.84	1341.27
Hind limb	*												
Femur	R	13	25	37	48	59	68	77	85	93	100 =	171.95	
	E	11	22	33	43	54	63	73	82	91	100 =		121.90
Patella	R	15	28	41	52	63	72	81	88	95	100 =	10.79	
	E	12	23	34	45	55	65	74	83	92	100 =		8.36
Tibia	R	13	25	36	47	57	67	76	85	93	100 =	151.98	
	E	11	22	33	43	54	63	73	82	91	100 =		104.63
Tarsus	R	16	31	44	56	67	76	84	91	96	100 =	53.39	
	E												38.51
TOTAL HINDLIMB	R	13	26	38	49	60	69	78	86	93	100 =	388.11	
	E	12	23	34	45	55	65	74	83	92	100 =		273.4
Axial Skeleton													
Pelvis + sacrum	R&E	9	18	27	37	47	57	67	78	89	100 =	248.53	167.41
Lumbar vertebrae	R	10	20	30	40	50	60	70	80	90	100 =	170.35	
	E	15	28	41	52	63	72	81	88	95	100 =		83.70
Thoracic vertebrae and ribs	R&E	8	17	26	36	46	56	66	77	88	100 =	999.6	587.93
TOTAL AXIS	R	9	18	27	37	47	57	67	78	89	100 =	1418.48	839.04
	E	9	18	28	38	48	58	68	78	89	100		
Forelimb													
Scapula	R&E	9	18	28	38	48	58	68	78	89	100 =	99.36	64.71
Humerus	R&E	13	24	36	47	57	67	76	84	93	100 =	132.73	89.59
Radius/Ulna	R&E	12	24	35	46	57	66	75	84	92	100 =	110.15	74.53
TOTAL FORELIMB	R&E	12	23	34	44	54	64	74	83	92	100 =	342.24	228.83

* R = Rams
E = Ewes

Linear Dimensions

Table 4.d.5. shows relative length and width of the limb bones of Merino rams and ewes. With the exception of the radius/ulna the length of which is similar in both sexes, the general pattern is that the ewe bones are about 0.9 of the length of the ram bones. However, the width of the long bones of ewes is around 0.85 that of the bones of rams.

The density of bones as measured by the weight:length ratio (Table 4.d.6.) shows the ram bones to be more dense in all bones measured with mean values for the rams of 0.69 compared with ewes 0.51.

Table 4.d.5. Linear dimensions of long bones of mature Merino rams and ewes (Data from Thompson, unpublished)

Individual bone	Rams	Ewes	Ewes as proportion of rams
Femur length	19.4	17.8	0.92
Tibia length	22.7	20.8	0.92
Scapula length	16.4	14.9	0.91
Humerus length	16.0	14.6	0.91
Radius/ulna length	20.3	19.6	0.97
Ischium length	22.8	20.3	0.89
Femur width	2.1	1.8	0.86
Tibia width	1.8	1.6	0.89
Humerus width	1.9	1.6	0.84
Radius/ulna width	2.1	1.8	0.86

Table 4.d.6. Weight:length ratio (g/mm) of bones of mature Merino rams and ewes (Data from Thompson, unpublished)

	Rams	Ewes
Femur	0.89	0.68
Tibia	0.67	0.50
Scapula	0.61	0.43
Humerus	0.83	0.61
Radius/ulna	0.54	0.38
Ischium	0.63	0.48
Mean	0.69	0.51

e. GROWTH WITHIN THE BODY FAT OF EWES RELATIVE TO RAMS

In many species a readily recognizable difference between the sexes is the smoothness of the surface of the female relative to the muscular definition of the male. This difference is brought about partly by the tendency for the female to have more abundant subcutaneous fat. The aesthetic appeal of this layer of fat in the meat animals of recent decades is less appreciated in the modern domestic meat animal where the trade is inclined to prefer male animals, even though castrated, as they believe the females are likely to be fatter at the same slaughter weight.

If, however, the female lays down fat preferentially in the subcutaneous depot and if carcases or live animals are assessed by measurement of subcutaneous fat, then females would have less fat in the total carcase at the same level of subcutaneous fat. It is, therefore, important that we understand the differences in fat partitioning.

Jones (1982) compared the "accumulation" of fat in four wholesale cuts of lambs slaughtered at liveweights ranging from 24 to 62 kg. He concluded in comparisons over this weight range that ewes fattened faster and earlier than rams, but that they partitioned their fat in a similar manner. He showed that the cuts from the ewes had slightly more intermuscular fat at the same total fatness than rams, but as this was a difference of only 24 g, and as the 'thin' cuts which he discarded could have drastically altered this finding in the whole carcase or sheep, it would be unwise to accept as usual that ewes partition more fat intermuscularly; in fact other studies show the opposite, or as in the study of Vezinhet and Prud'hou (1975) that there was no difference in fat partitioning between Merino rams and ewes.

We have discussed fat partitioning of rams and wethers in Chapter 3.e. and will use the study of Thompson (1983) as the main basis for this discussion of rams and ewes.

Table 4.e.1. Weights of fat partitions in mature Merino rams and ewes (From Thompson 1983)

Fat partition	Weight (kg) Rams (N = 18)	 Ewes (N = 16)
Subcutaneous	6.06	6.14
Intermuscular	6.06	4.84
Total carcase	12.12	10.98
Kidney	2.42	2.79
Omental	3.64	3.16
Mesenteric	1.41	1.30
Scrotal/Udder	0.61	0.37
Total non-carcase	8.08	7.62
Total body	20.2	18.6 (N.S.D.)

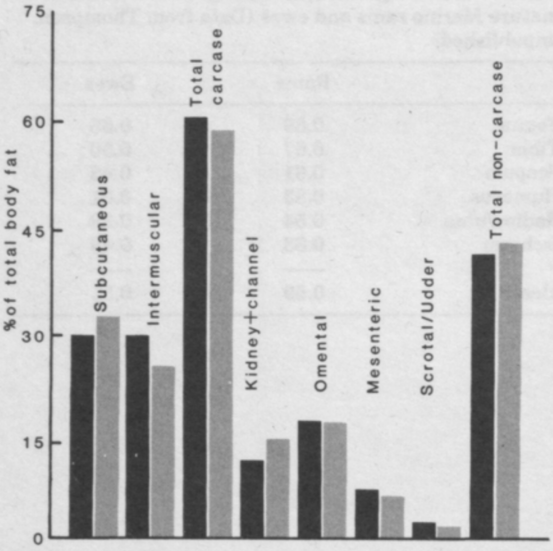


Figure 4.e.1.
Partitioning of fat. (Data from Table 4.e.2.)

Table 4.e.3. Maturity coefficients ('q') of fat partitions relative to total body fat of Merino rams and ewes (Adapted from Thompson 1983)

Fat partition	'q' Rams†	 Ewes	 Pooled
Subcutaneous	1.1	0.8	§
Intermuscular	1.3	1.2	1.2
Total carcase	1.2	1.0	1.1
Kidney	0.8	0.9	0.8
Omental	0.6	1.0	§
Mesenteric	1.0	1.2	*
Scrotal/Udder	1.2	1.5	1.3
Total non-carcase	0.8	1.0	0.9
Total body fat	1.0	1.0	1.0

† Ram and ewe values pooled over 'weight plus', 'random' and 'weight minus' strains.
* $P < 0.05$
§ $P < 0.01$

Table 4.e.1. shows the weight of fat in various partitions in mature Merino rams and ewes from Thompson's experiment. The data indicate a clear difference of partitioning of fat in rams and ewes (Table 4.e.2. and Figure 4.e.1.), although the total weight of fat was not significantly different in the two sexes.

Table 4.e.2. Weights of partitions of fat expressed as percentages of total body fat of mature Merino rams and ewes (Adapted from Thompson 1983)

Fat partition	Percent of total body fat Rams N = 18	 Ewes N = 16	Significance of difference	Ewes as % proportion of rams
Subcutaneous	30	33	*	1.10
Intermuscular	30	26	***	0.87
Total carcase	60	59		0.98
Kidney	12	15	**	1.25
Omental	18	17		0.94
Mesenteric	7	7		1.00
Scrotal/Udder	3	2	***	0.67
Total non-carcase	40	41		1.02
Total body	100	100		

Relative to total fat of rams, mature ewes had about three percentage units more of subcutaneous fat, three percentage units more of kidney fat, and four percentage units less of intermuscular fat. The scrotal fat of rams was about one percentage unit more than udder fat of ewes.

The commercially practical implications of the different fat partitioning of rams and ewes are centered in the carcase. The proportions of total carcase fat and total non-carcase fat are not different so that neither sex derives an advantage in dressing percentage from differences in partitioning of fat in mature animals. However, the greater proportions of subcutaneous fat in the ewes and of intermuscular fat in the rams have interesting implications at commercial slaughter weights, if indeed, these relationships are reflected at that stage. To examine this, the maturing patterns of the various partitions need to be studied.

In Table 4.e.3. are set out maturity coefficients for the fat partitions in Merino rams and ewes. The most important difference between the rams and ewes is in the maturing pattern of subcutaneous fat (rams 'q'= 1.05; ewes 'q' = 0.8). This difference means that the proportions of total fat represented by this partition will vary in such a way that, whereas the rams will have a higher proportion than the ewes up to about 60% of their mature weight, this will then be reversed. This is shown in Figure 4.e.2. adopted from Thompson (1983). As this reversal of proportions is not reflected in the intermuscular depot (see Figure 4.e.3.) the proportion of total carcase fat of rams relative to ewes must vary in an approximately similar way to subcutaneous fat (see Figure 4.e.4.).

For the most commercially useful comparison related to the carcases of rams and ewes it is instructive to study the subcutaneous and intermuscular partitions relative to the sum of their weights (i.e., total carcase fat) in Figure 4.e.5. Here it is seen that the subcutaneous fat grows at a greater impetus in ewes than in rams and exceeds the gross weight of intermuscular fat at lighter total carcase fat weight (approximately 7.5 cf 11.5 kg). At any same total carcase fat weight the rams at all stages have more intermuscular and less subcutaneous fat than the ewes.

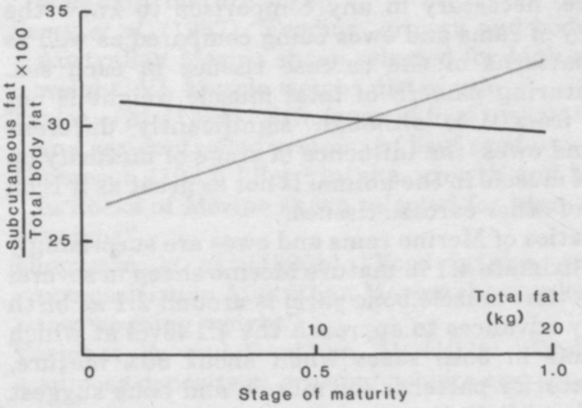


Figure 4.e.2.
The change in proportion of subcutaneous fat relative to total body fat in Merino rams and ewes. (From Thompson, 1985.)

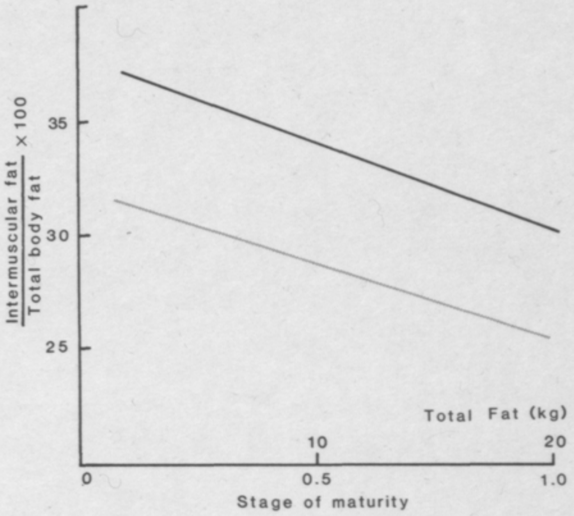


Figure 4.e.3.
The change in proportion of intermuscular fat relative to total body fat in Merino rams and ewes. (From Thompson, 1983.)

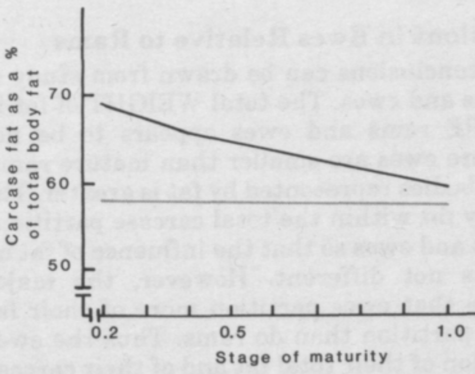


Figure 4.e.4.
The change in proportion of total carcase fat relative to total body fat in Merino rams and ewes. (Data from Thompson, 1983.)

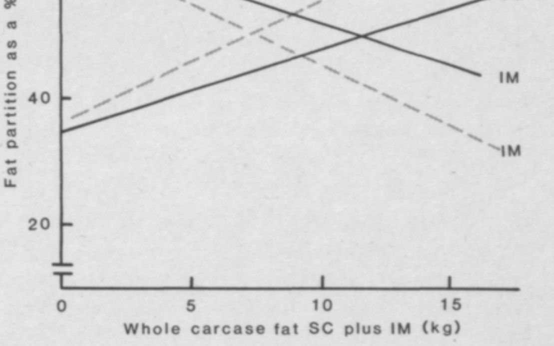


Figure 4.e.5.
Fat partitioning within the carcases of rams and ewes on the basis of total carcase fat (SC. + IM.). (Data from Thompson, 1983.)

f. CONCLUSIONS

Growth of Carcase Tissues

Rams and ewes differ in the proportions of carcase muscle, bone and fat at maturity. Rams contain greater proportions of muscle and bone and a smaller proportion of fat. The patterns of growth to maturity indicate that the carcase tissues follow different paths to their mature weights in rams and ewes.

It is, therefore, necessary in any comparison to know the stage of maturity of rams and ewes being compared as well as the maturing patterns of the carcase tissues in each sex. Because the maturing pattern of total muscle weight is not very different from 1.0, although significantly different between rams and ewes, the influence of stage of maturity on the proportion of muscle in the animal is not as great as it is on the proportions of other carcase tissues.

Muscle:bone ratios of Merino rams and ewes are surprisingly similar and approximate 4:1 in mature Merino sheep in several strains. It seems that muscle:bone ratio is around 2:1 at birth and quite rapidly advances to approach the 4:1 level at which it almost plateaus in both sexes when about 50% mature, although the maturity patterns for muscle and bone suggest that there must be a slight increase as muscle plus bone weight increases. Evidence from other breeds suggests that the similarity of muscle:bone ratio seen in Merino rams and ewes may be a peculiar breed characteristic as in Romney and Southdown sheep the ewes appear to have a higher muscle:bone ratio.

Muscle:fat ratio is markedly different in the sexes with ewes having a higher level of fat per unit of muscle. In both sexes muscle has a maturing pattern very similar to the whole animal, whereas fat has a high impetus pattern ('q' less than 1.0); thus the ratio of muscle to fat declines throughout progress to maturity.

Growth Within the Musculature

The major differences in the growth of the musculature of rams and ewes result from the post-pubertal high impetus growth of muscles in the cranial end of the rams.

Most evidence suggests that there is little difference in the pre-pubertal growth of the muscles of the two sexes and that the post-pubertal differences are produced either directly or indirectly by increased growth impetus in the muscles in the cranial end of the male sheep.

Growth of Fat Partitions in Ewes Relative to Rams

Several interesting conclusions can be drawn from study of fat partitioning of rams and ewes. The total WEIGHT of fat in the bodies of MATURE rams and ewes appears to be not different, but, as mature ewes are smaller than mature rams, the proportion of their bodies represented by fat is greater. The proportion of total body fat within the total carcase partitions is not different in rams and ewes so that the influence of fat on dressing percentage is not different. However, the major important difference is that ewes partition more of their fat into the subcutaneous partition than do rams. Thus the ewes have a smaller proportion of their total fat and of their carcase fat in the intermuscular partition.

However, due to different maturing patterns, the partitioning of fat during growth does not reflect that of the mature animals. Rams have a greater proportion of subcutaneous fat up to around 60% mature and from then to maturity the ewes have a greater proportion. As pointed out by McClelland *et al.* (1976), the majority of lambs in the United Kingdom, and probably elsewhere, are marketed at around 60% of their mature weight, and therefore the difference in partitioning of fat in slaughter animals of the two sexes may be small.

MAJOR REFERENCES FOR CHAPTER 4

Fourie *et al.* (1970) "Growth and development of sheep. II. Effect of breed and sex on the growth and carcass composition of the Southdown and Romney and their cross"

Jury *et al.* (1977) "Growth and development of sheep. IV. Growth of the musculature"

McClelland *et al.* (1976) "Breed differences in body composition of equally mature sheep"

Perry *et al.* (1987) "Feeding, growth and body composition in Australian Merino sheep selected for high and low weaning weight. VI. Muscle weight distribution"

Taylor *et al.* (1985) "Efficiency of food utilization in traditional and sex-controlled systems of beef production"

Thompson (1983) "Feed intake, growth and body composition in flocks of Merino sheep selected for high and low weaning weight"

Thompson *et al.* (1985b) "Food intake, growth and body composition in Australian Merino sheep selected for high and low weaning weight"

Vezinhet, A. and Prud'hon, M. (1975) "Evolution of various adipose deposits in growing rabbits and sheep"

CHAPTER 5

COMPARISON OF GROWTH AND DEVELOPMENT OF BREEDS

a. INTRODUCTION

It is difficult to embrace the subject of breed comparisons of sheep in any manner which will give the reader a comprehensive story. Breed comparisons in the literature are mostly confined to small numbers of breeds and small numbers of criteria under conditions which are specific to the particular comparison. Additionally, the breeds of interest differ from country to country and even within a breed there is often a wide spectrum of types or strains within and between countries. This is apparent, for example, in Merino sheep in Australia and within the Texel breed in the United Kingdom where results of studies by Wolf *et al.* (1980) and More O'Ferrall and Timon (1977a,b) differ from those of similar studies of Kempster *et al.* (1987) who suggest that the different results are due to the use of different strains of Texel sheep.

The studies of Kempster *et al.* (1987) and Croston *et al.* (1987), based on Meat and Livestock Commission data, are extremely large and comprehensive in that they were carried out over a five year period in 10 geographically-scattered commercial flocks of Scottish Blackface, Scotch Halfbred (Border Leicester x North Country Cheviot) and Mule (Blue-faced Leicester x Swaledale) ewes mated to 10 terminal sire breeds. Their analysis involved 3,360 lambs produced by an average of 43 randomly-selected rams per breed. The 10 breeds were: Border Leicester, Dorset Down, Hampshire Down, Ile de France, North Country Cheviot, Oxford Down, Southdown, Suffolk, Texel and Wensleydale. One side from each of 1,120 lambs was dissected into muscle, subcutaneous fat, intermuscular fat, bone and waste using the procedure of Cuthbertson, Harrington and Smith (1972); lambs were slaughtered at the same estimated subcutaneous fat content of 120 g/kg of carcase weight.

Among the significant findings from this study was the demonstration of different growth rates among breeds of similar body size. In particular, the Texel and the Suffolk grew faster than the similar-sized Oxford Down, Border Leicester and Wensleydales. When broken down to carcase muscle and fat growth Texel was superior to the Suffolk in muscle growth. A most important table from Kempster *et al.* (1987) is reproduced as Table 5.a.1. and shows that the Texel carcases had significantly more muscle and less fat than any other breed in the comparison.

There are, in some countries, remnants of breeds of sheep which have played a part in the past development of the local sheep breeds. An example of this is the Lincoln breed which was used in the development of the Corriedale in New Zealand and in Australia. It is well to remember that the Lincoln and other breeds have fallen into commercial oblivion on the basis of assessment in a very different era of commercial requirements to those prevailing now. It is, therefore, of interest to see that a relook at the Lincoln is taking place in the U.S.A. (Dahmen, Jacobs and Morrison, 1985). Although the comparisons made by Dahmen *et al.* demonstrated little if anything to recommend the reintroduction of the Lincoln as a commercial proposition in Idaho, U.S.A., it is well to keep in mind that more extensive testing under different conditions might well reveal valuable production characteristics of this and other now relatively obscure breeds.

In this chapter we will compare many characteristics of just two breeds from which considerable data have been collected under similar circumstances. Using the two breeds in the studies of Butterfield *et al.* (1983, 1984/5) which formed the basis of Chapters 2 and 3, i.e., Merinos and Dorset Horns, an attempt is made to present methods of comparison which might be used as data become available from further studies. The two breeds in this comparison represent the morphological extremes of the breeds widely used in the Australian sheep industry, although there are, in other parts of the world, sheep of more diverse types. The data come from two separate experiments, the conditions of which were almost identical. The feeding was *ad lib* and the diet was the same pelleted ration. The same housing was used and the preweaning (and pre-experiment) growth was in each case that which could be expected under Australian pastoral conditions; i.e. somewhat slow.

As pointed out in Chapter 2, the Merino breed in Australia is very diverse in that selection for various wool types and adaptability to the wide range of environments has resulted in sheep of a wide range of many characteristics, and this includes size. For this comparison the larger of the two strains available was used as it varies most in size from Dorset Horns. Few strains of Merinos have been directly selected for meat characteristics and certainly not the strain used in this comparison.

The Dorset Horn has been used in the Australian industry since 1895 (Australian Agricultural Year Book, 1985) and has been selected for meat characteristics. Initially its greatest use in Australia was as a sire of fat lamb mothers in a cross with the abundant Merino ewes. Over recent years this role has changed. Formerly, the Southdown was used as a terminal sire on crossbred ewes, including the Dorset x Merino ewe, but as the demand has grown for larger, leaner carcases, the Dorset Horn has replaced the Southdown as a terminal sire over a variety of dams, but most commonly the Border Leicester x Merino.

Table 5.a.1. Sire breed means from "Late Flocks" computed over three dam types (From Kempster et al. 1987)

	Border Leicester	Dorset Down	Hampshire Down	Ile de France	N. Country Cheviot	Oxford Down	Southdown	Suffolk	Texel	Wensleydale	Approx. s.e. of Mean
Age at slaughter (days)	286	218	236	253	242	271	234	249	247	287	6
Carcass weight (kg)	19.7	17.0	17.7	18.4	18.3	19.7	16.4	19.1	18.8	20.2	0.1
Daily carcass weight gain (g)	74	86	82	78	82	79	80	84	83	74	2
M. longissimus											
Width (A) (mm)	57.5	55.1	56.2	57.0	57.0	58.1	55.3	58.0	57.7	58.8	0.52
Depth (B) (mm)	26.3$_a$	26.0$_a$	25.5$_a$	27.5$_b$	25.7$_a$	26.3$_a$	25.8$_a$	26.4$_a$	27.4$_b$	26.1$_a$	0.35
Carcass conformation (15 point scale)	6.5$_a$	7.6$_{bc}$	7.5$_{bc}$	8.2$_c$	7.1$_{ab}$	6.9$_a$	8.3c	7.8$_c$	7.9$_c$	6.6$_a$	0.23
Tissue in carcass (g/kg)											
lean	562$_{ab}$	557$_a$	562$_{ab}$	571$_b$	568$_{ab}$	560$_{ab}$	559$_{ab}$	567$_{ab}$	590$_c$	567$_{ab}$	3.2
separable fat	257$_{bc}$	267$_{cd}$	263$_{bcd}$	255$_{bc}$	251$_b$	258$_{bc}$	273$_d$	252$_b$	240$_a$	253$_b$	3.3
Daily tissue weight gain in carcass (g)											
lean	40	47	45	43	45	42	43	46	47	40	1.0
separable fat	19	22	22	20	20	20	22	21	20	18	0.57

a, b, c, d means with the same subscript did not differ significantly ($P < 0.05$)

b. BREED DIFFERENCES IN GROWTH OF CARCASE TISSUES

McClelland and Russel (1972) suggested that "when animals of differing mature weight are slaughtered at the same stage of maturity, the proportion of fat in the body will be similar." They studied wethers fed set weights of either 200 or 100 g/day of a very high protein diet, and there was no breed difference between Dorset Horn and Corriedale in the deposition of protein, ash or fat. We might, therefore, expect that two breeds fed the same diet and compared at maturity would have similar proportions of total body fat and if the fat is partitioned similarly between the carcase and the remainder of the body, similar proportions of carcase fat.

Table 5.b.1. Carcase tissue weight of mature Merino and Dorset Horn rams

Whole carcase tissue	Weight (kg) Merino N = 4	 Dorset N = 5	Sig. Diff.
Muscle	25.9	24.7	NS
Bone	6.4	4.7	*
Fat	26.7	24.7	*
Liveweight	116.5	99.7	**

Table 5.b.2. Carcase tissues as percentages of shorn full liveweight of mature Merino and Dorset Horn rams

Whole carcase tissue	Percent of liveweight Merino N = 4	 Dorset Horn N = 5	Sig. Diff.
Muscle	22.3	24.8	*
Bone	5.5	4.7	NS
Fat	23.0	24.8	NS
Liveweight	100.0	100.0	-

Merinos and Dorset Horns are compared at maturity in Table 5.b.1. and 5.b.2. These sheep had similar proportions of both fat and bone and so support the hypothesis of McClelland and Russel at that final stage of growth. If the hypothesis regarding fat is to be fully supported by these data, it is necessary that the two breeds have, not only the same proportion of fat at maturity, but also that they achieved this level of fatness along the same maturing pattern, and that the proportion of total body fat partitioned into the carcase is the same. As will be shown in Section 5.e., this is so.

Table 5.b.3. Maturity coefficients ('q') for muscle, bone and fat relative to liveweight of Merino and Dorset Horn rams

Carcase tissue	'q' Merino	 Dorset	 Sig.	Pooled Diff.
Muscle	1.31	1.21	NS	1.26
Bone	1.33	1.63	*	-
Fat	0.07	0.05	NS	0.06

All values significantly different from 1.0.

In Table 5.b.3. are set out the maturity coefficients which show that there is no difference in the coefficients for fat over the period from 20% mature up to maturity. It can, therefore, be deduced that the proportion of fat in the bodies of the two breeds of rams was similar at all stages of progress to maturity and the hypothesis of McClelland and Russel is supported. These results cannot, of course, be extrapolated to cover all breeds as Wolf *et al.* (1980) have shown that the Texel breed is leaner (i.e., less fat) than would be expected from its mature size. This applies also in other species, such as the Pietran breed of pigs and Limousine cattle (Wood, 1982). Also Fourie *et al.* (1970) showed breed differences between Southdown, Romney and their cross, in the growth coefficients of total body fat against starved body weight.

Dorset Horn rams contain a higher proportion of muscle weight (2.5% of liveweight) than Merinos at maturity in this comparison (Table 5.b.2.). While this would not come as any surprise to those who regard the Dorset Horns as "meat" sheep and the Merinos as "wool" sheep; it is not consistent with results from Edinburgh (McClelland *et al.*, 1976; Thonney *et al.*, 1986) in which they showed no differences in the proportion of muscle to liveweight over diverse breeds when compared at the same degrees of maturity. That the superiority of the Dorset Horn was also apparent throughout growth, is shown by the maturity coefficients set out in Table 5.b.3. which indicate no significant difference in 'q' values for the two breeds. It is therefore concluded that, relative to liveweight, it can be expected that Dorset Horn rams will show a slight superiority throughout growth in the proportion of muscle weight to liveweight compared with Merinos. Fourie *et al.* (1970), on the other hand, showed no significant difference in liveweight and muscle weight at maturity, nor were the growth coefficients for muscle different in Southdown, Romney, and Southdown x Romney. Therefore, in their three genotypes, there was no difference in muscle weight to liveweight and as "Muscle growth occurs at almost exactly the same rate as starved liveweight" (Fourie *et al.*, 1970) comparisons on any basis should record similar proportions of muscle to liveweight in these three genotypes.

Bone provides an interesting comparison in Dorset Horns and Merinos. The difference in proportion at maturity approaches, but does not reach, significance and indicates that Merinos may have a slightly higher proportion of skeleton weight than

Dorset Horns. However, the main interest lies in the maturing patterns which are significantly different (Table 5.b.3. and Figure 5.b.1.) indicating that comparisons of the proportion of bone to liveweight will be different at different stages of maturity. Fourie *et al.* (1970) also showed breed differences in the growth coefficients ('b') of bone of Southdown, Romney and their cross. They claimed that this was one of the first experiments reported with domestic animals that had established significant within-species differences between breeds in allometric growth coefficients for bone.

Table 5.b.4. shows the progress to maturity of the three carcase tissues along their maturing patterns. They show, for example, that when liveweight is 50% mature, the proportion of fat and muscle was similar for both breeds but there were differences in bone; in Dorset Horn bone was 66% of its mature weight whereas in the Merino it was 58%. If there are similar differences in maturing patterns of bone or other tissues in various breeds, then this type of information is necessary before genetically-meaningful statements can be made about the relative composition of animals revealed during any comparison. Such comparisons will be possible between breeds as the data are accumulated on their mature weights and their maturing patterns.

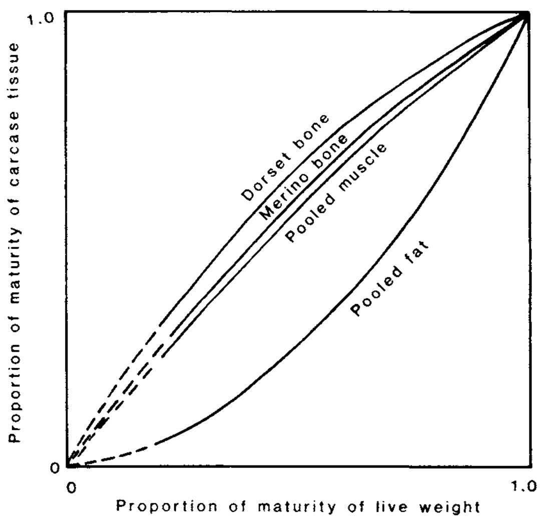


Figure 5.b.1.
Maturing patterns of carcase tissues of Merino and Dorset Horn rams (see Tables 5.b.3. and 5.b.4.).

The information in Table 5.b.4. could be used to calculate carcase composition at any chosen liveweight, or carcase weight. It is, of course, possible to decide from this information the answers to such questions as: What liveweight of sheep of each breed at around 50% mature would we need to yield a specified weight of muscle tissue or muscle plus fat tissue ("meat")?

Table 5.b.4. Progress to maturity of carcase tissues of Merino and Dorset Horn rams relative to progress to maturity of shorn full liveweight

		Percentage maturity								Mature weight Kg Merino	Mature weight Kg Dorset Horn
Liveweight	20	30	40	50	60	70	80	90	100 =	116.5	99.7
Muscle	24	35	46	57	66	75	84	92	100 =	25.9	24.7
Bone Merino	25	37	48	58	68	77	85	93	100 =	6.4	–
Dorset	30	43	55	66	75	83	90	96	100 =	–	4.7
Fat	5	10	17	27	37	50	65	82	100 =	26.7	24.7

Set out in Table 5.b.5. is an example of the actual weights of the tissues in the two breeds calculated from maturing patterns. When this type of information is available for many other breeds our ability to make definitive statements regarding the comparative body composition will be greatly enhanced. In Figure 5.b.2. are shown the increments of muscle, bone and fat during each 10% increase in liveweight from 20% mature up to maturity. This figure shows the overall similarity of the growth process of each tissue and highlights that differences in the mature weight of the tissues are contributed throughout the growth process. The pooled 'q' for muscle of 1.26 for Dorset Horns and Merinos indicates a small proportional change in muscle to liveweight throughout growth. However, due to the fact that the Merinos were 17 kg heavier than the Dorset Horns at maturity, there was a small increase in the difference in the relative proportions of muscle when compared at equal maturity, compared with comparison at equal liveweight (Table 5.b.6.) (and in Figure 5.b.3.).

Also the differences in the proportion of fat and bone were considerably reduced when compared at equal maturity and this reinforces the demonstration in Chapter 2 of the need for genetic comparisons to be made at equal maturity. However, due to the changing proportions in line with the maturing patterns of the tissues, the values at any stage of maturity will be unique to that stage of maturity. In the case of the muscle and fat, in which maturing patterns are common to the two breeds, there will be no crossover of values. However, the Dorset Horn rams had a lower proportion of bone at maturity and a higher 'q' value than the Merinos, hence in the early stages of growth the Dorset Horns had the greater proportion of bone, whereas after about 40% mature, the Merinos had proportionately more bone. In animals slaughtered between 20 and 60% mature there would be little difference between the breeds (see Figures 5.b.4. and 5.b.5.). The work of McClelland *et al.* (1976) showed that "while a large part of between-breed . . ...differences in body composition can be accounted for by stage of maturity, useful amounts of variation remain."

Table 5.b.5. Predicted weights of carcase tissues in Merino and Dorset Horn rams during progress to maturity.

Liveweight % maturity	20	30	40	50	60	70	80	90	100
Liveweight (kg)									
Merino	23.3	35.0	46.6	58.3	69.9	81.6	93.2	104.9	116.5
Dorset	19.9	29.9	39.9	49.9	59.8	69.8	79.8	89.7	99.7
Muscle (kg)									
Merino	6.2	9.5	11.9	14.8	17.1	19.4	21.8	23.8	25.9
Dorset	5.9	8.6	11.4	14.1	16.3	18.4	20.7	22.7	24.7
Bone (kg)									
Merino	1.6	2.4	3.1	3.7	4.3	4.9	5.5	6.0	6.4
Dorset	1.4	2.0	2.6	3.1	3.5	3.9	4.2	4.5	4.7
Fat (kg)									
Merino	1.3	2.7	4.5	7.2	9.9	13.4	17.4	21.9	26.7
Dorset	1.2	2.5	4.2	6.6	9.1	12.4	16.1	20.3	24.7

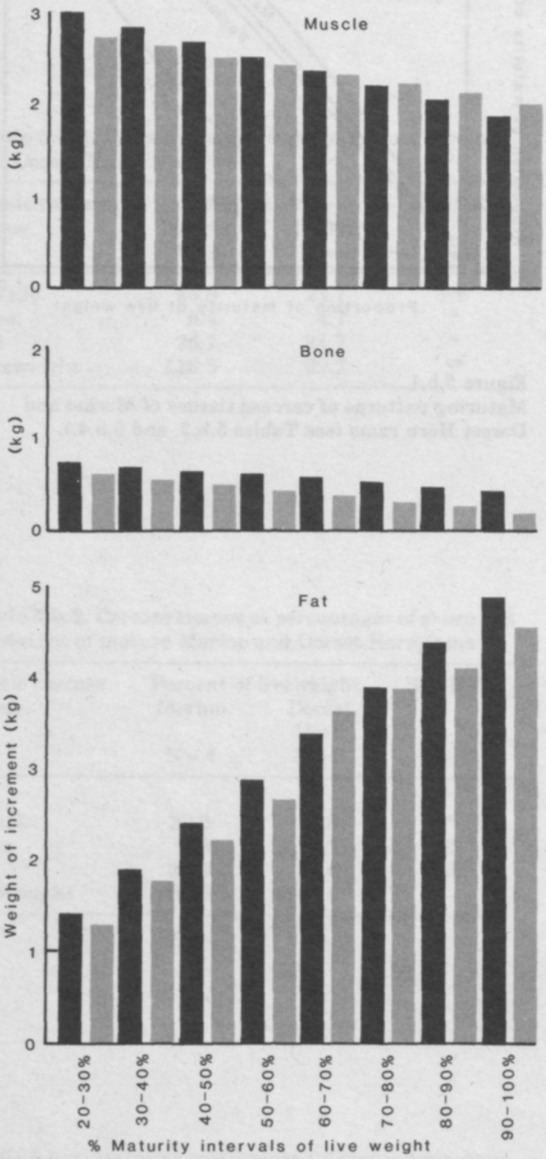


Figure 5.b.2.
Increments of muscle, bone and fat during each 10% increase in liveweight of Merino and Dorset Horn rams.

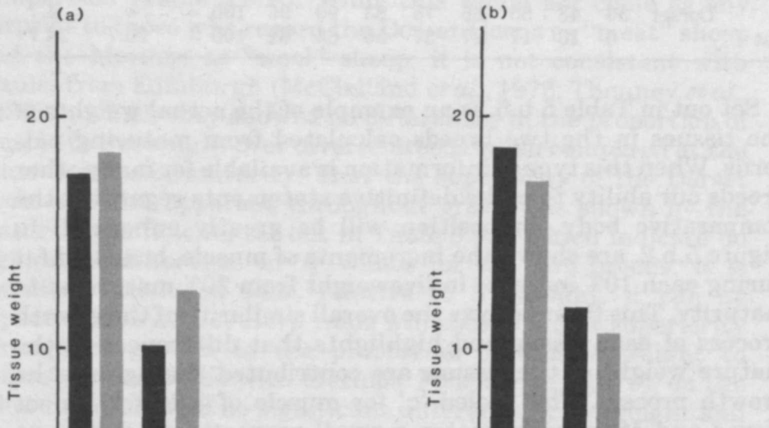


Figure 5.b.3.
Mean weight of carcase tissues of Dorset Horn and Merino rams (a) at equal liveweight (70 kg), and (b) at equal maturity (0.65).

Table 5.b.6. Predicted means of carcase tissues as percentages of liveweight of Merino and Dorset Horn rams at (i) The mean liveweight (70 kg) and (ii) The mean proportion of mature liveweight (0.65)

Tissue	At mean liveweight			At same proportion of mature liveweight		
	Merino	Dorset Horn	Dorset Horn as proportion of Merino	Merino	Dorset Horn	Dorset Horn as proportion of Merino
Muscle	24.9	26.3	1.06	24.6	26.6	1.08
Bone	6.2	5.6	0.90	6.1	5.8	0.95
Fat	14.4	17.8	1.24	15.5	16.5	1.06

MUSCLE:BONE RATIO

Kempster and Cuthbertson (1977) recorded a range of muscle:bone ratios in a comparison of seven breed types of lambs at equal subcutaneous fat percentage. These are set out in Table 5.b.7. The type groups were based on the weight and fatness of carcase usually produced (larger, e.g. Suffolk; intermediate, e.g. Dorset Down and Hampshire Down crosses; and smaller, Southdown crosses) and partly on genetic history (Welsh Mountain, Black-Faced Mountain, and British Longwools pure or crossbred).

There seems, from these results, to be no consistent relationship betweeen size and muscle:bone ratio nor do breed types as diverse as Southdown crosses and British Longwools differ in muscle:bone ratio. The Suffolk crossbreds have a lower muscle: bone ratio but it must be remembered that the dam base of these breed types differed. However, this may be a true breed characteristic as Wood, MacFie, Pomeroy and Twinn (1980) showed the Suffolk to have a lower muscle:bone ratio than Clun, Colbred and Hampshire over a range of carcase weights. Kempster, Croston and Jones (1981) showed that Texel progeny had higher muscle:bone ratio than other breeds surveyed, with a ratio of 3.75 compared with the lowest in the Oxford Down of 3.34. Although not all differences were significant, it is interesting to rank their breeds in an attempt to determine if there is a relationship between broad types of sheep and their muscle:bone ratios. The ranking is:

Texel,
Southdown,
Ile-de-France,
Hampshire Down,
Wensleydale, Oxford Down and Dorset Down,
Suffolk,
Border Leicester
and North Country Cheviot.

Although the author is not closely acquainted with some of these breeds, it seems that there is little relation between this ranking and general body type. Kempster *et al.* (1981) concluded that, although there were important differences between sire breeds in both conformation and muscle:bone ratio, there was little relationship between these two characteristics, and although the Texel stood out in muscle:bone ratio, its conformation was not sufficiently extreme for this to be assessed visually. Jackson and Mansour (1974) also showed that muscle:bone ratio was little effected by conformation

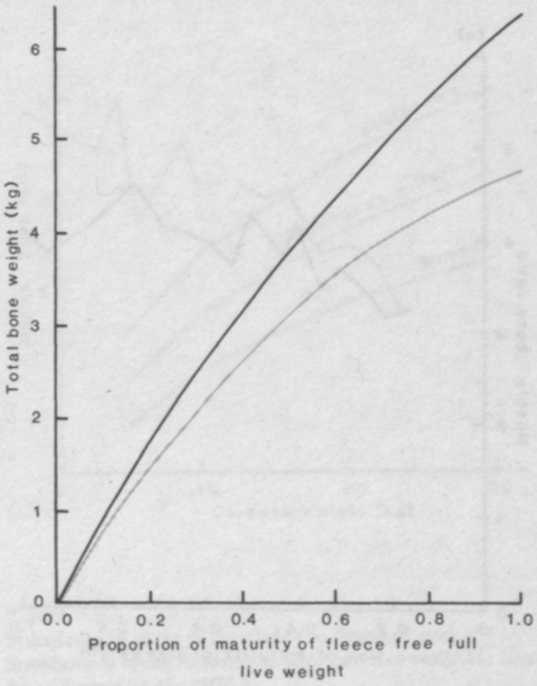


Figure 5.b.4.
The weight of carcase bone throughout progress to mature liveweight of Merino and Dorset Horn rams.

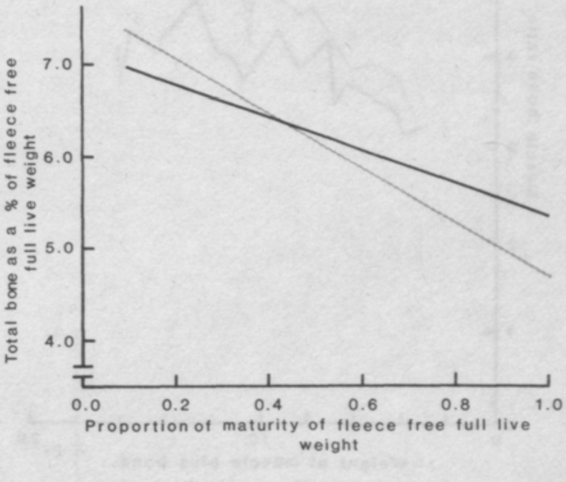


Figure 5.b.5.
The weight of carcase bone as a percentage of liveweight throughout progress to mature liveweight of Merino and Dorset Horn rams.

Table 5.b.7. Muscle:bone ratio of seven breed types (From Kempster and Cuthbertson, 1977)

Breed-type group	Muscle:bone *
Welsh Mountain	3.71^{c}
Blackfaced Mountain	3.52^{b}
British Longwool crosses	3.64^{bc}
Suffolk crosses	3.37^{a}
Intermediate†	3.80^{c}
Southdown crosses	3.68^{c}
British Longwool	3.76^{c}

* Values with same superscript do not differ ($P < 0.05$)
† By Dorset Down or Hampshire Down sires out of intermediate size ewes.

differences among a range of lambs of various British breeds selected for good and poor conformation. Butler-Hogg (1984) presented data on Southdown and Clun sheep which demonstrated a superior muscle:bone ratio in the Southdown. This difference was due entirely to heavier bone in the Cluns as in each breed the proportion of muscle to liveweight was similar. This highlights the advantage of studying the whole animal, as the basis of the difference in the muscle:bone ratio is immediately apparent.

Muscle:bone ratio is a commercially valuable statistic when the basis of comparison is stated, e.g., at equal fat thickness; equal carcase weight etc. As a biologically meaningful statistic it needs to be associated with other information such as the proportion of the total animal constituted by each tissue as was done by Butler-Hogg (1984).

As explained in Chapter 1, muscle:bone ratio may be assessed on several bases, so here we make comparison on the basis of stage of maturity of liveweight and on muscle plus bone weight (Figure 5.b.6.), and also by means of a simple plot of muscle weight against bone weight (Figure 5.b.7.). On each basis Dorset Horns were superior to Merinos and the presentation of such a clear difference would probably be convincing on almost any basis.

There is little doubt that the "meat" characteristics of the Dorset Horn are expressed in the superior muscle:bone ratio to that of the "wool" sheep. Similarly, Fourie *et al.* (1970), who studied Southdown, Romney and Southdown Romney cross sheep in New Zealand, showed that, from slaughter at four different carcase weights, Southdowns had superior muscle: bone ratio to Romneys and that the crossbreds lay in between (Figure 5.b.8.).

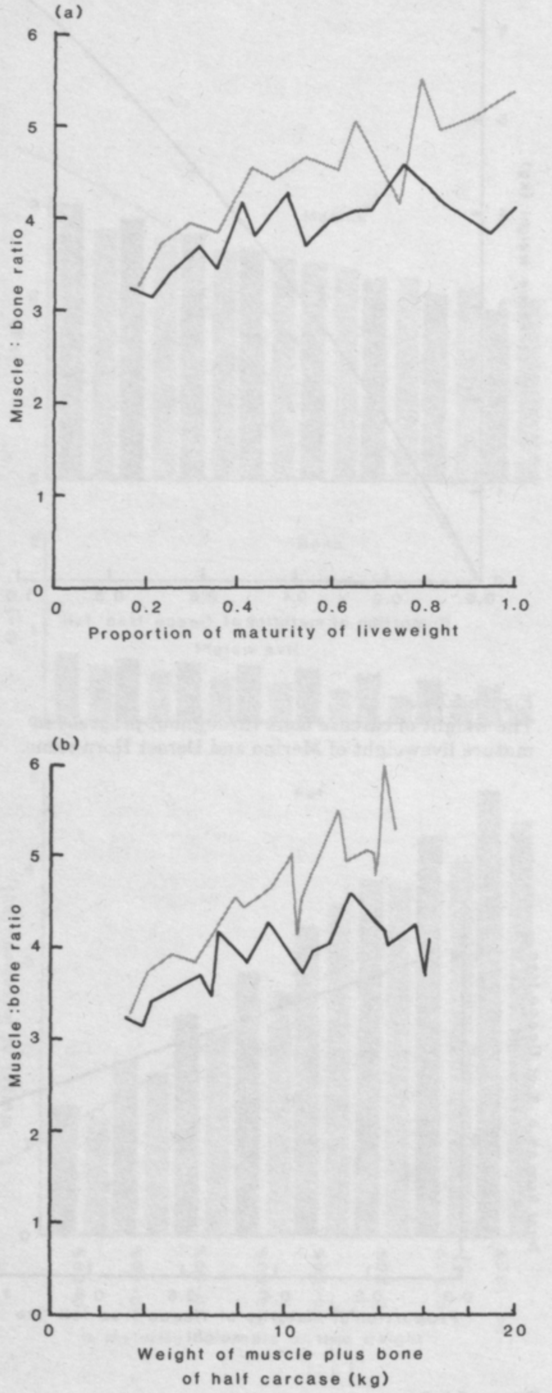


Figure 5.b.6.
Muscle:bone ratio vs (a) proportion of maturity of liveweight, and (b) muscle plus bone weight for Merino and Dorset Horn rams.

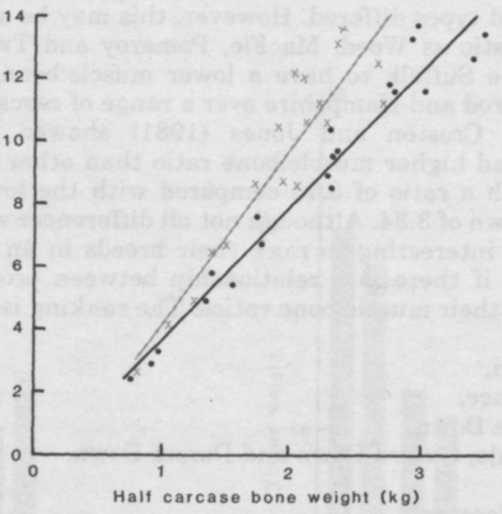


Figure 5.b.7.
Muscle weight against bone weight of Dorset Horn and Merino rams.

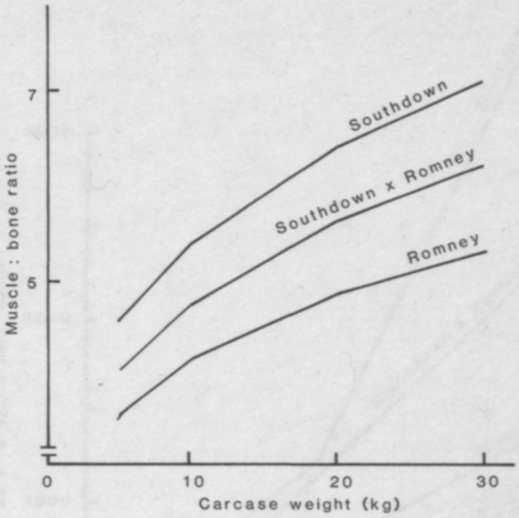


Figure 5.b.8.
Muscle:bone ratio of Southdown, Romney and Southdown cross Romney at four carcase weights. (Data from Fourie *et al.*, 1970.)

MUSCLE:FAT RATIO

The muscle:fat ratio of Dorset Horn and Merino rams is shown in Figure 5.b.9. on the basis of progression of liveweight to maturity. The difference in the ratios at light weights is a reflection of the poor preweaning nutrition of the Dorset Horn rams and is an unsatisfactory aspect of this study. Once the two groups had settled on to *ad lib* feeding there was little apparent difference between the breeds and this continued until maturity when the breeds did not differ with each having a muscle:fat ratio close to 1:1.

In order to remove any influence of the basis of comparison, the weight of fat relative to muscle weight is presented in Figure 5.b.10. and again shows the two breeds to be similar. It is interesting to note that, when plotted in this way, the early difference in the ratios, which was so apparent in Figure 5.b.9., is not so starkly demonstrated. This is, of course, one of the problems with the use of ratios of quantities of different dimensions in that they can exaggerate the importance of a difference among small quantities.

Fourie *et al.* (1970) presented data from Southdowns, Romneys and their crossbreds at four carcase weights and showed that the Romneys had superior muscle to fat ratio at all four weights with little difference between the Southdowns and the crossbreds.

It seems that there may be less correlation between "meat characteristics" and a desirable muscle:fat ratio than there is to a desirable muscle:bone ratio.

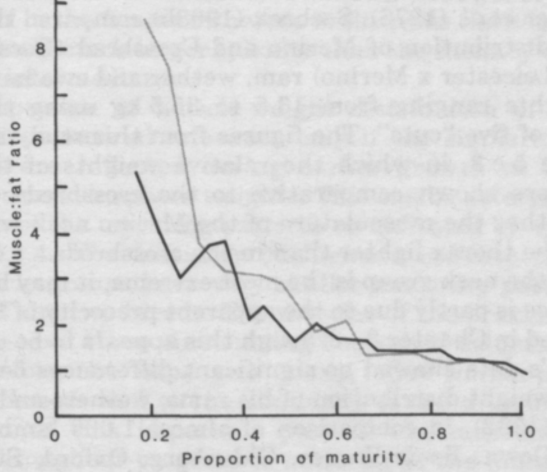


Figure 5.b.9.
Muscle:fat ratio against proportion of maturity of liveweight of Dorset Horn and Merino rams.

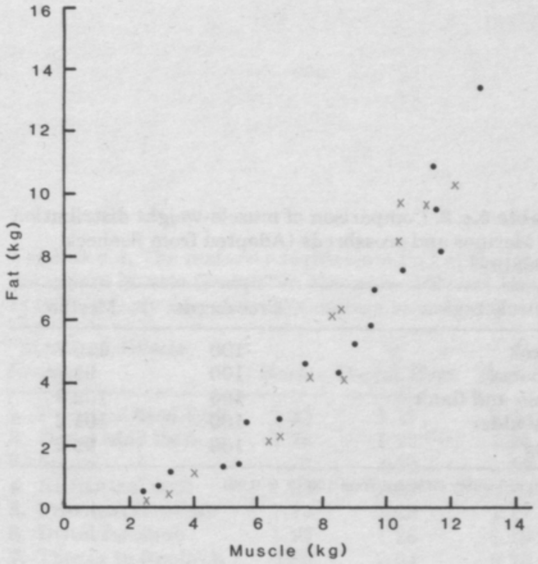


Figure 5.b.10.
Carcase fat weight against muscle weight of Merino and Dorset Horn rams.

c. BREED DIFFERENCES IN GROWTH WITHIN THE MUSCULATURE

In this section we use the same two groups of mature rams as in the foregoing sections to provide the composition of the mature musculature. In Table 5.c.1. are shown the actual weights of the "Standard Muscle Groups" and in Table 5.c.2. the weights of these groups are shown as percentages of total muscle weight. There is a general similarity between the breeds and it is not possible to say that either breed had a superior muscle-weight distribution compared with the other. This is particularly brought home by the comparison of the "Expensive Group" in which there is a 0.5% superiority in favour of the Merinos. It would not be safe to conclude from this that no meat breeds have any superiority in muscle-weight distribution. Thonney *et al.* (1986c), from less complete dissection, concluded that Southdowns were superior in this characteristic to Soay, Welsh Mountain, Finnish Landrace, Jacob, Wiltshire Horn and Oxford Down sheep. However, Jury *et al.* (1977), working with Southdown, Romney and their crossbreds, concluded that ". . . the supposedly superior blocky conformation of Southdown x Romney has conveyed no superiority in terms of distribution of the more valuable muscles relative to the leggier Romney." They also stated that these findings are in agreement with the earlier conclusions of Kirton and Pickering (1967), Jackson and Mansour (1974) and Kempster *et al.* (1976). Seebeck (1968b) compared the muscle-weight distribution of Merino and Crossbred (Dorset Horn x Border Leicester x Merino) ram, wether and ewe lambs at five liveweights ranging from 13.5 to 35.5 kg using the muscle content of five "cuts". The figures from this study are set out in Table 5.c.3. in which the relative weights of the muscle groups are shown comparative to the crossbreds = 100. He showed that the musculature of the Merino neck was heavier and of the thorax lighter than in the crossbreds.

Table 5.c.2. The percentage of total muscle weight of the "Standard Muscle Groups" of mature Merino and Dorset Horn rams

"Standard Muscle Groups"	% of total muscle weight Merino	% of total muscle weight Dorset Horn	Dorset Horn as proportion of Merino
1. Proximal hind limb	25.5	25.7	1.01
2. Distal hind limb	4.5	4.1	0.91
3. Spinal	15.4	15.3	0.99
4. Abdominal wall	10.3	13.8	1.34
5. Proximal forelimb	10.8	10.4	0.96
6. Distal forelimb	2.7	2.3	0.85
7. Thorax to forelimb	8.6	9.9	1.15
8. Neck to forelimb	7.6	7.1	0.93
9. Neck and thorax	12.2	9.7	0.80
Scrap muscle not included in a "Standard Muscle Group"	2.4	1.7	–
Total half-carcase muscle weight	100.0	100.0	–
"Expensive muscles (1+3+5)"	51.7	51.4	0.99

Table 5.c.1. The weight of muscle in the "Standard Muscle Groups" of mature Merino and Dorset Horn rams

"Standard Muscle Group"	Weight (g) Merino	Weight (g) Dorset Horn
1. Proximal hind limb	3301	3169
2. Distal hind limb	578	499
3. Spinal	1999	1881
4. Abdominal wall	1338	1707
5. Proximal forelimb	1403	1279
6. Distal forelimb	352	287
7. Thorax to forelimb	1111	1222
8. Neck to forelimb	983	874
9. Neck and thorax	1587	1199
Scrap muscle not included in a Standard Muscle Group	311	209
Total Half-carcase Muscle Weight	12963	12326

Table 5.c.3. Comparison of muscle-weight distribution of Merinos and crossbreds (Adapted from Seebeck, 1968b)

Muscle region	Crossbreds	Merino
Neck	100	115.7*
Thorax	100	93.8*
Loin and flank	100	102.3
Shoulder	100	101.2
Leg	100	99.2

* Significantly different from 100 ($P < 0.05$)

Since the neck group is the most extreme, it may be that the difference is partly due to the apparent precocity of Merinos as suggested in Chapter 3, although this appears to be unlikely as Seebeck's data showed no significant differences between the muscle-weight distribution of his rams, wethers and ewes.

Wolf (1982), in comparison of almost 1,000 lambs sired by Dorset Down, Ile-de-France, Oldenberg, Oxford, Suffolk and Texel rams, concluded that: ". . . differences between sheep breeds for lean tissue distribution at constant weight of total lean cannot be explained entirely in terms of differences of stage of maturity." and that "It may be possible to attribute commercial importance to small but significant differences in lean tissue distribution. . ."

Kempster and Cuthbertson (1977) showed that various breed types of British lambs differed significantly in the proportion of muscle weight distributed in the "higher-priced joints" but dismissed the small differences as being economically insignificant in that they affected the retail value of the carcase by only 1.0%. And so, it is not surprising that there is little difference in muscle-weight distribution between the leggy, poor conformation (for meat) Merinos, and the Dorset Horn.

At this stage of knowledge it seems that we can conclude that there is little evidence of the superiority of any one breed over any other in the characteristic of muscle-weight distribution. There are, however, some interesting but economically unimportant differences in the data in Table 5.c.2. The muscles of the abdominal wall are proportionally much heavier in the Dorset Horn rams at maturity than in the Merinos and it is interesting to reflect on why this may be. Berg and Butterfield (1976) showed in calves that the relative growth rate of the muscles of the abdominal wall could be modified by the type of feed. However, these rams in our current comparison were fed an identical pelleted ration. Additional work could be placed on the abdominal wall by any of several factors which might lead to increased abdominal load, such as increased gut fill, resulting from larger appetite or slower passage of ingesta; larger internal organs or larger internal fat stores. Each of these can be investigated from the available data and, as seen in Chapter 5.f., larger gut fill may be related to the heavier abdominal wall in the Dorset Horns.

The other marked difference between the two groups of rams is in the relative size of the intrinsic muscles of the thorax and neck. The Dorset Horns are noticeably lighter in the "Group 9" muscles which include all intrinsic muscles of the thorax and neck some of which are subject to considerable masculinization. It seems that there may be considerable variation between these two breeds as to the influence of androgens on this group, with the Merinos being more responsive than the Dorset Horns. It seems probable, therefore, that some breeds respond to male sex hormone in a more exaggerated manner than others. Therefore, comparisons of entire males, and particularly mature or nearly mature entire males, may show much more diverse muscle-weight distribution than comparisons of females or castrated males. This can be illustrated by drawing on data of Fourie (1965) which is shown in Figure 5.c.1. Here the weight of the most androgen-responsive muscle of the neck, the splenius, is shown as a percentage of its own weight at birth against age for two breeds and crosses. The three genotypes are very similar in the females whereas in the rams the Southdown has a relatively much larger splenius than the Romney with the crossbreds intermediate.

The comparison of muscle-weight distribution of mature rams is of commercial relevance only if the similarities and differences are reflected during earlier growth as animals proceed to usual slaughter weights. This can be determined by comparison of the maturing patterns as indicated by 'q' values in Table 5.c.4. The maturity coefficients indicate that the major muscle groups have very similar maturing patterns in the rams of the two breeds. The muscles of the proximal ends of the limbs and those surrounding the spinal column, which collectively form the "expensive" group, follow similar patterns in the two breeds and so the similarity of the muscle-weight distribution of this important part of the musculature is reflected throughout progress to maturity of the musculature of the two breeds. However, there are some large differences in the patterns of some of the economically less expensive muscle groups which could be reflected in quite large differences in the differential yield of muscle. "Group 4", the muscles of the

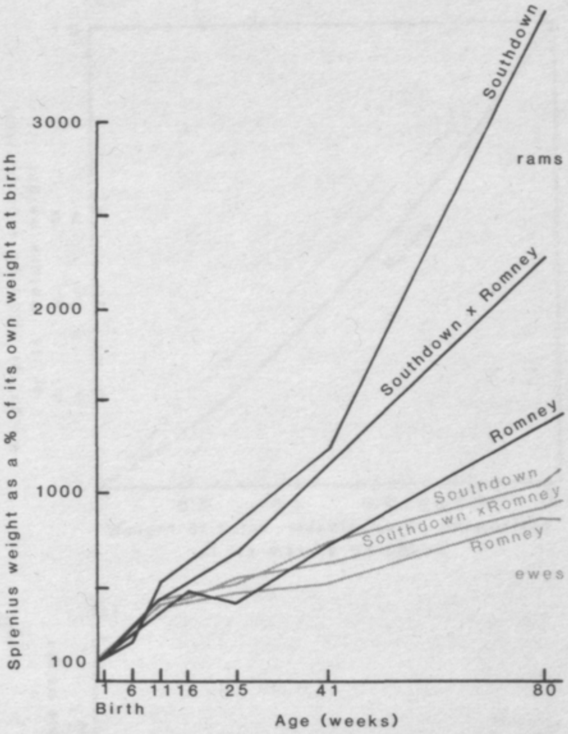


Figure 5.c.1.
Splenius weight as percentage of its own weight at birth versus age. (Data from Fourie, 1965.)

Table 5.c.4. The maturity coefficients ('q') of the "Standard Muscle Groups" in Merino and Dorset Horn rams from approximately 20% mature to maturity

"Standard Muscle Groups"	'q' Merino	'q' Dorset Horn	'q' Pooled
1. Proximal hind limb	1.23	1.17	1.20
2. Distal hind limb	1.26	1.22	1.24
3. Spinal	1.25	1.13	1.19
4. Abdominal wall	1.02	0.53	–
5. Proximal forelimb	1.12	1.23	1.17
6. Distal forelimb	1.13	1.26	1.19
7. Thorax to forelimb	0.86	0.64	0.75
8. Neck to forelimb	0.49	0.85	0.67
9. Neck and thorax	0.53	0.97	–
Expensive (1+3+5)	1.21	1.17	1.19

abdominal wall, have a higher impetus in the Dorset Horn than in the Merinos in pursuit of their final higher proportion of the mature musculature shown previously.

The patterns of the three forequarter groups associated with the axial skeleton of the neck and thorax have maturing patterns which reflect their different proportions in the musculature of the mature rams. Of particular interest is Group 9, the intrinsic muscles of the thorax and neck, in which the pattern of growth to maturity is very different in the two breeds. This is of considerable interest as it is probably due to a different level of hormonal modification of the effects of the genetic factors governing the growth of this group than to differences in the genetic factors themselves.

The breed differences shown in the maturing patterns of the muscles of the abdominal wall and of the intrinsic muscles of the neck and thorax are probably the largest and most striking differences for the same anatomical structures which are shown in any of the studies discussed in this book. Few breed differences are likely to be revealed of such large dimensions in the growth and development of the same structures within animals of any single species.

Using the data and maturity coefficients it is possible to make comparisons of the muscle-weight distribution of the two breeds at any chosen total muscle weight or degree of maturity of the musculature and it is, of course, possible to use the data in section 5.b. to select any desired liveweight or carcase weight should it be required to compare muscle-weight distribution on these criteria.

In Table 5.c.5. a comparison is made of the muscle-weight distribution of the two breeds of rams at the mean total side muscle weight of all the sheep from which data were available and the mean proportion of mature muscle weight. There is little difference in the results from the use of the two bases, i.e., about 9 kg total side muscle weight and 70% of mature muscle weight. The differences between the breeds are marginally less at equal maturity in all cases except Group 9 (neck and thorax). That the similarity in the two comparisons is largely the result of the choice of the two bases is seen by comparison at 100% mature in Table 5.c.2., where Groups 4 and 9 were very different in the two breeds. The difference in the proportion of the muscle weight in the abdominal wall, which was so apparent at maturity, had decreased by about one half when considered at 70% of maturity. Also, the large difference in the proportion of muscle in the neck and thorax had declined by about one third at the lower level of maturity. In this latter case, the closer proximity of the two breeds was achieved by the marked decline in the muscle group in the Merinos in line with their maturity coefficient of 0.53; whereas the proportion in the Dorset Horns remained almost stable in line with its 'q' of 0.97. This can be understood by reference to Figure 5.c.2. in

Table 5.c.5. Predicted means for weights of muscle groups as percentages of total muscle weight for Merino and Dorset Horn rams after adjustment to (i) the mean total muscle weight (8.8 kg), and (ii) the mean proportion of mature muscle weight (0.696)

	At the same total muscle weight			At the same proportion of maturity		
	Merino	Dorset Horn	Dorset Horn as % of Merino	Merino	Dorset Horn	Dorset Horn as proportion of Merino
1. Proximal hind limb	27.35	26.96	98.6	27.24	27.04	0.99
2. Distal hind limb	4.83	4.30	89.0	4.81	4.32	0.90
3. Spinal	16.86	15.83	93.9	16.79	15.86	0.95
4. Abdominal wall	10.39	11.98	115.3	10.38	11.87	1.14
5. Proximal forelimb	11.24	11.06	98.4	11.22	11.10	0.99
6. Distal forelimb	2.83	2.50	88.3	2.82	2.51	0.89
7. Thorax to forelimb	8.18	8.89	108.7	8.21	8.83	1.08
8. Neck to forelimb	6.34	6.79	107.1	6.41	6.77	1.06
9. Neck and thorax	10.22	9.64	94.3	10.32	9.64	0.93
Expensive muscles Groups 1 + 3 + 5	55.45	53.85	97.1	55.25	54.00	0.98

which the maturing patterns and resultant compositional changes are shown for Group 9 muscles. Comparison at about 45% of mature weight of total muscle would result in both breeds showing the same values for Group 9 as a percentage of total muscle weight.

It is indeed fortunate for the concept of comparison at equal maturity, that few structures are found to have different maturing patterns between breeds, as, if this were so, comparison at any chosen degree of maturity would give little idea of the composition at any other stage of maturity.

It is also fortunate that the two groups of muscles in this comparison, which have widely differing maturing patterns, are to a large degree complementary in their proportionate fluctuation and are both relatively "cheap" in terms of the commercial value of the carcase. Therefore, despite the differences in the fluctuations of the proportions of these two groups of muscles, the "expensive" portions of the carcase musculature retain similar maturing patterns and similar proportions of total muscle weight in the two breeds at the same degree of maturity.

In Table 5.c.6. the progress to maturity of the "Standard Muscle Groups" in Dorset Horn and Merino rams is shown and 4 is based on the 'q' values in Table 5.c.3. Calculation of the approximate weight of any muscle group at any stage of maturity is possible, e.g., when the total musculature of the half-carcase is 50% mature it will weigh 6.2 kg in Dorset Horns and 6.5 kg in Merinos, and Group 3 will weigh 1.0 kg in Dorset Horns and 1.1 kg in Merinos. The marked effect of the different 'q' values for each breed in Groups 4 and 9 are clearly seen.

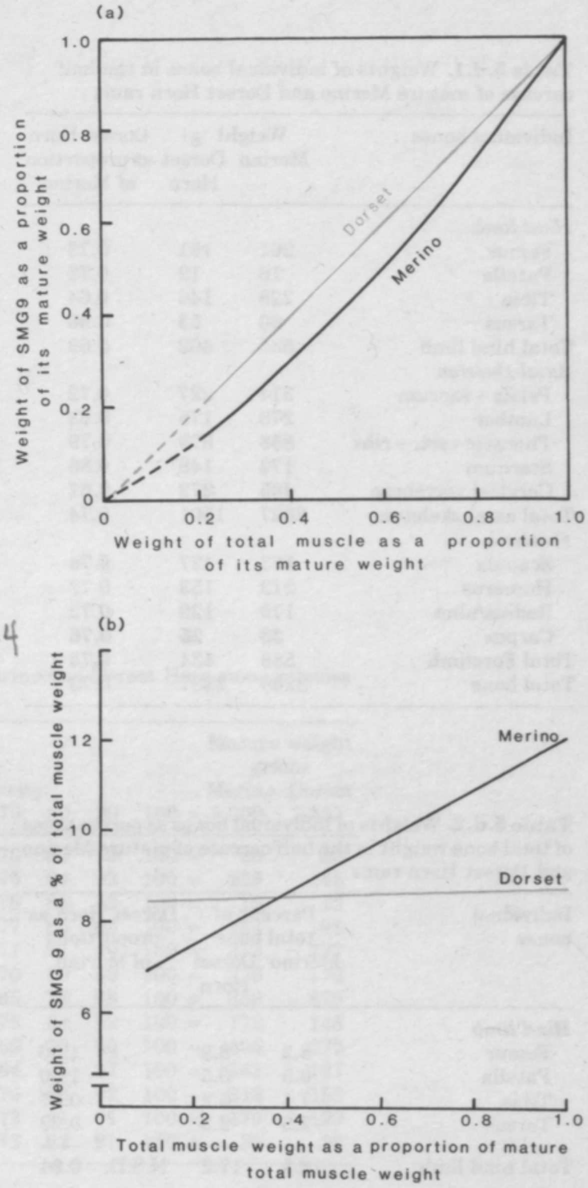


Figure 5.c.2.
Comparison of (a) the maturing patterns and (b) the proportional changes, of the weight of the intrinsic muscles of the thorax and neck relative to total muscle weight in Merino and Dorset Horn rams.

Table 5.c.6. The progress to maturity of "Standard Muscle Groups" of Dorset Horn rams and Merino rams relative to progress to maturity of total muscle weight

	Percentage maturity									Mature Weight Grams	
										Dorset Horn	Merino
Total muscle weight	20	30	40	50	60	70	80	90	100 =	12,326	12,963
1. Proximal hind limb	23	34	45	55	65	74	83	92	100 =	3,169	3,301
2. Distal hind limb	24	35	46	56	66	75	84	92	100 =	499	578
3. Spinal	23	34	45	55	65	74	83	92	100 =	1,881	2,023
4. Abdominal wall											
Merino	20	30	40	51	60	70	80	90	100 =	–	1,338
Dorset Horn	12	20	29	38	49	60	72	86	100 =	1,707	-
5. Proximal forelimb	23	34	44	54	64	74	83	92	100 =	1,279	1,403
6. Distal forelimb	23	34	45	55	65	74	83	92	100 =	287	352
7. Thorax to forelimb	16	25	34	44	54	65	76	88	100 =	1,222	1,111
8. Neck to forelimb	15	23	32	42	52	63	75	87	100 =	874	983
9. Neck and thorax											
Merino	12	20	29	38	49	60	72	86	100 =	–	1,561
Dorset Horn	20	29	39	49	59	69	80	90	100 =	1,199	–

d. BREED DIFFERENCES IN GROWTH WITHIN THE SKELETON

There is little reason to believe that there should be any major breed differences in the relative growth of the weight of bones except in so far as the differences in mature size of the animals may have an effect. This may be inferred from the comparison of two strains of different size (Chapter 2), where larger animals tended to have larger bones in the limbs as had been suggested in cattle by Callow (1962).

A comparison of the weights of the bones of mature Merino rams and smaller mature Dorset Horns is set out in Table 5.d.1. The weights are converted to percentages of total bone weight in Table 5.d.2. and demonstrate the anatomical harmony between the relative weights of the bones. The differences between the two breeds in the proportions within the skeleton are less than in the comparison of the large and small Merinos (Chapter 2). The four major weight-bearing bones (femur, tibia, humerus, and radius plus ulna) were all relatively heavier in larger Merino rams compared with a smaller strain of Merino, whereas in this breed comparison this applied to only two of the bones, the tibia and radius plus ulna, with the femur being the same and the humerus a smaller proportion in the heavier breed. All the differences were small and it is unlikely that the difference in the size of the two breeds made any contribution to a difference in bone-weight distribution. This is particularly evident when the weights of the total bone in each section of the appendicular skeleton and that of the axial skeleton are compared as shown in Table 5.d.2.

The general similarity of growth in the skeleton of the two breeds is further demonstrated by the maturity coefficients in Table 5.d.3. There are no significant differences in the 'q' values for the bones of the two breeds and this is an example of the similarity of the growth process across the breeds of a species. However, as many of the maturing patterns of the bones are different from that of the total skeleton, any comparisons of bone-weight distribution of breeds will require an understanding of these patterns. As shown in Table 5.d.4. Merinos and Dorset Horn rams are more alike in bone-weight distribution at the same degree of maturity of the skeleton than they are at equal skeleton weight.

As the maturity coefficients do not differ between Dorset Horn and Merino rams, pooled coefficients can be used to produce a table of progress to maturity (Table 5.d.5.) for these two breeds. It remains to be seen if this table will be appropriate for other breeds.

Table 5.d.1. Weights of individual bones in the half carcase of mature Merino and Dorset Horn rams

Individual bones	Weight (g) Merino	Weight (g) Dorset Horn	Dorset Horn as proportion of Merino
Hind limb			
Femur	261	191	0.73
Patella	16	12	0.75
Tibia	228	146	0.64
Tarsus	**80**	**53**	**0.66**
Total hind limb	585	402	0.69
Axial skeleton			
Pelvis + sacrum	314	227	0.72
Lumbar	278	175	0.63
Thoracic vert. + ribs	858	679	0.79
Sternum	172	148	0.86
Cervical vertebrae	**405**	**272**	**0.67**
Total axial skeleton	2027	1501	0.74
Forelimb			
Scapula	163	127	0.78
Humerus	213	153	0.72
Radius/ulna	179	129	0.72
Carpus	**33**	**25**	**0.76**
Total Forelimb	588	434	0.74
Total bone	3200	2337	0.73

Table 5.d.2. Weights of individual bones as percentages of total bone weight in the half carcase of mature Merino and Dorset Horn rams

Individual bones	Percent of total bone Merino	Percent of total bone Dorset Horn		Dorset Horn as proportions of Merino
Hind limb				
Femur	8.2	8.2		1.00
Patella	0.5	0.5		1.00
Tibia	7.1	6.2		0.87
Tarsus	2.5	2.3		0.92
Total hind limb	18.3	17.2	N.S.D.	0.94
Axial skeleton				
Pelvis	9.8	9.7		0.99
Lumbar	8.7	7.5		0.86
Thoracic vert. + ribs	26.8	29.1		1.09
Sternum	5.4	6.3		1.17
Cervical vert.	12.6	11.6		0.92
Total axial skeleton	63.3	64.2	N.S.D.	1.01
Forelimb				
Scapula	5.1	5.4		1.06
Humerus	6.7	6.6		0.99
Radius/ulna	5.6	5.5		0.98
Carpus	1.0	1.1		1.10
Total forelimb	18.4	18.6	N.S.D.	1.01
Total bone	100	100		-

Table 5.d.3. Maturity coefficients of bones in Merino and Dorset Horn rams. (Data from Butterfield *et al.*, 1983d, and Butterfield unpublished)

Bone	Maturity coefficient 'q' Merino	Dorset Horn	Pooled
Hind limb			
Femur	1.30	1.32	1.31
Patella	1.46	1.28	1.38
Tibia	1.24	1.23	1.24
Tarsus	1.25	1.53	1.38
Total hind limb	1.27	1.31	1.29
Axial skeleton			
Pelvis and sacrum	1.04	1.05	1.04
Lumbar	0.85	1.15	0.98
Thoracic vert. + ribs	0.85	0.69	0.77
Sternum	1.25	1.19	1.23
Cervical vertebra	0.87	1.04	0.95
Total axial skeleton	0.92	0.91	0.91
Forelimb			
Scapula	0.75	0.65	0.70
Humerus	1.15	1.24	1.19
Radius/ulna	1.10	1.06	1.08
Carpus	1.03	1.32	1.13
Total forelimb	1.02	1.02	1.02

Table 5.d.4. The weights of individual bones as percentages of total bone weight for Merino and Dorset Horn rams after adjustment to (i) the same total bone weight (2.0 kg), and (ii) the same proportion of mature total bone weight (0.74)

Bones	At same total bone weight			At same proportion of maturity of total bone		
	Merino	Dorset	Diff.	Merino	Dorset	Diff.
Pelvis and sacrum	10.1	10.1	–	10.1	10.1	–
Femur	10.1	10.7	0.6	10.4	10.5	0.1
Patella	0.7	0.7	–	0.7	0.7	–
Tibia	8.4	7.7	0.7	8.6	7.6	1.0
Tarsus	3.0	3.1	0.1	3.1	3.0	0.1
Scapula	4.1	3.9	0.2	4.0	4.0	–
Humerus	7.4	7.8	0.4	7.5	7.7	0.2
Radius and ulna	6.0	6.0	–	6.1	6.0	0.1
Carpus	1.0	1.2	0.2	1.0	1.2	0.2
Cervical vertebra	11.4	11.1	0.3	11.2	11.1	0.1
Thoracic vertebra and ribs	23.7	22.5	1.2	23.2	23.1	0.1
Lumbar vertebrae	7.7	7.4	0.3	7.5	7.3	0.2
Sternum	6.4	7.8	1.4	6.6	7.7	1.1
TOTAL DIFF.	–	–	5.4	–	–	3.2

Table 5.d.5. The progress to maturity of bones of Merino and Dorset Horn rams relative to the progress to maturity of total bone weight

	Percentage maturity									Mature weight grams	
										Merino	Dorset
Total bone weight	20	30	40	50	60	70	80	90	100 =	3,200	2,337
Tarsus	26	38	49	60	69	78	86	93	100 =	80	53
Tibia	24	35	46	56	66	75	84	92	100 =	228	146
Patella	26	38	49	60	69	78	86	93	100 =	16	12
Femur	25	37	47	58	67	77	85	93	100 =	261	191
Pelvis and sacrum	21	31	41	51	61	71	81	90	100 =	314	227
Lumbar vertebra	20	30	40	50	60	70	80	90	100 =	278	175
Thoracic vertebra & ribs	16	25	34	44	54	65	76	88	100 =	858	679
Sternum	24	35	46	56	66	75	84	92	100 =	172	148
Cervical vertebra	19	29	39	49	59	69	79	90	100 =	405	272
Scapula	15	24	33	43	53	64	75	87	100 =	163	127
Humerus	23	34	45	55	65	74	83	92	100 =	213	153
Radius and ulna	21	32	42	52	62	72	81	91	100 =	179	129
Carpus	22	33	43	53	63	73	82	91	100 =	33	25

e. BREED DIFFERENCES IN THE GROWTH OF THE FAT PARTITIONS

Kempster (1980) reviewed knowledge then current on fat partitioning in sheep and pointed out that it had been recorded by Hammond (1932) that sheep differed considerably in the manner in which they partitioned their body fat. The first suggestion that this difference of partitioning may be related to the environmental origin of breeds appears to have come from Palsson's (1940) report that mountain breeds partition more of their fat internally than other sheep.

Kempster further discussed the work of Donald *et al.* (1970) who reported that lambs by Soay sires had a higher proportion of kidney fat than Southdown-and Oxford Down-sired lambs, whereas McClelland and Russel (1972) found that Finnish Landrace deposited a higher proportion of fat in the body cavity than did Scottish Blackface. Wood *et al.* (1979) later reported that meat-type sire breeds in the form of Suffolk and Hampshire had less internal body fat than the ewe-type breeds, Clun and Colbred.

All of the foregoing tends to support the statement by Wood (1982) that "The partitioning of total fat between carcass . . . and abdominal . . . sites is not influenced by mature size but rather by breed itself . . ." and further "There is no difference in fat partitioning of mature animals of different breeds which can be related to their mature size. However, if the mature sizes of breeds are different, this will have an effect on the fat partitioning of animals killed at the same body weight or same weight of fat because fat depots grow at characteristic rates. Thus, intermuscular fat would form a higher proportion of total fat in a late maturing breed (large body size) and subcutaneous fat would form a higher proportion in an early maturing breed".

"If different breeds are compared at the same stage of maturity of body fat, and differences in fat partitioning are found, then a true breed effect exists. However, subcutaneous fat alone cannot be used to describe stage of maturity of fat since it may itself be contributing to the difference in fat partitioning." (Wood, Pers. Com. 1985)

Kempster, in attempting to summarize the position regarding relative partitioning within the carcase, stated that "the British sire breeds in general, showed a similar fat partition to the Suffolk" which he used as a benchmark. He then gave the exceptions as:

1. The Wensleydale had particularly high subcutaneous to intermuscular fat ratio.
2. The Oldenburg, Oxford Down and, in particular, the Texel, also had a high subcutaneous to intermuscular fat ratio.

The demonstration by Wood, MacFie, Pomeroy and Twinn (1980) that "ewe" breeds (noted for milking ability) partitioned their fat in a different manner to "ram" breeds (noted as sires for meat production), was one of considerable importance. As the consumers swing rapidly away from fat, the problem arises of finding sheep with adequate fat stores to enable them to survive in stressful environments, whilst at the same time producing offspring whose carcases contain only small amounts of carcase fat at market weights.

Undoubtedly the knowledge that sheep vary in the proportion of their total fat stores which comprise part of the commercial carcase, allows for examination of the potential to select animals which will have adequate total body fat which is largely removed at slaughter. McClelland and Russel (1972) showed that Finnish Landrace tended towards more intra-abdominal fat than Scottish Blackface and Butler-Hogg (1984) showed that Cluns deposited proportionately more fat intra-abdominally than did Southdowns. These studies open up an exciting opportunity for the meat animal production industry to comply with the demands for leaner meat whilst still retaining the productive insulation of adequate total body fat stores. Gaili (1978) showed that there are some quite significant differences in the distribution of intermuscular fat in three breeds, the Hampshire, Dorset Horn and Clun; the most striking being the considerably less intermuscular fat in the neck and thorax of the Hampshire compared with the other two breeds. Geenty, Clarke and Jury (1979) showed that lambs with Dorset or Corriedale genes partitioned more fat to internal depots than did Romneys.

There is some difference of opinion, which may be based partly on breed differences, regarding the degree of difference of relative growth rates of fat partitions in sheep. Butler-Hogg (1984) was not impressed with the finding of Butterfield and Thompson (1983) that there was no significant difference of any importance from total body fat in the maturing patterns of fat partitions of Merino rams where total carcase fat was regarded as a single partition. If Butterfield and Thompson's results are applicable to sheep other than their Merinos, it would mean that the stage of maturity of sheep at slaughter would have no important effect on the partitioning of fat between carcase and non-carcase, whereas the differences shown by Butler-Hogg suggest that comparisons of fat partitioning could give different answers at different stages of maturity. Butler-Hogg and Johnsson (1986) also showed in Hampshire Down x Mule ewe lambs that carcase fat (intermuscular plus subcutaneous) increased as a proportion of total body fat from 693 g/kg at four weeks to 739 g/kg at 36 weeks of age.

Such disagreement may mean that the differences are of debatable economic significance relative to other factors or that there are real breed differences between Merinos and other breeds. As the sheep in the Butterfield and Thompson study were reared up to weaning in conditions of less than the optimum nutrition, which would be essential in prime lamb production, it seems wise at this stage to treat their results on fat partitioning with some caution, and the results of Butler-Hogg and Johnsson seem likely to be more truly indicative of the likely situation in commercial lamb production irrespective of breed.

In Table 5.e.1. and 2 are shown the weights and proportions of carcase and non-carcase fat of Merino and Dorset Horn rams fed on the same diet to maturity. There is obviously only a small difference in the partitioning of fat at maturity and should more work, based on many more rams, show these figures to be indicative of the true breed picture, then there is little to choose between these two breeds, with the Merino having a slightly greater proportion of its total fat in the non-carcase partition. The maturity coefficients shown in Table 5.e.3. indicate no significant difference between partitions or between breeds and suggest that stage of maturity has little bearing on comparisons in these two breeds. However, it is well to remember that the numbers are small and the individual variation high so that it would be rash to form firm opinions about breed differences until much more data are available.

Seebeck (1968b) studied the distribution of fat within the subcutaneous and intermuscular partitions of Merinos and Dorset Horn-sired crossbreds (Dorset Horn x Border Leicester x Merino) and showed breed differences in both partitions, in that Merinos had less subcutaneous fat in the thorax and more in the loin plus flank; whereas they had more intermuscular fat in the neck and loin plus flank and less in the thorax than the crossbreds. It is difficult to relate these findings to variation in commercial value due to the combination of the expensive loin and inexpensive flank in a single "cut".

The maturing patterns of fat partitions of Merino and Dorset Horn rams are similar and hence compositional differences are similar on each of the two bases of comparison in Table 5.e.4. However, had the separate patterns of subcutaneous and intermuscular fat been available for this comparison it is probable that it would be necessary for comparisons to be made at equal maturity to be genetically useful.

Table 5.e.4. Predicted means of fat depots as percentage of total fat at (i) equal total fat (20.3 kg) and (ii) equal maturity of total fat (0.52)

Fat depot	At same total fat weight			At same proportion of maturity of total fat		
	Merino	Dorset Horn	Diff.	Merino	Dorset Horn	Diff.
Carcase	64.3	68.3	4.0	64.3	68.3	4.0
Kidney plus channel	9.4	8.8	0.6	9.4	8.7	0.7
Omental	17.2	13.7	3.5	17.2	13.7	3.5
Mesenteric	7.6	6.1	1.5	7.6	6.1	1.5
Scrotal	1.5	2.2	0.7	1.5	2.2	0.7

Table 5.e.1. Weight of partitions of fat in mature Merino and Dorset Horn rams (Data from Butterfield *et al.*, 1983d and Butterfield *et al.* 1985c)

Fat Partition	Weight (kg)	
	Merino	Dorset Horn
Carcase	27.37	24.68
Kidney plus channel	4.20	3.30
Omental	7.20	4.87
Mesenteric	3.20	2.16
Scrotal	0.80	0.99
Total body	42.77	36.29

Table 5.e.2. Fat partitions as percentages of total body fat weight in mature Merino and Dorset Horn rams

Fat Partition	Percent of total fat	
	Merino	Dorset Horn
Carcase	64	68
Kidney plus channel	10	9
Omental	17	13
Mesenteric	7	6
Scrotal	2	3
Total body	100	100

Table 5.e.3. Maturity coefficients of fat partitions of Merino and Dorset rams relative to progress to maturity of total body fat

Fat partition	'q'		
	Merino Rams	Dorset Horn Rams	Pooled
Carcase	1.01	1.00	1.01
Kidney plus channel	0.80	1.05	0.92
Omental	1.10	0.97	1.04
Mesenteric	1.06	1.01	1.04
Scrotal	0.50	0.68	0.58

Set out in Table 5.e.5. is the progress to maturity of the fat partitions and as the 'q' values are not different for the breeds, similar values apply to both breeds. How widely across other breeds this table could be used will have to await further work.

Table 5.e.5. Progress to maturity of fat partitions relative to total body fat in Dorset Horn and Merino rams

	Percentage of mature weight										Merino	Dorset Horn
											Mature weights (kg)	
Total body fat	20	30	40	50	60	70	80	90	100	=	42.77	36.29
Total carcase fat	20	30	40	50	60	70	80	90	100	=	27.37	24.68
Non-carcase Depots												
Kidney & channel fat	19	28	38	48	58	68	79	89	100	=	4.20	3.30
Omental fat	21	31	41	51	61	71	81	90	100	=	7.20	4.87
Mesenteric	21	31	41	51	61	71	81	90	100	=	3.20	2.16
Scrotal	13	21	30	40	50	61	73	86	100	=	0.80	0.99
Total non-carcase fat										=	15.40	11.61

f. BREED DIFFERENCES IN THE GROWTH OF BODY ORGANS

Truscott (1980) showed that Friesian steers had "higher proportions of abdominal organs" than Hereford steers killed at equal liveweight. As Truscott stated, "Thus it is not surprising, considering the breed differences in mature size, that these early developing components should be heavier in the larger, faster growing Friesians at equal body weights." It may well be therefore that, in this respect, there is no genetic difference between dairy-type and beef-type cattle.

In this section we compare the relative growth of body organs of Dorset Horn rams and Merino rams which are representative of meat-type and wool-type sheep respectively. In Table 5.f.1. are set out the weights and percentages of total body weight at maturity of the body organs. The contents of the digestive tract are relatively heavier in the Dorset Horns whereas the tract itself is not different.

The heavier content of the digestive tract seems to align with the relatively heavier abdominal wall muscles in the Dorset Horn rams discussed in Chapter 5.c. Neither the weights of the liver nor of the tract itself suggest any great difference in the activity of the digestive system of the two breeds. It may well be that the major difference is slower passage of digestive tract contents in the Dorset Horns.

The head is relatively heavier in the Dorset Horns and this may be due to heavier horns, although no data are available on this. Also, the hide is heavier in the Merino rams, apparently in response to the much more active wool-growing function in the Merino.

Apart from the few examples mentioned above, it seems that the proportion of the total body weight, represented by each of the body organs, is very similar in both breeds of sheep and there is no suggestion that the specialized use of each breed is reflected in any great change in body organs except skin.

In Table 5.f.2. are shown the maturity coefficients of the body organs of the two breeds. There is little difference in the maturing pattern of the alimentary tract in total, however, the small intestine has a much higher 'q' in the Dorset Horn than in the Merinos. The alimentary tract contents in the breeds follow the general pattern of the tract as a whole and reflects again the high 'q' value for the small intestine. The 'q' values for the abomasum contents are meaningless due to the extreme scatter of the values.

Table 5.f.1. Weights of individual organs and organ contents and their percentage of shorn full liveweight (SFLW) of mature Merino and Dorset Horn rams

	Weight (kg)		Percent of SFLW	
	Merino	Dorset Horn	Merino	Dorset Horn
Alimentary tract				
Oesophagus	0.10	0.09	0.08	0.09
Ruminoreticulum	1.13	1.19	0.94	1.19
Omasum	0.13	0.11	0.11	0.11
Abomasum	0.27	0.30	0.23	0.30
Small intestine	0.66	0.36	0.55	0.36
Large intestine	0.58	0.44	0.49	0.44
Total	2.87	2.49	2.40	2.50
Alimentary tract contents				
Ruminoreticulum contents	5.02	6.13	4.19	6.15
Omasum contents	0.15	0.10	0.13	0.10
Abomasum contents	0.34	1.38	0.28	1.38
Small intestine contents	0.77	0.51	0.64	0.51
Large intestine contents	1.06	0.87	0.89	0.87
Total	7.34	8.99	6.13	9.02
Other major internal organs				
Liver	1.26	0.94	1.05	0.94
Kidneys	0.21	0.18	0.17	0.18
Spleen	0.14	0.09	0.12	0.09
Heart	0.35	0.30	0.29	0.30
Trachea	0.08	0.06	0.07	0.06
Lungs	0.53	0.41	0.44	0.41
Thyroid	0.02	0.01	0.02	0.01
Pancreas	0.07	0.08	0.06	0.08
Total	2.66	2.07	2.22	2.08
Central nervous system				
Brain	0.11	0.09	0.09	0.09
Eyes	0.03	0.03	0.03	0.03
Total	0.14	0.12	0.12	0.12
Miscellaneous components				
Blood	4.50	3.09	3.76	3.10
Head	6.84	6.23	5.72	6.25
Penis + bladder	0.11	0.09	0.09	0.09
Hide	9.86	6.06	8.24	6.08
Distal limbs	1.65	1.25	1.38	1.25
Total	22.96	16.72	19.19	16.77
Shorn empty liveweight	112.32	90.74	93.87	90.99
Shorn full liveweight	119.66	99.72	100.00	100.00

* rounding of numbers may lead to differences between sum of components and total

Of the major solid organs the liver, as expected, follows the trend of the small intestine in having a higher value in the Dorset Horn. The only other organ with a significantly different maturity coefficient is the kidney. No ready explanation of this is forthcoming. Table 5.f.3. shows the maturing patterns of small intestine, small intestine content, liver and kidney in all of which Dorset Horns have significantly larger 'q' values. All of these four maturing patterns suggest that the organs decline in actual, as well as relative, size as the Dorset Horns approach maturity. There is little if any such decline in the liver and kidney of the Merinos. Such results make us wonder regarding the adequacy of the fit of our statistically calculated pattern to the data and so in Figure 5.f.1. are shown the simple plots of the data for the kidney and liver. Although the 'q' value tends to underestimate for both the organs in the early growth of the Merinos, the difference between the two breeds, suggested by the 'q' values, is clearly apparent.

Table 5.f.4. shows a comparison of the percentages of liveweight comprised by the body organs at the mean liveweight of the available animals and also at the mean proportion of mature liveweight. The results are predictable from the knowledge of the mature values and the maturing patterns. For instance, the total weight of the gastrointestinal tract appears

Table 5.f.2 Maturity coefficients of body organs and organ contents of Merino and Dorset Horn rams, relative to the progress to maturity of shorn full liveweight from 20% mature to maturity (Data from Butterfield *et al.*, 1983c and Butterfield *et al.*, 1984a)

		Maturity coefficients 'q'		
		Merino	Dorset Horn	Pooled
Alimentary tract				
Oesophagus		1.82	1.63	1.74
Ruminoreticulum		2.48	2.12	2.32
Omasum		2.76	3.22	2.97
Abomasum		2.20	2.27	2.23
Small intestine		5.13	9.48	–
Large intestine		3.60	3.44	3.54
Total		3.28	3.47	3.37
Alimentary tract contents				
Ruminoreticulum contents		2.33	1.46	1.93
Omasum contents		3.09	3.22	3.15
Abomasum contents		1.77	0.14	1.03
Small intestine contents		4.19	6.83	–
Large intestine contents		3.05	3.34	3.18
Total		2.62	1.77	2.23
Other major internal organs				
Liver		2.40	4.43	–
Kidneys		2.05	3.11	–
Spleen		1.33	1.81	1.55
Heart		1.90	2.02	1.95
Trachea		2.39	2.32	2.36
Lungs		2.45	3.14	2.76
Thyroid		3.55	3.31	3.45
Pancreas		1.96	2.04	2.00
Total		2.26	3.44	2.80
Central nervous system				
Brain	'b'† =	0.25	0.26	
Eyes	'b' =	0.40	0.42	
Total	'b' =	0.29	0.30	
Miscellaneous components				
Blood		1.51	1.76	1.62
Head		1.40	1.08	1.25
Penis + bladder		1.05	1.68	1.34
Hide		1.11	1.53	1.30
Distal limbs		1.98	1.84	1.92
Total		1.34	1.43	1.38
Shorn empty liveweight		0.89	0.92	0.91

† 'b' The values given under 'q' for eyes and brain are not 'q' values as quadratic regressions were unsuitable to represent the maturing patterns of these organs. The linear regression $y = a + bx$ (constrained to pass through (1, 1)) was used to calculate the progress to maturity of these organs.

to be relatively greater in the Merinos at equal weight but greater in Dorsets at equal maturity. The liver provides an interesting exercise in mental gymnastics in that the mature livers of the Merinos were 320 g heavier and as a percentage of liveweight 0.11% heavier. However, at equal liveweight (71 kg.), the Merino liver was 0.2% lighter, and at equal maturity (0.65 mature) the Merino liver was 0.5% lighter. These apparent contradictions come about because of the different composition at maturity and because of the different maturing patterns of the liver in the two breeds, and highlight the dangers of simplistic approaches to comparative studies of body proportions. In Table 5.f.3. are shown the maturing patterns of four organs whose 'q' values are different in Dorset Horn and Merino rams. These patterns highlight the fact that comparison of the genetic proportions of body organs within the total body must be approached from considerable knowledge of the changes occurring with growth. Truly we are wandering in a "forest of moving trees."

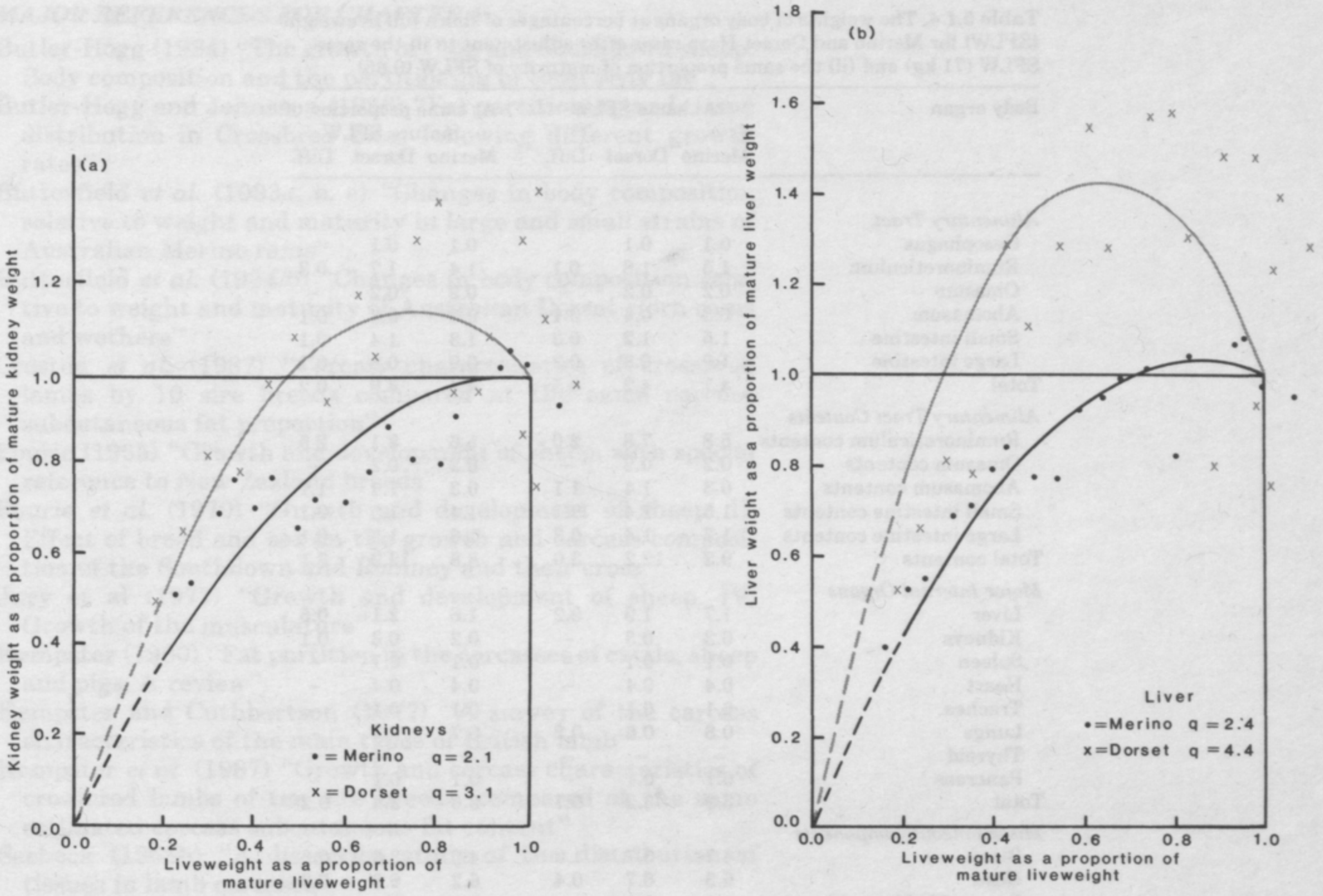


Figure 5.f.1.
Plots of progress to maturity of (a) kidney, and (b) liver of Dorset Horn and Merino rams. (Data from Butterfield *et al.*, 1983, 1984a.)

Table 5.f.3. Progress to maturity of those body organs of Merino and Dorset Horn rams which differ in the two breeds*

	Percentage maturity									Mature weight (kg)	
										Merino	Dorset Horn
Shorn full liveweight	20	30	40	50	60	70	80	90	100 =	119.7	99.7
Small intestine											
Merino	86	117	139	153	159	157	146	127	100 =	0.66	–
Dorset Horn	156	208	244	262	264	248	216	166	100 =	–	0.36
Small intestine contents											
Merino	71	97	117	130	137	137	131	119	100 =	0.77	–
Dorset Horn	113	152	180	196	200	192	173	142	100 =	–	0.51
Liver											
Merino	42	59	74	85	94	99	102	103	100 =	1.26	–
Dorset Horn	75	102	122	136	142	142	135	121	100 =	–	0.94
Kidneys											
Merino	37	52	65	76	85	92	97	99	100 =	0.21	–
Dorset Horn	54	74	91	103	111	114	114	109	100 =	–	0.18

* Maturing patterns of the remainder of the organs given in Table 1.f.3. are appropriate for both Merino and Dorset Horn rams as their maturity coefficients do not differ. Mature weights of these organs are found in Table 5.f.1. for Merinos and Dorset Horns.

Table 5.f.4. The weights of body organs as percentages of shorn full liveweight (SFLW) for Merino and Dorset Horn rams after adjustment to (i) the same SFLW (71 kg) and (ii) the same proportion of maturity of SFLW (0.65)

Body organ	At same SFLW			At same proportion of mature SFLW		
	Merino	Dorset	Diff.	Merino	Dorset	Diff.
Alimentary Tract						
Oesophagus	0.1	0.1	–	0.1	0.1	–
Ruminoreticulum	1.5	1.6	0.1	1.4	1.7	0.3
Omasum	0.2	0.2	–	0.2	0.2	–
Abomasum	0.3	0.4	0.1	0.3	0.4	0.1
Small intestine	1.5	1.2	0.3	1.3	1.4	0.1
Large intestine	1.0	0.8	0.2	0.9	0.8	0.1
Total	4.7	4.2	0.5	4.4	4.6	0.2
Alimentary Tract Contents						
Ruminoreticulum contents	5.8	7.8	2.0	5.6	8.1	2.5
Omasum contents	0.2	0.2	–	0.2	0.2	–
Abomasum contents	0.3	1.4	1.1	0.3	1.4	1.1
Small intestine contents	1.5	1.4	0.1	1.4	1.5	0.1
Large intestine contents	1.7	1.4	0.3	1.6	1.5	0.1
Total contents	9.2	12.2	3.0	8.8	12.9	3.1
Major Internal Organs						
Liver	1.7	1.9	0.2	1.6	2.1	0.5
Kidneys	0.3	0.3	–	0.2	0.3	0.1
Spleen	0.1	0.1	–	0.1	0.1	–
Heart	0.4	0.4	–	0.4	0.4	–
Trachea	0.1	0.1	–	0.1	0.1	–
Lungs	0.8	0.6	0.2	0.7	0.7	–
Thyroid	–	–	–	–	–	–
Pancreas	0.1	0.1	–	0.1	0.1	–
Total	3.9	3.2	0.7	3.6	3.4	0.2
Miscellaneous components						
Blood	4.7	3.7	1.0	4.6	3.8	0.8
Head	6.3	6.7	0.4	6.2	6.8	0.6
Penis + bladder	0.1	0.1	–	0.1	0.1	–
Hide	9.2	6.6	2.6	9.1	6.7	2.4
Distal limbs	1.9	1.6	0.3	1.8	1.7	0.1
Total	22.2	18.6	3.6	21.7	19.0	2.7
Shorn empty liveweight	90.4	88.6	1.8	90.9	88.2	2.7

g. CONCLUSIONS

As stated in the Introduction to this chapter, it is difficult to present a comprehensive comparison of breeds and so the main emphasis has been on the presentation of methods that may be considered for use in future studies.

There is some excellent published work on breed comparisons, but it is not clear to what extent the results may apply to other breeds or other conditions of nutrition or husbandry.

It is suggested that comparisons need to be made of the growth of carcase tissues relative to the growth of the whole animal and of the ratios of muscle:bone and muscle:fat. The partitioning of fat between the carcase and non-carcase, and between subcutaneous and intermuscular partitions, are suggested as the most fruitful methods of study of fat.

Studies of the relative sizes of muscles and bones are likely to yield less useful information due to the small variation between breeds. However, there is still much to be learned about the factors involved in the small apparent differences in muscle-weight distribution of breeds. While comparison at an equal degree of maturity reduces the differences revealed at equal weight; there may still be differences at equal maturity due to genetic variation and variation in fatness and hormone levels which are still poorly understood. This is not an area of pressing economic importance, however, it is of considerable biological interest.

MAJOR REFERENCES FOR CHAPTER 5

Butler-Hogg (1984) "The growth of Clun and Southdown sheep: Body composition and the partitioning of total body fat"

Butler-Hogg and Johnsson (1986) "Fat partitioning and tissue distribution in Crossbred ewes following different growth rates"

Butterfield *et al.* (1983a, b, c) "Changes in body composition relative to weight and maturity in large and small strains of Australian Merino rams"

Butterfield *et al.* (1984/5) "Changes in body composition relative to weight and maturity of Australian Dorset Horn rams and wethers"

Croston *et al.* (1987) "Carcass characteristics of crossbred lambs by 10 sire breeds compared at the same carcase subcutaneous fat proportion"

Fourie (1965) "Growth and development of sheep, with special reference to New Zealand breeds"

Fourie *et al.* (1970) "Growth and development of sheep. II. Effect of breed and sex on the growth and carcass composition of the Southdown and Romney and their cross"

Jury et al (1977) "Growth and development of sheep. IV. Growth of the musculature"

Kempster (1980) "Fat partition in the carcasses of cattle, sheep and pigs: A review"

Kempster and Cuthbertson (1977) "A survey of the carcass characteristics of the main types of British lamb"

Kempster *et al.* (1987) "Growth and carcass characteristics of crossbred lambs of ten sire breeds, compared at the same estimated carcass subcutaneous fat content"

Seebeck (1968b) "A dissection study of the distribution of tissues in lamb carcases"

Thonney *et al.* (1986c) "Breed and sex differences in muscle distribution of equally mature sheep and goats"

Wood *et al.* (1980) "Carcass composition in four sheep breeds: The importance of type of breed and stage of maturity"

APPENDIX 1

TERMINOLOGY

"We therefore wish to propose the following agreed terminology to avoid confusion" (Huxley and Teissier, 1936).

"Although some of the terminology of biology is of the functional, workaday kind we expect of a complex and busy science, all too much of it is a mixture of grandiloquence and linguistic offenses." (Medawar and Medawar, 1983).

a. THE PROBLEM

The terminology of biology provides a series of shorthand summaries of processes and phenomena to allow less tedious description when repeatedly used. However, some of the terms associated with studies of growth and development have been exploited to cover such broad spectra that their unqualified use is either meaningless or misleading; so that redefinition is a prerequisite of all studies in which they are used.

In "Final Considerations" at the Ghent seminar on "Patterns of Growth and Development in Cattle" in 1977, J.H. Oslage stated, "I would like to stress particularly the overall necessity of . . . a better and clearer definition of the technical terminology we use and, if possible, the use of the same definition of a particular term in the institutes in the various countries. In any country we will always find people who want to create new terms, which of course are always better in their understanding. I am not against improvements in our special terminology but, on the other hand, I am not in favour of misunderstandings arising through the use of different terms or definitions for the same thing." To this he might well have added "the use of the same term or definition for different things."

New terms often spring from a sound basis only to be distorted by expediency. None of us is innocent of the abuse and yet we are often caught between the unsavoury alternatives of twisting the meaning of an existing term or of introducing a new one, to further clutter the literature.

It is the feeling of insecurity regarding definitions which is so evident in Oslage's comment which makes it necessary to include in this monograph a section on terminology as reference for the reader. In the short history of growth studies a large body of terms and definitions has grown up, which can be reviewed in light of current knowledge. It is not suggested that my conclusion, from consideration of any term, will be that which would be reached by another author confronted with a different text, however, it is suggested that discussion of terminology and the culling of some terms, could lead us to more general use of terms meaning the same to us all.

b. A DISCUSSION OF SOME KEY DEFINITIONS

GROWTH

"IS AN INCREASE IN SIZE"

Growth is the *sine qua non* of animal production; the central theme of many books, monographs and scientific papers and the core of the life's work of many scientists; and yet no single definition is accepted by all.

A.E. Needham (1964), in his introductory chapter to "The Growth Process in Animals", traced the confusion in the definition of growth from the last century and quoted many different definitions, some simple and some which had sown ". . . unnecessary seeds of confusion". Needham fancied those definitions which fitted the viewpoint that "Growth plus Differentiation equals Development", and was not at all enthusiastic about definitions which implied: Differentiation (Development) plus Other phases equals Growth" which was his interpretation of Robbins (1928) when he said ". . . this phase of growth is commonly called differentiation or development . . ."

Needham's desire for a simple definition is not helped by the definition of Falkner and Tanner (1978) that "Growth, as we conceive it, is the study of change in an organism not yet mature." This definition is unique in that it states that growth is a "study" rather than a biological phenomenon. Perhaps this is to be expected as the scene was set by Weiss (1949) for the inclusion of almost anything in a definition of growth with his attempt "Growth is a word, a term, a notion, covering a variety of diverse and complex phenomena." As Falkner and Tanner explain, their definition makes no distinction between growth and development as development is the product of differential growth.

The early definition of T.H. Huxley (quoted by Needham), that growth means "increase in size", is the type of fundamental definition which can remain unaltered across all types of studies. In the majority of cases no further detail is required to ensure absolute understanding of what is meant by "growth", however the rider of Widdowson (1980) ". . . but an increase in size has many implications.", alerts us to the need for specific qualifications for special occasions but leaves the fundamental definition intact: "Growth is an increase in size".

In attempting to reach the most appropriate definition of growth, the theme of Needham's discussion was that there was a need for a simple basic definition along with a clear recognition of the need to qualify (not modify) this definition to suit genuinely complex circumstances. For specific purposes it is often necessary to define which tissues or tissue-components are included in, or excluded from, a particular growth study and this can be done without losing the basic concept of an increase in size. For example, Cheek (1968) found it necessary to produce his own definition of growth as " . . . the physiologic accretion of new tissue which is reflected by the acquisition of protein and water." and thereby eliminated fat from the specific considerations of growth in his study. In a later chapter, the same author went even further with "We can define growth as the replication of DNA and accretion of protein.", so that only the fractions of the body of immediate concern were embraced by the definition. In the same book another author, Blizzard, also found it necessary to produce his own definition: "Growth implies permanent enlargement or increase in total mass and does not encompass fluctuations such as excessive storage of fat or water.", so that only some fat was accepted in the growth process. These definitions by Cheek and Blizzard do not depart from the basic concept that growth is an increase in size but merely qualify it by defining the components which they are studying.

Falkner and Tanner stated that all change, and this would include development, in the immature animal, is growth. Whilst it is indeed convenient to include development in the definition of growth it can also be argued that it is unnecessarily complicating, as differential growth which produces developmental change is a special consequence of growth rather than an essential part of the fundamental process.

There are surprisingly few attempts to define growth in the animal production literature. Hammond (1940) described it as "increases in weight until mature size is reached" which may have been worded to exclude increases in fat beyond that which accrued during the growth of the other body tissues, whilst Purdom (1980) in a more physiological approach, and referring specifically to fish, interpreted growth as "the sum of anabolic profit and catabolic loss". An essential difference between these two definitions is that Hammond's definition embraces only increases in weight whilst that of Purdom also includes weight loss. It is unnecessary for our purposes in this monograph to dwell on the need to encompass "negative growth", however, in the broad field of growth studies it will often be necessary to embrace weight or size loss and the term seems appropriate.

Parks (1982) gave a simple definition of "the change of size, live weight or biomass with time or some other variable." and discussed the reluctance of scientists to accept a simple definition of growth in the following terms ". . . there is a tendency among bioscientists to wait and work for complete microdescription of growth before accounting for the simple and obvious macroscopic phenomenological aspects." Fortunately we are not constrained by a need to embrace anything but "obvious macroscopic aspects" of growth and so the unqualified definition that "growth is an increase in size", is adequate.

DEVELOPMENT

"CHANGES IN SHAPE AND BODY PROPORTIONS ASSOCIATED WITH GROWTH."

Although the word "development" is the most common companion of the word "growth", it appears to have stimulated few attempts at accurate definition in terms of meat animal growth. A dictionary definition of the biological use of the word is ". . . to cause to go from an embryonic state to a later and more complex or perfect one." (Paul Hamlyn, 1971). This is very similar to Hammond's (1940) definition which indicated that development to him meant changes in body proportions and shape and "bringing its various functions and faculties into full being."

Butterfield (1964b) used the terms "early developing", "late developing" etc. to indicate the stage of growth when proportionate increases within the musculature occurred. This followed the use of the terms by Luitingh (1962) who used "maturing" and "developing" as though synonymous. From a strictly anatomical viewpoint, i.e., ignoring the physiological implications, development may be adequately defined as: Changes in shape and body proportions associated with growth.

The qualifying terms of "early", "average", "late", and "very late" were used by Butterfield (1964b) to indicate the following during post-natal life:

Early developing: structures which at birth constitute a greater proportion of the animal than in the mature animal.

Late developing: structures which at birth constitute a smaller proportion of the animal than at maturity but which make rapid growth immediately following birth.

Very late developing: structures which at birth constitute a smaller proportion of the animal than at maturity and which do not increase until late in life.

Average developing: structures which retain a constant proportional weight relation with the whole animal throughout postnatal life.

In earlier work we used the "development" terminology to avoid the use of the word "maturing" which seemed inappropriate to describe the early post-natal changes in the musculature, so far removed from the mature state (Butterfield, 1964b). However, Butterfield and Berg (1966c) pointed out that the "development" terminology did not adequately describe the growth patterns and changing proportions within the musculature and that the use of the term "late developing" had "led to the erroneous conclusion that rapid progression through the phases of relative growth by better nutrition or use of early-maturing breeds, would increase the proportion of these muscles." Nevertheless, it is suggested that these terms, i.e. "early developing", "late developing" etc., could be substituted for "early-and late-maturing" in many instances in the terminology of growth and development studies. This would result in a sensible synthesis of the measurement of "growth" as the basic phenomenon and "development" as the detailed qualification. It is usual to talk of "growth and development" not "growth and maturing". Qualifications of "development", such as "early" and "late", provide only a rough indication of the timing and direction of the "changes in body proportions associated with growth". (See p. 000 for definitions.)

GROWTH IMPETUS:

Refers to the relative growth rates of body parts and is, therefore, a means of expressing the developmental changes occurring within the body. It is usually expressed relative to either the total animal, and this concept was used by McMeekan (1940), or the total tissue of which the structure is an intrinsic unit, suggested by

Wallace (1948). In 1966, in search of a method of expressing relative growth which would be more precise than the rather vague terms in general use at that time, Butterfield and Berg (1966a) developed a classification of the patterns of growth of muscles relative to that of total muscle weight. In this system the growth impetus of a muscle was measured by the "Growth Coefficient" ('b') of Huxley (1932) within each of several phases of post-natal growth and the growth impetus of each muscle in each phase described as "High", "Low" or "Average" according to its growth rate relative to that of total muscle. Fowler (1980a) commented that this system "... was very descriptive of a complex biological problem.", although he suggested that the inclusion of a quadratic term in the regression may have resulted in a better fit to the data. The system of Butterfield and Berg was later used by Richmond and Berg (1971b) and in the same year refined by Lohse *et al.* (1971) when the arbitrary growth phases were replaced by phases which were defined as multiples of birth weight.

Growth impetus is described by the terms "High" indicating a 'b' value significantly greater than 1.0; "Average", a 'b' not significantly different from 1.0; and "Low", significantly less than 1.0. Throughout the total life span from conception several changes in impetus may occur in some structures, and hence "Impetus patterns" (Butterfield and Berg, 1966a, b) indicate growth impetus and changes therein.

Growth impetus can be determined just as readily from Butterfield *et al.*'s (1983a) 'q' values as from Huxley's 'b' values. ('q' less than 1.0 = high: equal to 1.0 = average and greater than 1.0 = low impetus. Growth impetus patterns are shown in Appendix 1 Figure 1.

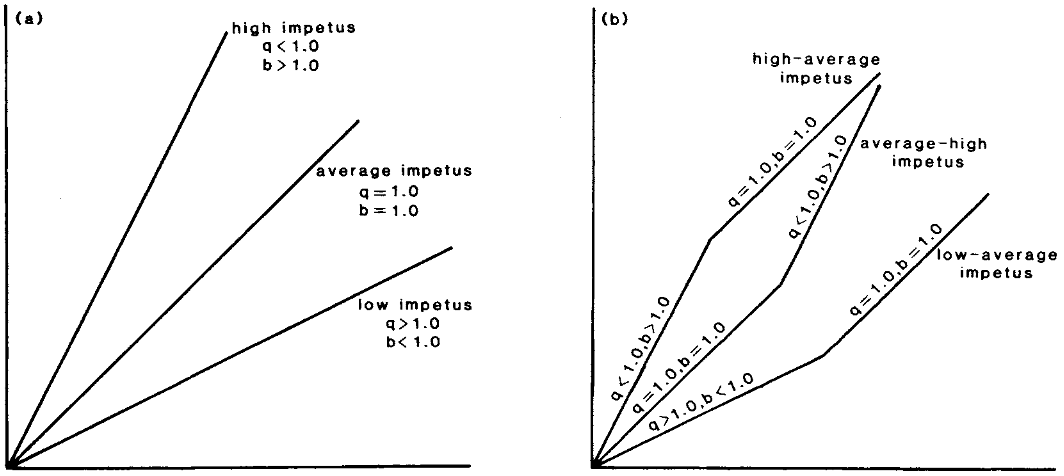


Figure 1
Growth impetus patterns.
(a) Monophasic. (b) Diphasic.

'q' values = Butterfield *et al.*, (1983a) coefficient.
'b' values = Huxley (1932) coefficient.

MATURITY

THE STATE OF ANATOMICAL EQUILIBRIUM ACHIEVED WHEN AN ANIMAL HAS CEASED TO GROW.

"... but what exactly is maturity?" (J. Robelin, in discussion at E.E.C. Seminar, 1977.)

"A state of ripeness or completed growth." (Stedman's Medical Dictionary. 21st Ed.)

"A definition of mature body weight that meets most purposes is the body weight of a normally grown, skeletally mature, normally active adult animal maintained in a state of body weight equilibrium on a standard diet, in a thermo-neutral, disease-free environment with, or adjusted to, a chemical body fat of 20%." (Taylor, 1985a).

"Body size is usually measured in a mature individual because that is the only period in an animal's life when body size is normally or potentially in an unchanging state." (Taylor, 1982)

"... an animal was accepted as mature when it had reached at least 0.85 of its asymptote for the exponential relationship between body weight and cumulative food consumed ..., and the average weekly increment in body weight for at least 10 weeks prior to slaughter was not significantly different from zero ..." Thompson et al. (1985b).

Animals which have ceased to grow at about the weight at which their earlier growth and food consumption suggest is a likely mature weight, can be presumed to be mature. It is simple to state a definition of maturity; it is much more difficult to be sure that a particular animal is mature and the degree to which its state at maturity has been influenced by various factors.

What is the effect on mature weight and mature composition of the nutritional, microbiological, metabolic, environmental and other sub-clinical disease experiences encountered during life? How long does the animal remain in a state of maturity before commencing to become senile? Does growth of fat mask the onset of senility of other body structures? There are, no doubt, many answers to these questions and these answers will vary according to the degree of departure from optimum of the many influences and the stage of the growth process when the departures occur.

Taylor, in presenting a course on Growth and Development at Göttingen for the German Society of Animal Science (Taylor, 1985b), listed the following factors as those likely to influence adult size:

1. GENOTYPE—species, breed, sex, individual, major genes.
2. NUTRITION—amount, quality, availability (feeding system).
3. DISEASE—

4. PHYSICAL ENVIRONMENT—temperature.
5. ACTIVITY—none, normal, exceptional loads.
6. SOCIAL ENVIRONMENT—competition, facilitation.
7. AGE—all adult ages acceptable.

And so Taylor defined the "Characteristic Adult Size" of a genotype in terms of "a dynamic equilibrium maintained under standard specified conditions after normal growth is over."

Mature liveweight achieved by individuals or groups of animals will be influenced by the factors listed above and hence "the unqualified use of mature liveweight becomes almost worthless" Taylor (1965) under many circumstances. We have only to study lists of mature weights published for sheep grown at pasture and compare these with weights achieved on ad lib feeding to realise that this is so, however, this does not mean that sets of mature weights developed for sheep under pastoral conditons are not of great value as it is usually the comparative mature weights, rather than the actual weights which are of value. It is sufficient for us here to draw attention to the possibility that mature weight determined under even the best controlled conditions may be influenced by non-genetic factors.

We have been primarily concerned in this book with measures of weight, however, it is well to note that other characteristics of animals, such as linear dimensions, reach a mature state and that some of these features, such as bone length, are less susceptible to environmental influences than is liveweight.

Brinks *et al.* (1962) and Fitzhugh, Cartwright and Temple (1967) weighed cows annually over many years and used the mean values as mature weights. Fitzhugh and Taylor (1971) suggested that this mean value might, in some circumstances, be estimated from the asymptote of a fitted growth curve as reported by Joandet and Cartwright (1969).

Taylor (1982) introduced the concept of mature weight being defined at a specified fatness with his definition "that meets most purposes" as follows: "a mature equilibrium weight containing 15% chemical fat". This was extended to, (Taylor, 1985a) "Mature weight is the body weight of a normally grown, skeletally mature, normally active adult animal maintained in a state of body weight equilibrium on a standard diet, in a thermo-neutral, disease-free environment with, or adjusted to, a chemical body fat of 20%." As Taylor explained the 20% chemical fat stated is perhaps only one of many standard levels of fat which might be set to suit various mammalian types.

On the other hand it may not be acceptable in some circumstances to standardise the level of fat if the actual amounts of fat in mature animals vary greatly. After all, fat is a body tissue and although its growth is less determinate than other body tissues, this does not mean that it is not important. In fact its variability is the most important characteristic in determining the relative commercial value of many animals. McClelland and Russel (1972) suggested that, at the same stage of maturity, sheep of all breeds may contain a similar proportion of fat and if this is even approximately correct then Taylor's suggestion will be a most practical definition.

Workers will need to supplement a simple definition of maturity in line with the practicalities of each particular experimental situation. The simple definition could be that an animal is mature when it ceases to grow. The important thing is that there should be no doubt regarding the criteria adopted as measures of the cessation of growth and the conditions under which the growth took place.

Simple weight against time growth curves show that growth is asymptotic to a mature weight (Brody, 1945; Joandet and Cartwright, 1969; Parks, 1982) but as growth is more closely related to food intake than to time, it seems logical to relate the maturing phenomenon to food intake and so Parks (1982) incorporated this in his definition of mature age, which reads ". . . the age when an animal . . . has reached (or almost reached) its steady state liveweight and food intake, but before the age the animal is considered senile". Based on this concept Thompson (1983) suggested the following working definition for maturity in *ad lib* fed sheep: "animals were accepted as mature when they had reached at least 85% of their asymptote for the exponential relationship between body weight and cumulative feed consumed, and the average increment in weekly body weight at least ten weeks prior to slaughter were not significantly different from zero ($P<0.05$)". This definition of Thompson's is a useful working definition which describes an animal within which there is an approximate anatomical equilibrium in all structures except fat. However, the approximation implied by the 85% suggests that this definition could be improved.

Terms in which "maturity" is qualified

The terms "early maturity" and "late maturity", are undoubtedly the most inappropriately used of any terms common to the scientific and commercial animal industries. They are applied in an unqualified form to weight, to fatness, to linear and chemical measurements of live animals, to carcases, tissues and organs. They are also applied as an index of fatness, or of rate of growth or of achievement of a physiological state such as puberty. Problems would be minimised if these terms were appropriately qualified in the form, e.g. "early maturing for fat" or "late maturing for growth rate". However, the confusion surrounding their meaning is so deeply ingrained in the collective thinking of animal scientists and stockmen that alternate, more specific terms are sought.

In this discussion we ignore those applications of the terms which are not of an anatomical nature but this still leaves us with a confused list. Wenham, Fowler and McDonald (1973) in a study of the skeleton, drew attention to the possibility that ". . . the uncritical use of accepted terminology such as early and late maturing may tend to obscure an understanding of the manner in which certain components of the skeleton develop." and further, Elsley (1976) drew attention to the major problem with these terms when he wrote: "The convention of 'early and late maturity' can also be an inhibition of thought if it is viewed as anything other than a simplified convenience in the description of the relative growth of tissues.", and so we should analyse their use before adding further to existing "inhibition of thought."

The words in the term "early maturing" imply that the structure under discussion matures earlier than some baseline which is usually the total animal. That is, it gains its final size and ceases to grow at an earlier point in time, or after less food is eaten, than the whole animal. But, of course, that is not what is meant by most authors, as a sample of quotes shows:

Early Maturity: "Some . . . breeds . . . have a fattening phase which begins at a relatively early age. They can be described as 'early maturing'." (Allen and Kilkenny, 1980)

Early maturing: ". . . it possesses the genetic capacity to synthesise fatty tissue at an earlier age . . ." (Preston and Willis, 1970)

Late Maturity: ". . . many . . . breeds . . . are very lean and have a late fattening phase. They are 'late maturing'." (Allen and Kilkenny, 1980)

Early and Late Maturity: "Hammond's description of parts as 'early'- or 'late'-maturing relates to the sequence in which they reach their maximal absolute growth rate . . ." (Fowler, 1980b)

Early and Late Maturity: "Tissues which were 'early maturing' exhibited their maximum growth intensity early in the life of the animal and thereafter there were waves of growth which affected each part in turn, the last to develop being the 'late maturing' parts. These phases were considered to be time dependent . . ." (From Fowler 1980a, commenting on a general hypothesis of The Hammond Group.)

Early Maturity: "The small Soay breed matured significantly earlier (by 36 days on average) than the large Oxford Down breed. The Finnish Landrace, though twice as heavy at maturity as the Soay, was almost equally early maturing." McClelland *et al.* (1976).

Early Maturity: "An early maturing tissue is . . . one which, at any stage of growth, prior to maturity, has achieved a greater proportion of its mature weight than has the whole body of its mature weight." (Butterfield *et al.* 1983a).

Early and Late Maturity: "By convention, tissues which are a greater proportion of their mature weight than is body weight or which increase in weight at a slower relative rate than body weight over the postnatal period are classified as early maturing. Tissues which have the converse characteristics are classified as late maturing. "(Black, 1983).

Early maturing: ". . . rather than by the phrase 'early maturing' which implies an early cessation of growth" (Wenham, Fowler, and McDonald, 1973).

There is a general similarity in these definitions and statements yet sufficient difference to leave considerable doubt as to any precise scientific definition of early and late maturity. Equally, these definitions have very little to do with maturity.

Butterfield *et al.* (1983a) and Black (1983) have taken the advantage of knowledge of mature weights, and hence of proportions of mature weights, to place an objective framework around the use of these terms on the few occasions when such information is available, however, this does not really make the terms any more sensible. The words "early maturing" cannot be twisted to mean "increased proportions in early life".

The issue is further confused by the somewhat different use of the term as an index of fatness. Here the term really revolves around "maturity" of a carcase relative to the criteria of excellence of a trade, even when it is applied to the live animal. In this arena the term is more acceptable as it can be taken to mean that the animal reaches a prescribed level of fatness "earlier" than others and that this level of fatness is that which is required in a "mature" carcase. So that with the term "early", indicating either more rapid growth or lighter weight, and "mature" indicating a precise level of fat, the term "early maturing" makes sense in this context, although the alternatives of either time or weight must introduce some confusion in the application of the term.

The above has been largely confined to "early" maturity. "Late" maturity is, of course, the opposite and subject to the same problems, although it is nonsense to talk of a tissue or organ maturing later than the whole animal.

It seems that it would be advisable to avoid the use of early and late maturity other than in the context of the total animal where the terms are understood to relate to the mature carcase. Studies within the body tissues may be much better served by use of precise terms which accurately reflect the relative growth rates of the tissues thus avoiding confusing generalities.

It is interesting to consider the appropriateness of the use of terms relating to maturity in the three main phases of growth:

(1) *The antenatal phase:* during which the goal of all growth is a viable new-born animal, is clearly defined from conception to birth, and as the foetus at the moment of birth can be precisely measured as the mature foetus, then it may be appropriate to use terms such as "early maturing" to describe antenatal growth of a structure which reaches its birth weight before the whole foetus. There clearly cannot be any "late maturing" structures in this context, only early maturing and the remainder. Johnson (1974) used the terminology of early and late maturing when studying antenatal and early postnatal growth in calves and commented that his results "underline the restrictive description afforded by the 'early-maturing—late-maturing' terminology . . ."

There are some problems associated with using birth as a landmark in growth and development. Obviously the onset of parturition is determined by a host of factors not associated with the growth process of the foetus: there are sex differences in the stage at which the average fetus is expelled (about 4% of mature weight in ram lambs and 5-6% in ewe lambs) (Taylor, Pers.Com.); there are species differences which are very wide, e.g. parturition occurs at about 0.6% of mature weight in pigs and 7% in cattle. These differences are of little consequence when making intrinsic comparisons of tissues within an animal, however they could be of considerable importance in comparisons across species or sexes.

(2) *The immediate postnatal phase:* during which the processes of growth are directed to the rapid achievement of maximum functional efficiency. Although the commencement of this phase is precisely defined it has no precise ending. It seems, therefore, inappropriate to use terminology based around the concept of maturity for a phase which has no state of maturity as its goal and it is in this phase that much of the change of growth impetus, particularly within the musculature which is the basis of "maturity" classification in the Hammond sense, takes place.

In line with the suggestions of Fitzhugh and Taylor (1971) and Taylor and Fitzhugh (1971), a precise endpoint for this phase could be an arbitrarily chosen proportion of mature body weight (say 20%) (which is the procedure adopted in Chapter1) and that the terminology of 'early and late' maturing could then be appropriately based on this endpoint as the 'mature' state of this phase. This does have the disadvantage of arbitrary selection of a point of variable biological significance among the structures of the body.

Puberty is a tempting landmark for the end of the immediate post-natal period as it is a physiologically important event. However, the problems associated with its detection and the gradualness of its achieval, make it impractical for most growth and development studies.

(3) *The maturing phase:* during which the whole process of growth is aimed at the achievement of a genetically-predetermined mature body composition.

Although the commencement of this phase cannot be precisely determined and undoubtedly is different for many structures, it seems that, in sheep, once an animal has reached 20% of its mature weight almost all of its tissues are on their final paths to maturity. The use of terms based on the concept of maturity may therefore be appropriate for this phase.

We are left with maturity terminology which could be appropriate in a limited way for only two of the three phases of growth and it seems therefore that, in order that we might embrace the whole of the lifespan of animals, a system which objectively describes the relative growth impetus of tissues and which makes no assumptions about the ultimate endpoint of any phase of growth should be sought. Therefore, throughout this book; although "early", "late" and "average maturing" have been used extensively in the papers on which the text is largely based; the use of stage of "development" and "relative impetus" have replaced references to "early and late maturity" where considered appropriate.

There are, nevertheless, other ways of approaching the problem of the suitability or otherwise of the terms 'late' and 'early' maturing, and these are to be found in papers by Fitzhugh and Taylor (1971) and Taylor and Fitzhugh (1971). They suggested that a stage of maturity (say 50% of mature body weight) be nominated and then the age at which each structure reaches this stage be recorded. The set of ages gives a variable which can be called "time taken to become 50% mature". Those structures which take a shorter time than the whole to reach 50% of their mature weight can be called "early" maturing at that nominated point. The point would not necessarily be a proportion of mature weight of the whole as it could, for example, be a nominated age, however, in order that the progress of individual organs be known in proportions of their mature weight, it would be necessary to know mature weights of the organs.

It will have become clear that the terms "early and late maturing" have been avoided in this text except in quotations. I have found no difficulty in this avoidance, but rather a feeling of satisfaction that terms such as high and low growth impetus, which have been used, leave no doubt as to their meaning. The position is analogous to the discussion of the word "allometry", by Needham and Lerner in 1940 when they wrote, "The term allometry was considered by Huxley and Teissier to be advantageous in that it could be applied both to phenomena of growth and to phenomena of proportionate size. Since terminology, which does not distinguish between differences during growth, at any given stage of growth, or after its completion, is bound to lead to ambiguous interpretation in many instances, the advantages of an all-embracing term are doubtful." The all-embracing usage of "early and late maturing" has led to a great deal of "ambiguous interpretation" and there would be little lost by the discontinuation of their use.

Conformation

"Beauty is in the eye of the beholder."

" the function of an animal is, . . ., related to its form, *the development of which is a growth phenomenon." (Brody, 1945)*

"As has already been said, the body should be nearly square. The vital currents moving in short lines are more effective than when moving in those of great length. The blood moving from the heart along very extended channels, flows with much less force as it recedes from the cause which set it in motion. The same is probably true of the nervous currents. The great vitalizing organs are located near the center of the system—a provision of nature by which the vital currents are shorter than under any other arrangement. "Russell Manning, (1880)

"If I could breed a cow fifty feet long, I would." Tom Lasater. *(Lasater, 1972).*

As applied to animal assessment, the term "conformation" has many different meanings. Individual animal breeders and scientists usually have a personal impression of conformation but rarely can they clearly define this for others.

Conformation of the carcase and that of the live animal are, of course, closely related, yet it is usual for a breeder to be talking about an entirely different concept from that of the butcher when using the word "conformation". In this discussion it seems useful to work backward from the carcase to the live animal to decide if it is feasible to use a common definition of conformation for both, or whether a chosen definition for the carcase can be a component of that of the live animal.

Historically there has been confusion as to whether conformation referred to the proportional size of body parts, or to the relationship of the skeletal size to the thickness of soft tissues, or to both, as in the reference by Palsson (1955) that "... developmental changes in different anatomical regions, and in the major tissues and organs of the body, which added together account for the changes in the conformation of the animal from birth to maturity". Whereas Hammond (1940) referred his reader in his index to "Body Proportions" when "Conformation" was sought, he nevertheless stated "Improvement of beef conformation has consisted in shortening the bones, particularly of the extremities, and so in thickening the muscles which lie over them." Berg and Butterfield (1976) stated "Conformation has been largely used as being synonymous with shape.", yet the same authors in 1966 in describing carcase merit quoted conformation as "the proportion of more expensive joints.". Luitingh (1962) and Taylor (1964) showed how the fattening process can affect carcase conformation (defined as the relative proportions of the various parts of the body) as well as composition.

It seems, therefore, that two different views have been extant. On the one hand conformation was an expression of the relative proportions within the carcase and particularly between high-priced and low-priced regions. On the other hand it was regarded as the relationship between skeletal size, particularly length, and soft tissue thickness. A welding of the two ideas appeared in the definition given by Alliston (1983) namely: "Conformation can be defined as the visual shape of the body of an animal, particularly the relationship between the skeleton and the covering of muscle and fat."

Workers located in the European Economic Community (E.E.C.) seem to be heading towards an acceptable definition of carcase conformation based on the relationship between the length of bones and the thickness of muscle plus fat. This has been stated in a variety of ways, e.g. "The relative plus weight of the carcass with regard to the average weight at its slaughter length." (Verbeke and Van de Voorde, 1978); "The thickness of muscle and fat in relation to skeletal size." (Kempster, 1978); "Conformation as defined in most countries is the visual assessment of the thickness of muscle and fat in relation to the size of the skeleton, blockier carcasses with good hindleg development being given higher scores." (Kempster; 1981) "Conformation (thickness of muscle plus fat) ..." (Allen and Kilkenny, 1980).

As with the definition of "growth" itself, workers have been unable to resist the ephemeral advantages of complicating the simple definition of conformation. It also seems that there has been difficulty in choosing between proportions of the body in a regional sense and proportions in a tissue sense as the simple basic definition.

Both of these simple concepts embrace differences in shape and so shape can be seen as a consequence of whichever simple definition is used. However, it seems that Hammond's definition in 1940 is to be reinstated after 40 years of being distorted to include regional proportions. He wrote: "Improvement for beef conformation consists in shortening the bones, particularly of the extremities and so thickening the muscles which lie over them. This gives a carcase with blocky joints and great depth of flesh.", which is very similar to the type of definition emerging from the E.E.C. countries at present. As the modern trend is against fat, there is a need to be more explicit in our separation of muscle and fat and this has led to the more specific definition of "muscularity" in which the components of the "flesh" (i.e. muscle and fat) in Hammond's definition are separated.

Let us accept that:

Carcase conformation is: "The thickness of muscle and fat in relation to skeletal size." as proposed by Kempster (1978) even though this definition provides us with no guide as to how to measure conformation.

What then of the conformation of the live animal?

The first consideration is, can the same definition cover both the live animal and the carcase? This seems to be desirable and possible in so far as slaughter stock are concerned if we accept the statement of Barton (1967) in his extensive review of conformation in cattle that "... conformation is generally regarded as a characteristic of the animal which gives an external indication of the desirability of the carcass and its meat." However, breeding stock comprise a quite different problem. It is in breeding stock that physical suitability for maximum productivity may be associated with quite different characteristics to those sought in a slaughter animal or carcase. The ideal carcase conformation may be highly incompatible with many productive characteristics and particularly with reproductive efficiency both in the male and the female and with locomotion, and so the breeder uses conformation as a term to embrace the entire structure of the animal and under these circumstances it is as Barton (1967) stated "... impossible to define conformation objectively."

Conformation to the breeder embraces the manner in which the total animal conforms to his preconceived ideal animal. It is primarily shape, but involves much more than the simple relationship we have accepted for a definition of carcase conformation. Not only does it involve the relationship of soft tissue to bone, but also the distribution of tissues, the shape of the skeleton, the angulation of joints, the partitioning of fat and many more. A large part of this conformation is determined by genetic makeup of the animal but is constantly moulded by the changes of age and environment. Attempts are made to lay down the most salient points of the conformation of an ideal animal in various breed standards.

c. DEFINITIONS

The following definitions are presented to ensure that the reader is in no doubt when a term is encountered in the text. In some cases minor comment is made regarding general problems in the use of a particular term beyond the scope of this text.

Allometry:

From the Greek allometron. "... that by which anything is measured." (Huxley and Tessier, 1936)

"... allometric formulas reveal certain beautiful regularities in nature, describing a pattern in the comparisons of animals as different in size as the shrew and the whale, and this can be as delightful in its own way as the view through a microscope." (McMahon and Bonner, 1983).

(See "Growth Coefficient". p. 129).

Bone:

"Bone is the general name for each of the distinct parts which unitedly make up the skeleton of vertebrate animals" (Oxford).

Total bone weight: The aggregate weight of all the bones included in the commercial carcase. (It may be specified as "total half-carcase bone weight" to mean the weight of all the bones in half a carcase divided in the median plane).

Bone-weight distribution: The relative weights of individual bones or groups of bones expressed as percentages of total bone weight.

Dissectible (dissected) bone: Individual bones and groups of bones freed from all surface soft tissue except periosteum. (In some studies to which reference is made in this text, e.g. those of the Cambridge School, and some New Zealand studies, the periosteum was removed.)

Carcase (Carcass)

The skinned and eviscerated body from which the head has been removed at the atlanto-occipital joint, the tail at the articulation of the second and third caudal vertebrae and the limbs at the carpo-metacarpal and tarso-metatarsal joints. The kidneys and associated fat have been removed. The fat lining the pelvic canal ("pelvic fat", "channel fat", "retroperitoneal fat") has been removed also. (It is necessary to define the carcase as the wide diversity of procedures in commerce result in many minor variations in carcases.)

Hot carcase weight: The weight of the carcase at the end of the "dressing" procedure and within one hour of slaughter. (It may be necessary to specify the relationship to washing in commercial situations.)

Cold carcase weight: The weight of the carcase after a specified time under standard conditions. The conditions usually approximate hanging for 24 hours at 4°C.

Mature carcase: a carcase with the prescribed level of fat for a particular market.

Conformation (see discussion p. 126)

Carcase conformation: "Thickness of muscle and fat in relation to skeletal size". (Kempster, 1978) Measured by the relationship between length of leg (Kirton and Pickering, 1967) relative to carcase weight.

Live animal conformation in slaughter stock: Thickness of muscle and fat in relation to skeletal size.

Live animal conformation in breeding stock: The manner in which the whole animal conforms to the preconception of an ideal animal by the beholder. "Beauty is in the eye of the beholder".

Development:

The changes in the body proportions associated with growth.

Early development: A consequence of rapid relative growth rate early in life which results in the structure being a greater proportion of the whole (animal or tissue) at a specified stage of maturity than at maturity.

Late development: A consequence of slow relative growth rate early in life which results in the structure being a smaller proportion of the whole (animal or tissue) at a specified stage of maturity than at maturity.

Dissectible (Dissected) Tissues

Those tissues which can be separated by simple macroscopic dissection. ("Dissectible" is often misspelt "dissectable" in the literature.)

Dissect: To cut apart an animal body to examine the structure, relation of parts, or the like. (Paul Hamlyn, 1971)

To cut asunder, cut in pieces, divide by cutting. (Oxford, 1967)

Dressing percentage

Is the value derived by expressing the weight of the commercial carcase as a percentage of liveweight. This statistic requires precise definition of the conditions of recording of both liveweight and carcase weight and a clear definition of what constitutes the carcase.

Fat

The adipose tissues of the animal.

Total body dissectible fat: all the adipose tissue, including minor connective tissues which can be removed from the whole animal by simple macroscopic dissection.

Total body chemical fat: all fat which can be extracted from the whole animal by a specified chemical method.

Dissectible carcase fat: the sum of the subcutaneous and intermuscular fat partitions.

Chemical fat: fat which is extracted by a specified chemical method.

Chemical carcase fat: The sum of intermuscular, subcutaneous, intramuscular and intraosseus fat as extracted by a specified chemical method.

Pelvic fat ("retroperitoneal", "channel"): the fat lining the pelvic canal extending cranially to the external iliac vein.

Cardiac fat: the fat within the pericardium.

Fat partitioning: the divisions of the body fat into layers (e.g. subcutaneous and intermuscular) and regions (e.g. mesenteric and omental).

Fat depots: arbitrarily-defined regions within fat partitions.

Fat-weight distribution: the relative weights of the fat depots expressed as percentages of the weight of the fat partition within which they lie.

Intermuscular fat: the fat between the muscles. It includes all carcase fat with the exclusion of intramuscular, intraosseus and subcutaneous fat.

Intramuscular fat: the fat within muscles. May be subjectively estimated or chemically determined.

Intra-abdominal fat: the summed weights of omental, mesenteric and perirenal (kidney).

Intraosseus fat: the fat within bones. May be measured chemically.

Mesenteric fat: the fat within the mesentery attached to the large and small intestine.

Omental fat: all the fatty tissue associated with the rumen, reticulum, omasum, abomasum and the cranial and descending parts of the duodenum.

Non-carcase fat: (body cavity fat): all body fat not included in the subcutaneous, intermuscular, interosseus and intramuscular depots.

Perirenal (kidney) fat: the fat associated with the kidneys extending caudally to the external iliac vein.

Retroperitoneal fat: this term has been used (Kempster, 1981 and Butler-Hogg, 1985) to replace the inelegant "channel fat". However, it is rather all-embracing. Certainly the fat within the pelvic cavity, of which this term is proposed as a definition, lies behind the peritoneum (i.e., it is retroperitoneal) but so also is the kidney fat and other lesser depots lining the body cavity. If the term "channel" offends then "pelvic" fat is anatomically more acceptable than "retroperitoneal".

Scrotal fat: the fat associated with the scrotum. Is a depot within the subcutaneous partition.

Mediastinal fat: the fat within the mediastinum of the thorax.

Mammary (udder) fat: the fat in the inguinal region associated with the udder. Is a depot within the subcutaneous partition.

Subcutaneous fat: the fat immediately deep to the skin and superficial to all other tissues of the carcase, but including the fat deep to the M. cutaneous trunci et omobrachialis.

Growth

An increase in size.

Relative growth: the relationship between the changes in size of parts of the body.

Relative growth rate: the rate of growth per unit weight.

Negative growth: loss of size.

Growth coefficient: is a measure of the ratio of the rate of growth per unit weight of an organ to the rate of growth per unit weight of the body.

Accepting that the rate of growth per unit weight may be expressed as "relative growth rate", the definition may be restated as:

"The ratio of the relative growth rate of the organ to the relative growth rate of the body." (Huxley, 1932).

In Huxley (1932) the growth coefficient was represented by the constant 'k' in the formula:

$y = bx^k$

where:

y = the magnitude (weight) of the organ,
x = the magnitude (weight) of the body,
b = the value of 'y' when 'x' = 1.0,
k = the ratio of the rate of growth per unit weight of the organ to the rate of growth per unit weight of the body.

As mentioned by Huxley and Teissier (1936), the notation of the simple allometry formula has seen a list of different symbols confusingly applied. They listed: $y = Kx^a$ (Teissier, 1934); $y = bx^k$ (Huxley, 1932); $a = Kb^x$ (Nomura, 1926); $p = aw^K$ (Weymouth and Mackay, 1934), and then suggested that the "agreed" notation should be, $y = bx^{\mathrm{alpha}}$. They expressed the hope that "other workers in this field will see fit to adopt these suggestions." This was not to be.

The notation in Huxley's original formula fell from common usage, but not to be replaced by his 1936 suggestion along with Teissier as the formula is now most commonly written as: $y = ax^b$, so that the ratio of the relative growth rates of the part and the whole is represented by the symbol 'b' which is the commonly used "Growth Coefficient".

The formula is most commonly used in its logarithmic form:

$\log y = \log a + b \log x$, so that from the slope of the resultant straight line the value of 'b' can be read off.

It should not be presumed that Huxley 'invented' the use of the formula for the study of growth phenomena for, as pointed out by Brody (1945): "The parabola $Y = aX^b$ has been used in biology for perhaps a century and since 1890 for relating organ weight to body weight."

Impetus:

Is a term which describes the relationship between the relative growth rate of an organ and the relative growth rate of the body. It can be measured by the 'Growth Coefficient' of Huxley (1932) or the 'Maturity Coefficient' of Butterfield *et al.* (1983a).

Impetus patterns: the patterns of growth impetus measured throughout phases or periods of growth.

Impetus groups of muscles: muscles grouped according to their growth impetus patterns.

Liveweight

The weight of the live animal. ("Biomass", Parks, 1982). May be "full" or "fasted" for a specified time.

Full liveweight: the weight of an animal direct from feed.

Empty liveweight: the weight of an animal less the weight of the contents of the gastrointestinal and urinary tracts.

Shorn liveweight: the weight of an animal after wool is removed by commercial shearing.

Starved liveweight: the weight of an animal after a specified time during which there is a specified deprivation of food or water or both.

Fleece-free liveweight: the weight of an animal less the weight of wool shaved to skin level.

Standardized liveweight: the weight of an animal recorded at a set time of day under *ad lib* feeding or free-range grazing, or at a set time relative to time of controlled feeding.

Maturity

The state of anatomical equilibrium achieved when an animal has ceased to grow. (See discussion p. 123)

Mature body weight (adult body weight): is the weight of a mature animal.

Mature carcase: a carcase with the prescribed level of fat for a particular market.

Maturing pattern: the progress to maturity of an organ or part relative to the progress to maturity of the whole animal or total tissue.

Maturity coefficient: (Butterfield *et al.*, 1983a) The value 'q' in the quadratic equation:

$$y = p + qx + rx^2$$

which when constrained to pass through 0,0. representing conception and 1,1. representing maturity, implies that $p = 0$ and $r = 1-q$ and may thus be rewritten:

$$y = qx + (1-q)x^2$$

where:

y= the weight of an organ divided by its own mature weight (I/I_m)

x= the weight of the total (animal or tissue) divided by its own mature weight (T/T_m)

q= the relationship between y and x.

(See Appendix 4).

Muscle:

i "Any one of the contractile fibrous (sic) bands or bundles, having the function of producing movement in the animal body." (Oxford Dictionary)

ii "Muscle; one of the contractile organs of the body by which movements of the various organs and parts are affected." (Stedman's Medical Dictionary)

iii the red meat of the carcase.

Fusiform muscles: are those in which the fibres are approximately parallel to the line of pull.

Multipennate muscles: are complex muscles in which the fibres are oblique to the line of pull. (Pennate = feather-like)

"Standard Muscle Groups"

Nine anatomically-defined groups of muscles. These groups were defined by Butterfield (1963) for use in beef cattle studies. They have been used in cattle studies by Butterfield and Berg (1966a,b,) Berg and Mukhoty (1970) Berg and Butterfield (1974).

They have been slightly modified for sheep studies by Lohse (1971), Lohse *et al.* (1971) and Hilmi (1975), but used unmodified in others (Jury *et al.*, 1977; Butterfield *et al.*, 1983b, 1984b; Thompson, 1983; Perry *et al.*, 1987). Thonney *et al.* (1986c) arranged selected muscles according to these "Standard Muscle Groups".

They have been used as a basis, but appropriately modified for studies of elephant seals (Bryden, 1967), and kangaroos (Hopwood, 1976).

As originally defined the groups are (see Figure 1.c.1.):

Group 1—Those muscles of the pelvic limb which arise from the os coxae, together with the vasti and articularis genu muscles ("Proximal hind").

Group 2—Those muscles which arise from the distal half of the femur, from the tibia or fibula, excluding the vasti and articularis genu muscles. ("Distal hind").

Group 3—The muscles surrounding the spinal column in the thorax and lumbar region. ("Spinal")

Group 4—The muscles of the abdominal wall. ("Abdominal")

Group 5—Those intrinsic muscles of the thoracic limb which arise from the scapula and the proximal half of the humerus. ("Proximal forelimb")

Group 6—Those intrinsic muscles of the thoracic limb which arise from the distal half of the humerus, from the radius or the ulna. ("Distal forelimb")

Group 7—The muscles of the thorax which are attached to the thoracic limb. ("Thorax to foreleg")
Group 8—The muscles of the neck which are attached to the thoracic limb. ("Neck to leg").
Group 9—The intrinsic muscles of the neck and thorax. ("Neck and thorax")

A somewhat different set of "Standard" muscle groups was used by Bergstrom (1978).

Expensive muscle:

A composite group known as "Expensive Muscles" made up of the combined "Standard Muscle Groups 1, 3, and 5" (Butterfield, 1963).

The concept of "Expensive muscle groups" was extended by Richmond and Berg (1971b), who proposed three alternative "expensive" groupings for the musculature of pigs. These groupings were:

A. "Standard Muscle Groups 1 & 2." That is the muscles of the hind limb groups.

B. "Standard Muscle Groups 1, 2, & 3." That is all the muscles of the hind limb plus those surrounding the spinal column.

C. "Standard Muscle Groups 1, 2, 3 & 5." That is the muscles of the hindleg, those surrounding the spinal column and those of the proximal part of the forelimb.

Organ

"A part or member of an animal . . . body adapted by its structure for a particular vital function . . ." (Oxford) e.g. heart, liver, brain.

Sex

Ram: An entire male sheep of any age.
Wether: A castrated male sheep of any age.
Ewe: A female sheep of any age.

Tissue

A complete anatomical system such as the musculature, the skeleton, the adipose tissue.

APPENDIX 2

TECHNIQUES OF DISSECTION FOR STUDY OF BODY COMPOSITION

The data used in this monograph have been derived largely from studies carried out in the Department of Veterinary Anatomy in The University of Sydney. The dissection technique is similar to that previously described by Butterfield (1964a), Butterfield and May (1966), Butterfield and Berg (1966a) and Berg and Butterfield (1976) for cattle. In the case of sheep, the basic anatomical text of May (1970) provides a suitable description of the anatomy with minor up-dating of the terminology to approximate that of N.A.V. (1983).

All measurements of those structures which are removed from the carcase before storage are carried out as soon as possible after slaughter, and are usually completed within an hour. Many of these weight measures are of a simple nature, and can be carried out with a minimum of procedure for such structures as the liver and kidneys. However, it is necessary, if worthwhile data is to result, to determine in preliminary studies exactly what the endpoints of trimming are to be with each organ. For example, the heart is an organ about which it is difficult to lay down very precise trimming instructions, and so it is necessary for a single operator to do this trimming to a set procedure devised ahead of the commencement of the study. Also, with the hollow organs, which are to be emptied of their contents, standard procedures must be devised and preferably carried out by the one operator to ensure the uniformity of procedure and of endpoints of cleanliness. With organs such as the intestine it is not possible to achieve absolute emptiness and cleanliness of the lumen and so standardized procedures are essential.

The carcase is best handled by hanging in the usual commercial manner until set and assessment needs to be made of the possibility of the effect of non-uniform weight loss during this period, as draping of very young carcases may be essential to prevent unacceptable weight loss, particularly from the musculature. Any storage beyond the period of a few hours of the setting of the carcases will require that they should be draped in impervious material to prevent weight loss.

Carcases may be halved by various procedures. If both sides are needed for study then there is little alternative to careful sawing in the median plane. High levels of skill can be achieved by some operators, with appropriate equipment, however, once again it is necessary that preliminary practise be carried out to determine the ability of the staff and equipment to carry out this task efficiently. Alternatively, carcases may be separated in a paramedian plane leaving the vertebral column intact. Whole vertebrae can then be weighed and half weights used in the data from the side being dissected.

Usually it is desirable to divide the half carcase into arbitrarily-defined quarters as this exposes the minimum of tissue to drying during the dissection process.

It is desirable to work in a high humidity, cool, draught-free environment and under these conditions draping should not be necessary. Subcutaneous fat is removed only as necessary to reveal the underlying tissues deep to it. However, if such an environment is not available, draping is needed to avoid extensive dissection loss due to evaporation. Cuthbertson *et al.* (1972) suggested that the expense of careful temperature and humidity control was seldom warranted and this is agreed. Nevertheless, dissection projects have been carried out in a wide variety of conditions, mostly in environments with temperature and humidity ranges which were not extreme. However, some of the older data were collected under difficult circumstances, for example that of Wilson (1958) in temperatures of 90F and relative humidity of 50%. Under all conditions those tissues, such as fat, which are accumulated progressively during dissection must be placed in covered containers.

Unlike cattle dissection, in which, in our laboratory, butchers' knives are used; scalpels and forceps are more suitable for the smaller units in the tissues of sheep, although Cuthbertson, Harrington and Smith (1972) recommended the use of a butcher's knife in sheep dissection unless "one is interested in the details of individual muscle growth". Knives have been successfully used over large numbers of sheep by M.L.C. workers (Kempster *et al.* 1986). The choice of a knife has many advantages in the hands of skilled butchers who are also skilled knife sharpeners. If dissection is being carried out by technical staff who are more skilled in anatomy but less skilled in knife sharpening, then scalpels are probably to be preferred, as with disposable blades a high standard of sharpness is maintained. On the other hand, there is always a tendency to pick at tissues with a scalpel and this is unsatisfactory, whereas with a knife the natural inclination is to sweep across the tissues. However, technical staff can be trained to use large scalpel blades in an appropriate manner.

The muscles are removed in the order set out below:

Order of dissection of muscles of the hindquarter:

1. M. cutaneus trunci
2. M. tensor fasciae latae
3. M. biceps femoris
4. M. glutaeus medius
5. M. vastus lateralis
6. M. glutaeus accessorius
7. M. glutaeus profundus
8. M. rectus femoris
9 M. semitendinosus
10. M. gracilis
11. M. semimembranosus
12. M. adductor femoris
13. M. gastrocnemius et M. soleus
14. M. flexor digitorum superficialis
15. M. pectineus
16. M. sartorius
17. M. gemellus
18. M. quadratus femoris
19. M. obturator internus et M. obturator externus
20. M. vastus medialis
21. M. vastus intermedius
22. M. articularis genu
23. M. peroneus tertius
24. M. extensor digitorum longus
25. M. extensor digitorum brevis
26. M. extensor digitorum medius
27. M. peroneus longus
28. M. extensor digitorum lateralis
29. M. tibialis cranialis
30. M. tibialis caudalis
31. M. popliteus
32. M. flexor digitorum longus
33. M. flexor hallucis longus
34. M. psoas minor
35. M. psoas major
36. M. psoas major
37. Mm. intertransversarii lumborum
38. M. iliacus
39. M. latissimus dorsi
40. M. trapezius thoracica
41. M. serratus dorsalis caudalis
42. M. iliocostalis
43. M. longissimus dorsi
44. M. spinalis
45. M. multifidus dorsi
46. M. obliquus externus abdominis
47. M. retractor costae
48. M. obliquus internus abdominis
49. M. transversus abdominis
50. M. rectus abdominis
51. Mm. sacrococcygeus, ventralis, lateralis et dorsalis
52. M. levator ani
53. Mm. intercostales externiet interni
54. Mm. levatores costarum

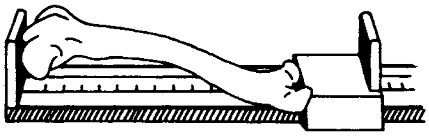


Figure 1
Method of measuring length of bones

Order of dissection of the muscles of the forequarter:

1. M. cutaneus trunci
2. M. trapezius cervicalis
3. M. trapezius thoracalis
4. M. deltoideus
5. M. infraspinatus
6. M. triceps brachii (caput laterale)
7. M. teres minor
8. M. triceps brachii (caput longum)
9. M. tensor fasciae antibrachii
10. M. extensor carpi radialis
11. M. extensor digiti tertii proprius
12. M. extensor digitorum communis
13. M. extensor digiti quarti proprius
14. M. extensor carpi ulnaris
15. M. extensor carpi obliquus
16. M. latissimus dorsi
17. M. protractor preputii
18. M. omotransversarius
19. M. serratus ventralis cervicis
20. M. serratus ventralis thoracis
21. M. pectoralis profundus
22. M. pectoralis superficialis
23. M. supraspinatus
24. M. biceps brachii
25. M. teres major
26. M. coracobrachialis
27. M. subscapularis
28. M. brachialis
29. M. brachiocephalicus
30. M. triceps brachii (caput mediale)
31. M. flexor carpi radialis
32. M. flexor carpi ulnaris
33. M. flexor digitorum superficialis
34. M. flexor digitorum profundus
35. M. anconaeus
36. M. serratus dorsalis cranialis
37. M. scalenus dorsalis
38. M. cervicohyoideus
39. M. iliocostalis
40. M. longissimus dorsi
41. M. longissimus cervicis
42. M. splenius
43. M. sternocephalicus
44. M. scalenus ventralis
45. M. longus capitis
46. M. intertransversarius longus
47. M. longissimus capitis
48. M. longissimus atlantis
49. Mm. intertransversarii cervicis
50. M. semispinalis capitis
51. M. spinalis dorsi
52. M. rectus capitis dorsalis major
53. M. obliquus capitis caudalis
54. M. rectus thoracis
55. M. obliquus abdominis externus
56. M. rectus abdominis
57. M. transversus abdominis
58. Diaphragm
59. M. transversus thoracis
60. M. longus colli
61. M. multifidus cervicis
62. M. multifidus dorsi
63. Mm. intercostales externi et interni
64. Mm. levator costarum

Each muscle is trimmed from its tendons and aponeuroses at the level of the last vestige of muscle tissue so that there may be some tendinous tissue left on the muscle, but no muscle tissue is removed with the tendon. The surfaces of the muscles are cleaned of all fat and connective tissues.

The bones are cleaned of all loose tissues but the periosteum is left intact on the bones. Linear measurements of bones are best made by use of a device which enables the bone to be placed between two plain surfaces, between which also lies a linear scale (see Figure Appendix 2 Figure 1). Measurements of length should be made between articular surfaces and should not include bony prominences. For example, measurement of the femur should be made from the most proximal surface of the head rather than the proximal surface of the greater trochanter. In this way the measure is of the functional length of the bone and does not include the prominences, the growth of which may be governed by other criteria than the functional length.

Each muscle and bone is weighed immediately dissected whereas the remaining tissues are accumulated and weighed at the completion of the dissection of the quarter-carcase.

Due to the difficulty posed by the increasing invasion of the connective tissues with fat as the animals become fatter, it is usually best to include all connective tissue in the dissected intermuscular fat, and that has been the procedure in all recent studies in The University of Sydney. However, in studies which involve animals which are not very fat, it may be more desirable to differentiate between fat and the more gross connective tissues, such as large tendons, ligaments and lymph nodes.

Muscle-weight distribution

The history of the study of muscle-weight distribution is quite brief and the first data for sheep produced by individual muscle dissection of the whole carcase came from Fourie (1965) working in New Zealand, where he expanded Daintree Walker's work in cattle to a study of sheep growth. Walker appears to have been the first to undertake individual muscle dissection of the entire carcase musculature as a means of studying muscle-weight distribution. Butterfield (1963) streamlined Walker's technique in cattle to reduce the labour input.

Individual muscle dissection has a great number of advantages over other dissection methods used to study the musculature. It also has the serious disadvantages of high cost and slowness so that it is used most often in studies of small numbers of animals. The high cost is due, not only to labour, but also to the reduction of the carcase to commercially unattractive units. The dissection of a side of lamb will usually be accomplished in an eight-hour working day by a single skilled and experienced dissector. However, if the carcase is very fat it may require considerable additional time.

The advantages of individual muscle dissection are:

i. The technique requires few arbitrary decisions and hence produces data in which can be felt a high degree of confidence, if the dissection is performed by dedicated workers.

ii. The data for each individual muscle are a record of a single unique functional unit of the highly active musculature. Each muscle being "individual" in its function and its consequent growth pattern.

iii. The data can be handled in any number of chosen groupings, e.g., as individual muscles, as anatomically-defined groups (Butterfield, 1963; Fowler, 1968), as 'impetus groups' (Butterfield and Berg, 1966a); or according to colour, size, anatomical structure, function, juiciness, tenderness, flavour or any other desired parameter. Many of these groupings are as yet unexploited in attempts to understand the complex changes within the musculature.

iv. The anatomical similarity of the musculature of mammals allows comparisons across the species.

v. The psychological stimulation to the dissectors of discrete anatomical structures is highly developed, and so the boredom associated with the gross separation of meat into muscle, bone and fat is largely overcome. The 'dedicated workers' mentioned as so important in i. above are wooed by the fascination of individual muscle dissection.

vi. The anatomical terminology of muscle names is international and so results are freely understood in all countries. This is assured by the adoption of *Nomina Anatomica Veterinarius* (1983) terminology.

There is little doubt that individual muscle dissection is the method of choice for precise studies of the musculature at the gross anatomical level, however, there are many situations where the number of animals to be assessed is such that quicker methods must be found. Nevertheless, it is clear that studies which lay claim to providing information about muscle, must be based on dissection of muscle. No useful information regarding the growth of the musculature can be gleaned from dissection procedures in which muscle is shrouded in variable amounts of subcutaneous and intermuscular fat. So the pragmatic approach to the problem of dissection of large numbers of animals is to dissect some large and anatomically-defined intrinsic units of the musculature, i.e., individual muscles or groups (Hewetson, 1962) and from these to remove all fat. If this is not possible the worker should confine his thinking to a study of that which he is dissecting, NOT muscle, but muscle plus some fat ("flesh"). However, if all fat can be removed, then quite useful studies can be made of muscle growth using regions or units, of the musculature which are representative of the whole. However, it is necessary to ensure that the muscles chosen to represent total muscle are a truly representative sample for the characteristics being studied. Wynn and Thwaites (1981) made an unfortunate choice of 24 muscles to represent total muscle weight. Twenty-two of their chosen muscles had a lower growth impetus than total muscle and hence formed an inappropriate sample for studying growth patterns relative to total muscle.

There is nothing wrong with studies of the distribution of commercial cuts of meat, and, in fact, many will see these as more commercially applicable than the airy-fairy dissection of individual muscles. However, those who undertake these studies must resist the temptation to extrapolate from their results, on their possible meaning in terms of muscle-weight distribution, as the variables involved in such studies are often much larger than the biological niceties of variation in muscle-weight distribution.

The analysis of muscle growth using any procedure which bulks a large number of muscles into a small number of units, such as "Standard Muscle Groups", must result in the masking of the growth characteristics of individual muscles. This is appreciated and so attempts are made to identify individual muscles of special interest within groups where it is apparent that their peculiar characteristics are either moderated or completely obliterated by the characteristics of the group as a whole. Each muscle has a unique role to play in the mobility of the animal, it is built accordingly and it grows accordingly. It would therefore be improbable for all muscles in the same anatomical region to follow a similar growth pattern.

Wallace (1948) was the first to suggest that the growth of units within a system, such as the musculature, should be assessed relative to the total system rather than the total animal. Total muscle weight is usually represented by all of the muscle from one side of the commercial carcase, i.e., one side of the animal less the head muscles and the tail muscles. Butterfield (1963) showed in cattle carcases that, although there were minor differences between the left and right sides of the musculature, these did not follow any consistent pattern and that it was acceptable to use the musculature of one side as an index of the whole. Tail muscles are usually removed at docking or "marking" in sheep in Australia. Heads are removed at slaughter.

The muscles of the head are commonly excluded from studies of the carcase musculature, not only because the head is removed at slaughter but also because the complexity and size of the head muscles is such that their dissection would require a great deal of effort for a very small return. It is safe to assume that the muscles of the head are very early developing and, therefore, their post-natal growth impetus is low, as they are so essential to the vital functions, particularly suckling, of the newborn.

Fat Partitioning and Distribution

Fat is accumulated during the dissection process as a virtual by-product of the dissection of muscle and bone. Little difficulty is experienced in making arbitrary decisions regarding the classification of fat into its partitions of "subcutaneous" and "intermuscular" in animals with low levels of total fat. However, divisions of the partitions into various depots for study of fat distribution needs to be carefully planned if the study is to include very fat animals. It is as well to obtain, before a study commences, animals representative of the degrees of fatness likely to be encountered during the study to assist in deciding on appropriate anatomical landmarks which can be easily determined at all degrees of fatness. Even so, it is not easy to ensure that the boundaries of depots are unaltered by mounting fatness.

As animals become fatter so the constitution of the connective tissue matrix of the dissectible fat stores comes to constitute a declining proportion of dissectible fat weight. However, this decline will not be uniform throughout the depots and so, whereas the mesenteric fat depot in the very fat animal will still contain a large proportion of connective tissues including blood vessels and lymphatic structures, the subcutaneous fat will contain only a very small proportion of connective tissues.

APPENDIX 3

SOME INDICES OF CHANGING BODY COMPOSITION DURING GROWTH

"On the face of it, the curve of growth . . . embodies a straightforward and entirely uncomplicated concept, yet the more deeply it is probed the more complicated it turns out to be." (Medawar and Medawar, 1983).

MUSCLE WEIGHT AS A PROPORTION OF LIVEWEIGHT

> *"It is the highest creatures that take the longest to mature, and are the most helpless during their immaturity." George Bernard Shaw, Back to Methuselah 1921.*
>
> *"I am indebted to Prof. D.M.S. Watson, F.R.S., for drawing my attention to the remarkable fact that, in beef animals, the muscular tissue is about one third of the live weight, irrespective of their fatness." Callow, E.H. (1944)*

This most important characteristic of meat animals has received scant attention and yet it offers what is perhaps the most important simple link between the commercial value of the live animal and the commercial value of the carcase. With muscle becoming increasingly *the* sought-after tissue, whilst fat and bone are increasingly regarded as unwanted, it is indeed surprising that so little effort has been placed into obtaining an understanding of this relationship between muscle weight and liveweight.

Callow (1944) first brought to notice the relative constancy of muscle to liveweight in cattle when he reported advice from Professor D.M.S. Watson in 1942 that one third of liveweight was muscle. McClelland *et al.* (1976), using a very diverse group of sheep breeds, showed that their muscle proportions varied very little from 28% of fleece-free empty body weight. Thonney *et al.* (1986b), with similar but extended material, showed muscle to be 30% of fleece-free empty body weight or 24% of shorn liveweight.

Truscott (1980), reporting the dissection of Hereford and Friesian steers between 181 and 623 days, stated "Carcase muscle as a proportion of liveweight appeared to be almost invariant with breed or age being very close to 31 per cent at all ages. Truscott *et al.* (1976) had found a similar result when comparing Angus and Friesian steers."

Understandably there are differences in species which are mobile at birth and those which are not, and George Bernard Shaw's quote, which is used as an introduction to this section, is probably based on this anatomical phenomenon. Human babies contain about 20% of muscle and are notoriously immobile, but increase to above 40% as time goes by (Appendix 3 Figure 1.). In the Macaca, Grand (1983a) showed that muscle rose from 24% of body weight at birth to 40% when 6 months old. Very young kangaroos similarly have less muscle than adults (Hopwood, 1976) (Appendix 3 Fig 2.). All of our conventional meat-producing animals need to be mobile from birth and, hence, at birth have well-developed musculature which can be a barrier in some species to enthusiastic selection for more muscular animals (Butterfield, 1985), as increased muscle in the full-term foetus is an invitation to dystokia. It is difficult to understand why one common domestic animal, the goat, should differ in this characteristic of almost invariant muscle proportion of liveweight. But Wilson (1958b) reported that East African Dwarf goats achieved "a large increase in the proportion of muscle (from 32 to 46%)". No data are available on "modern" goats.

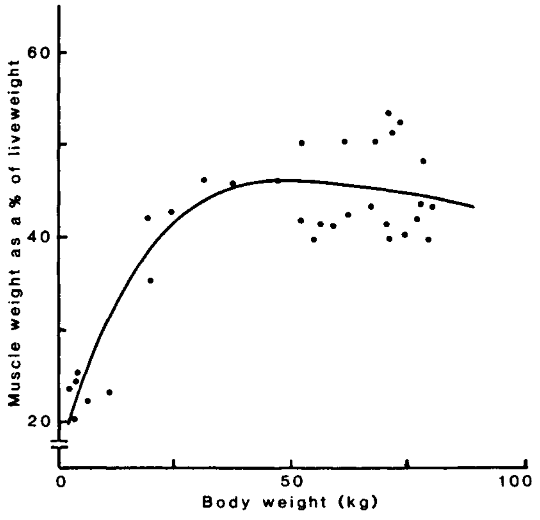


Figure 1
Muscle weight as a percentage of body weight in growing human beings. (Data from Malina, 1969.)

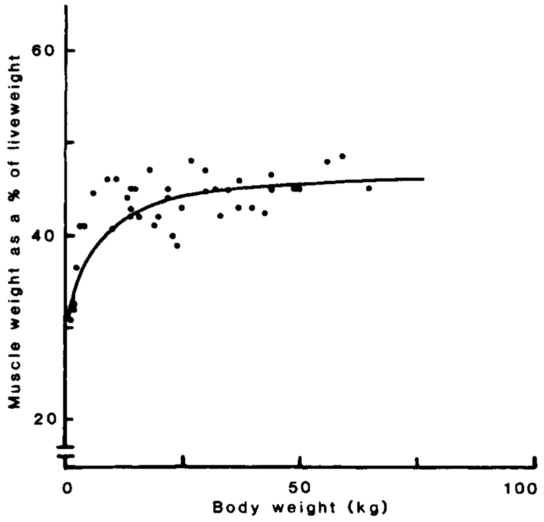


Figure 2
Muscle weight as a percentage of body weight in growing kangaroos. (Data from Hopwood, 1976.)

There is little information on the generalized atrophy of muscle after maturity in our meat animals, but the evidence for humans indicates that they have a slow loss of strength from about 30 years and a loss of fibres and size from 50 years (Sinclair, 1973). Data from human females (Appendix 3 Figure 1) shows the decline from around 50 kg body weight. The relative contribution of muscular atrophy and obesity is not clear, although both probably play a part in some individuals.

Animals within a species do differ in their proportion of muscle as shown by Berg and Shahin (1983) who reported mean values of 33% for Herefords, 39% for synthetics (hybrids) and 41% for double-muscled animals. They also reported extreme values of up to 50% for individual double-muscled animals. Just how far normal physiological function can be maintained as animals approach the upper limits of such a huge difference is yet to be determined, but it certainly seems to be one of the more fruitful areas for investigation.

In Appendix 3 Figure 3 the relationship between muscle weight and liveweight is shown for a variety of species which have been reported in the literature. There are some differences in the definition of liveweight in some of the species shown and so the actual values are not critically comparative, however, it is clear that there are species specific values and that these persist throughout life from soon after birth to maturity at least in the *conventional* meat-producing animals, with the possible exception of the goat. There is also an interesting illustration in this figure in that there is a clear depression of muscle weight as a percentage of liveweight as a result of castration in pigs; and in this case all the pig data are comparable as they are all derived from the same study of Walstra (1980).

In this book we have not produced any new evidence on the importance of this characteristic but hopefully some of the information presented may demonstrate principles which will lead to its study on a sound basis.

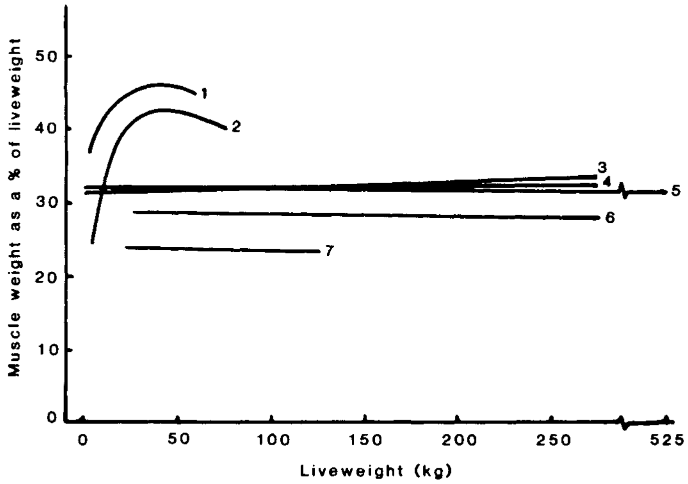


Figure 3
Relationship between muscle weight and live weight of several species during growth. Based on data from:
1. Kangaroos (Hopwood, 1976) 1–65 kg
2. Humans (Malina, 1969) 0.5–73 kg
3. Sows (Walstra, 1980) 1–296 kg
4. Boars (Walstra, 1980) 1.5–297 kg
5. Cattle (Butterfield, 1963) 21–514 kg
6. Pig castrates (Walstra, 1980) 26–296 kg
7. Large and small Merino rams (Butterfield *et al.*, 1983) 20–127 kg

MUSCLE:BONE RATIO

Whereas the previous subject appears to be a future basis of comparison of live animals, it may be that muscle:bone ratio is one of the two most important measures of carcase excellence.

The first significant publication on muscle:bone ratio was that in cattle by Hankins, Knapp and Phillips (1943) who displayed the range of this ratio in two types of Shorthorn cattle.

Although the basis on which they made their comparison may be disputed in light of new knowledge, there was little doubt that different animals had different muscle:bone ratios and maybe here is an index of carcase excellence which could be measured with certainty in the carcase and maybe in the future in live animals.

The major problem with this measure of carcase desirability is that the two components can be measured with accuracy only by expensive and time-consuming methods and so, although there have been attempts from time to time to elevate it to a position of importance as an index of carcase composition (Berg and Butterfield, 1966), little seems to have penetrated to the commercial or scientific level. Kempster and Cuthbertson (1977) showed significant differences in muscle:bone ratio between breed types of sheep ranging from Mountain sheep to Southdowns and the values ranged from 3.37 to 3.76 so that, although not large, the differences would appear to be worth further study.

As reported by Berg and Butterfield (1976), Berg and Mukhoty (unpublished) found breed differences in cattle in rate of muscle growth relative to that of bone in data where comparisons of growth coefficients of muscle had revealed no significant difference. They concluded that the use of bone as a baseline 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." Nevertheless, for commercial purposes comparison of muscle:bone ratio at equal carcase weight, or equal fatness or equal muscle plus bone weight, may be more applicable. It is possible that the ratio may be shown to have a maturing pattern which, by its similarity or diversity across animal types, can be of value in comparisons.

MUSCLE:FAT RATIO

Although the ratio of muscle to fat is undoubtedly the most important quantitative assessment which is made by the housewife, it has received scant attention by the scientific community. It tends to be submerged in the general assessment of the fatness of carcases. Kirton (pers comm.) advises that New Zealand workers are now highlighting muscle:fat ratio because of the tendency for muscle:fat ratio to be lower in animals with higher muscle:bone ratio, as in Fourie *et al.* (1970) and Kirton, Woods and Duganzick (1983).

MUSCLE-WEIGHT DISTRIBUTION

"I would rather make a rancher out of a boy off the streets of New York or Tokyo than a boy raised on a conventional ranch." Tom Lasater. quoted by Lasater (1972).

Due primarily to the belief that the expert judges of the past were able to determine fine differences in the relative size of muscle groups, there grew up a belief that such differences were of major importance to those attempting to "improve" various meat animals. Considerable evidence was gathered in the U.S.A. from cattle as far back as 1893 that such differences were probably small, as little variation had been shown in the yield of high-priced cuts between beef and dairy cattle (Wilson and Curtis, 1893), between comprest and conventional Herefords (Willey *et al.*, 1951; Stonaker *et al.*, 1952) and between various British breeds and Brahman crosses (Carroll *et al.*, 1955; Riggs and Maddox, 1955; Butler *et al.*, 1956a; Carpenter *et al.*, 1961). One of the major reasons that few saw these results as indicating a degree of constancy of muscle-weight distribution was, probably, that they had been determined by the assessment of commercial cuts of beef and it was appreciated that a confusing amount of fat was included in the data. Also, there was a long history of conditioning to believe that it was within the power of man to change the proportionate weight of body parts as Bakewell (1725-1795) is credited with the statement:" You can get beasts to weigh where you want them to weigh" (Smith, 1975), and so we had yet another example of Cantor's Law of Conservation of Ignorance: "A false conclusion once arrived at and widely accepted is not easily dislodged and the less it is understood the more tenaciously it is held" (Heusner, 1985).

It was not until Daintree Walker in New Zealand commenced studying individual muscle weights that the possibility existed to determine the full story of muscle-weight distribution. Numerous studies were to follow which have caused far more debate than the problem deserved. However, the firmly-held belief regarding the importance of the characteristic resulted in a long haul to the general acceptance of the idea that stock breeders could be much better occupied than in trying to improve this characteristic, which has displayed a remarkable resistance to man's attempts to alter it to the benefit of the butcher.

There have also been many studies which have reported the findings on muscle-weight distribution in only an approximate way and these have resulted in some confusion. For this reason the current knowledge, as it is believed to be across the species, is restated here:

The first anatomical study of breed differences in cattle was that reported by Butterfield (1963, 1964a,b) in which a most heterogeneous collection of animals was used. Despite the limitations imposed by the available cattle, it was clear that there existed a high degree of "anatomical harmony" (Boccard, 1978).

Since the early sixties a large number of cattle have been dissected by a range of workers in many countries and it is not disputed that there is only small genetic variation of muscle-weight distribution between breeds or between individual animals within breeds, provided we confine comparison to single sexes of normal cattle and make comparisons at the same stage of maturity. As will have become clear in this monograph, some of the past comparisons obviously were confounded by genetic difference in mature size. This was particularly so in comparisons of entire males for reasons discussed in Chapter 3.

There was considerable debate at the conclusion of the EEC Conference at Ghent in 1977 on the need, or otherwise, for further research of muscle-weight distribution based on whether or not there was sufficient genetic variation in cattle to make it a fruitful line of endeavour. There was, of course, a range of opinions, however, the statement by Kempster that "... here we are talking about a character such as lean distribution which, in overall economic terms, is one sixteenth as important as fat distribution, and one fourth as important as lean/bone ratio ..." did a great deal to place this characteristic in its correct perspective.

The current state of knowledge is that:

1. Within "normal" animals (i.e. excluding muscular hypertrophied animals) there is:
   (a) Only very small variation in muscle-weight distribution of animals of the same sex, fatness and stage of maturity of the musculature.
   (b) A difference between entire males and other sexes which increases as the musculature approaches maturity.
   (c) Change in muscle-weight distribution which is maximal in early growth in all sexes, becomes minimal during adolescence in all sexes and considerable in the adult entire male. There are minor changes in the adult castrate which are faint replications of the changes in the adult entire male and probably not any changes in the adult female unless induced by work in the abdominal wall by pregnancy.
   (d) Muscle-weight distribution is affected by the level of fatness of animals (Butterfield, 1964b) in a manner which is not understood (Johnson, Pryor and Butterfield, 1973)
2. In muscular-hypertrophied animals there is a shift of muscle weight into the more fleshy muscles particularly of the proximal limbs (Vissac, Menissier and Perreau,1971; Hanset and Ansay, 1972; Shahin, 1985).

Following the initial work in cattle, the "anatomical harmony" of muscle-weight distribution has been demonstrated within other species and particularly pigs (Richmond and Berg, 1971b; Davies, 1974a,b) and sheep (Fourie, 1965; Fourie et al 1970; Lohse, 1971; Jury et al, 1977). As for sheep, the information in Chapter 5 supports the very practical assessment made by Kempster and Cuthbertson (1977) that the largest difference in proportion of joint weights seen in their survey of British sheep resulted in a 1% difference in carcase value of lambs. Some of this small difference may have been due to other factors although the coefficient of variation of joint weight distribution and muscle-weight distribution were the same.

In this monograph a considerable amount of attention is given to the factors involved in muscle-weight distribution in sheep so that principles can be devised to provide the appropriate basis for comparisons of this characteristic of animals of any species, sex or stage of maturity.

FAT PARTITIONING

"Life is cut to allow for growth . . . one may vigorously put on weight before one fills it out entirely". (Ranier Maria Rilke, letter to Alfred Walther von Heymel, Oct. 12. 1941.)

This characteristic is one of considerable importance for a variety of reasons, both quantitative and qualitative. As fat is the most variable of carcase tissues it is the logical target for measurements aimed at describing the differences in carcases. The value of such measurements as an index of carcase composition depend on a knowledge of the factors likely to affect the proportion of total fat to be found in each fat partition. "If there is a poor genetic relationship between the growth of different depots selection based on one depot is unlikely to provide an effective reduction in other fat depots." (Kempster, 1980). Their value also depends on knowledge that the relationship between fat score and subcutaneous fat content (weight) is dependent on the weight of the carcase (or animal). As pointed out by Kempster this knowledge can be used to understand the need for both weight and fat thickness measures to be known when placing relative values on carcases.

Unfortunately anatomists and other body composition workers find the dissection of fat a psychologically unrewarding pursuit and accordingly during the 1960's most studies tended to concentrate on the anatomically more discrete and interesting muscles and bones. More recently, as knowledge of fat growth has become more important in line with its reduced popularity in human diets, there has been a considerable input into fat studies. This trend has been associated with the tendency for more studies to be based in large well-funded institutions where much of the dissection is done by professional butchers.

Among the most significant studies in sheep are those of Kirton *et al.* (1972); Warren (1974); Kempster and Cuthbertson (1977); Kempster (1980); Butler-Hogg and Wood (1982); Wood (1982); Butler-Hogg (1984); Thompson *et al.* (1985b); and Butler-Hogg and Johnsson (1986).

It is not only the differential deposition of fat in the carcase depots which is of importance but the proportion of fat in the body cavity (non-carcase) depots relative to each other and particularly relative to the total carcase fat. This partitioning also is of vital physiological as well as meat industry importance. Several studies (e.g. Wright and Russel, 1984) have reported on the correlation between the proportion of fat laid down in the body cavity depots and the overall productive demands in the form of milk or multiparity.

Studies of fat partitioning can be soundly based only if the changing proportions within the total growth span are understood so that principles can be developed on which to base assessment. However, it will take extensive study of very large numbers of animals to fully understand the phenomena involved as the individual variation is high and the precision of dissection less acute than in other body systems.

The study of the partitioning and distribution of fat within the body appears to have become, to some degree, over-complicated by the division of the body fat into many small partitions and depots. It is contended that the really important issues in fat studies should be the proportionate growth of carcase versus non-carcase fat and the growth of subcutaneous fat versus intermuscular fat. It is really of little importance commercially, although of admitted biological interest, whether internal fat is found in the omentum or the mesentery or surrounding the kidney. Although anatomically the term "non-carcase" fat is somewhat offensive it leaves no doubt of its commercial relevance.

It is important to differentiate between the growth of subcutaneous and intermuscular fat for several reasons. Firstly, it has been shown that there are factors such as sex which have a marked influence on their relative growth. Commercially they are very different in their trimability as subcutaneous fat can often be reduced with little effect on the integrity of the meat; whereas intermuscular fat is almost always difficult to trim without distortion of the meat. This will be of variable importance according to the nature of the trade. Subcutaneous fat is regularly used as an index of the total fatness of the carcase and it is of considerable importance to understand if measures of subcutaneous fat can be used across breeds and sexes and across sheep fed in various ways. In some circumstances subcutaneous fat acts as a protective wrapper to the underlying meat preventing drying and discolouration during storage.

FAT WEIGHT DISTRIBUTION

In studies of dissectible fat this term is confined to the subcutaneous and intermuscular partitions, whereas in studies involving chemical analysis the intramuscular fat and even the intraosseus fat may also be involved.

Individual animals distribute their fat differently but in general the patterns of distribution tend to be similar within a breed. The variation in fat weight distribution is largely associated with the shape of the underlying tissues (Riley, 1971). Flat muscle profiles and bony prominences tend to result in uneven fat distribution, whereas rounded, bulging muscular outlines and the consequently buried bony prominences, lead to even distribution of fat.

The degree of variation of fat distribution is particularly important, and probably greatest, in the subcutaneous partition for a variety of reasons. Just as differences of fat partitioning can effect the value of fat measurements in the subcutaneous depot as indices of total fat, so can the variation from site to site within the subcutaneous depot. As put by Kempster and Cuthbertson (1977) "The accuracy of measures of subcutaneous fat development . . . as predictors of total carcass fat content depends on the constancy of fat distribution."

Because the subcutaneous fat is physically constrained by only the skin, it is free to develop in a variety of ways whereas the intermuscular depot is, to a large extent, moulded by the relatively more restrictive musculature, and is, therefore, unlikely to vary as much as the subcutaneous partition.

As with other criteria, it is necessary to understand the changes which take place in the fat depots throughout the growth process if we are to understand the variations seen.

VISCERAL PROPORTIONS

The viscera, both solid and hollow, comprise along with contents, a considerable proportion of the living animal and it is only by understanding the changes which take place in the viscera that we can fully understand the changes in the carcase tissues.

Studies of viscera are commonly related to the whole animal and so, for example, heart weight is expressed as a proportion of body weight. This seems to be a sensible procedure as the function of each visceral organ is likely to be correlated with that of the total body. It is also possible that certain organs may be more closely functionally linked to other organs than to the total animal and so it is worth exploring, for example, the relationship between the growth of the liver and that of the digestive tract. Kirton *et al.* (1972) presented a considerable amount of data from Romney, Southdown and their crossbreds and along with data on Merinos and Dorset Horns in Australian studies there is now a useful body of information.

The influence of visceral proportions on dressing percentage has been largely ignored in the past yet it seems likely that the emphasis previously placed on increasing fatness as a cause of increased dressing percentage should be shared with the declining proportions of visceral organs in sheep.

Watson (1943) pointed out that in cattle "factors other than the degree of fatness" influenced dressing percentage. It is apparent that the proportion of the whole body represented by the viscera has a marked affect on changes in dressing percentage.

APPENDIX 4

THE DEVELOPMENT AND USE OF THE RELATIVE MATURING RATE COEFFICIENT 'Q'

"Non-additivity of two or more allometric equations, which make it conceptually illogical and methodologically difficult. Is some new additive form possible?" (TAYLOR, 1978)

In 1976 a Sydney group set out to plan an experiment "To determine the effect of mature size on the growth patterns of body components of sheep" and, in order to achieve this aim, it was necessary to decide on the most appropriate data and most appropriate method or methods of analysis of these data. It was decided that we needed to know the composition of mature animals and to analyse the progress to maturity in terms of units of mature weights of both the whole animal and its component anatomical structures.

The first step was to accumulate appropriate data and this was achieved by the serial slaughter of animals from 18 kg liveweight up to maturity, all grown on *ad lib* feeding of the same high quality pelleted ration. The period from birth to 18 kg liveweight was purposely avoided as previous work (Butterfield and Berg 1966a, b; Lohse *et al.*, 1971) had shown that, during this period, changes occurred, particularly in the musculature, which were unique to that period, and which seemed to be governed by priorities not closely related to the maturing process. Animal slaughter was scattered along the growth curve at intervals of 6 kg and with the available numbers of sheep this was thought to be likely to leave several sheep which would not ever reach their target weights. This was a process of great uncertainty as there was not available any one estimate of the likely mature size, which could be reliably assumed to be better than the many other available estimates which varied widely. As it turned out an estimate by Dr. Helen Newton-Turner was the closest. This period of uncertainty in undertaking such an experiment was well described by McClelland, Bonaiti and Taylor (1976): "There is also the impossibility of having an accurately observed mature weight in advance, and hence a persisting feeling of lack of precision in the conduct of the experiment."

Several mature sheep were required to fix, from mean values, the best estimate of mature composition which was to form the basis of all our analyses. Having achieved these values, all data were converted to proportions of these mature values, e.g., the liveweight of each sheep slaughtered was converted to a proportion of mature liveweight; the weight of each extensor carpi radialis muscle dissected was converted to a proportion of the weight of the mature extensor carpi radialis muscle; the weight of each liver dissected was converted to a proportion of mature liver weight. These proportions were then used for simple plotting of the progress to maturity of the structures (see Figure 1.b.1., page 5). Where appropriate, these plots were on the basis of the progress to maturity of liveweight, e.g., total systems, such as the musculature or skeleton; where appropriate they were on the basis of a total system, e.g., individual muscle weights as proportions of their mature individual muscle weights were plotted against total muscle weight as proportions of mature total muscle weight, individual bone proportions against the total skeleton proportions. Although aware of Taylor's (1978) statement that "A remarkable degree of understanding of quantitative data on growth and development can be achieved by simple graphical representation", it was necessary to find some simple statistical value to describe the mass of information available for each structure and so, having achieved these plots, the biometrical advice of Dr. David Griffiths was sought to determine the statistical method best able to describe the data and hopefully be appropriate for all or most of our anatomical structures. A direct quote from Butterfield *et al.* (1983a) describes the evolution of the maturity coefficient from this point:

> "Dissected weights of body components and shorn full live weight at slaughter were each expressed as proportions of their own weight in the mature rams . . . (i.e. as a fraction generally between 0 and 1). The development of body components to maturity was then assessed relative to the development of shorn full live weight to maturity, by fitting a quadratic curve, constrained to pass through the origin (0,0) and the point (1,1). This was consistent with an animal whose components are of zero size when the animal is zero size and whose components are mature when the whole animal is mature.
>
> "The two constraints on the quadratic equation $y = p + qx + rx^2$ imply $p = 0$ and $r = 1{-}q$. (Here $y = I/I_m$ and $x = T/T_m$, where I is the weight of the individual component, I_m is the mature weight of that component, T is shorn full live weight and T_m is the mature shorn full live weight).
>
> "The quadratic relationship may be thus rewritten
>
> $y = qx + (1{-}q)x^2$
>
> "For statistical analysis it is convenient to transform to $y^1 = y - x^2$ and $x^1 = x - x^2$ so that the relationship becomes $y^1 = qx^1$: a straight line through the origin for the transformed variables. The error structure of the response variable is unchanged by the transformation.
>
> "When q equals one, the relationship becomes $y = x$ and describes structures which mature at the same rate as the whole body. When q is greater than one, it represents an early maturing tissue, and when it is less than one, it represents a late maturing tissue, relative to the maturity of shorn full live weight."

Thus, we now had a method of simple description of the maturing patterns of almost all of our dissected structures from about 20% mature up to maturity (see Figure 1.b.2., p. 5). Only three structures could not be adequately described by our quadratic relationship and these were the brain and eyes which were already too far advanced towards their mature weights, and the testes which, by going from a low growth impetus to a high, and then back to low, defied description by a single parameter 'q'.

The answer to Taylor's (1978) question with which this chapter began is: Yes, because 'q' values are additive, "i.e., a q value can be calculated for the sum of a number of components from the sum of the individual q values weighted according to the proportion of the mature weight of the individual components relative to the mature weight of the sum of the components." (Butterfield *et al.* 1983a), or simply weighted by actual weights of mature tissues. (Appendix 4 Table 1.)

Maturing patterns and 'q' values are used extensively in this book and in the series of papers by Butterfield *et al.* (1983 and 1984); Thompson *et al.* (1985); Perry *et al.* (1987) and Thonney *et al.* (1986). The survival of the 'q' value as a useful tool will depend on the degree of its acceptance by other workers and on the extent of research based on knowledge of mature size and composition.

Thonney *et al.* (1986b) pointed out that there are mathematical problems of highly intractable equations in attempting to express compositional maturities of one characteristic solely as a function of another using 'q' values. They summed up the relative properties of maturity and growth coefficients as "The price paid for additivity in *q* is the inability to express relative growth easily whereas the price paid for expressing relative growth easily in terms of the allometric equation is non-additivity."

APPENDIX 4 – TABLE 1 Demonstrating the additivity of the maturity coefficient 'q'

Example 1

Structure	'q'		Percentage of mature carcase weight		Weighted value
Muscle	1.3	x	50	=	65.0
Bone	1.4	x	15	=	21.0
Carcase Fat	0.1	x	35	=	3.5
			100 (A)		89.5 (B)

$$\text{'q' for carcase} = \frac{(B)}{(A)} = \frac{\text{Total weighted value}}{100} = \frac{89.5}{100} = 0.9$$

Example 2

Structure	'q'		Weight (kg)		Weighted value
Muscle	1.3	x	25.0	=	32.5
Bone	1.4	x	7.5	=	10.5
Fat	0.1	x	17.5	=	1.75
			50.0 (A)		44.75 (B)

$$\text{'q' for carcase } \frac{(B)}{(A)} = \frac{\text{Total Weighted value}}{\text{Total Weight}} = \frac{44.75}{50} = 0.9$$

Just as Huxley's coefficients ('b' values) can be used to indicate changing body composition (Seebeck, 1978) so can 'q' values:

i. A 'q' value greater than 1.0 means a lesser rate of growth, i.e., "low impetus" relative to that of the whole animal and therefore a declining proportion of the whole.
ii. A 'q' value less than one means a greater rate of growth, i.e., "high impetus" relative to that of the whole animal and therefore an increasing proportion of the whole.
iii. A 'q' value not different from 1.0 means that the structure and the whole are growing at the same relative rate, i.e., "average impetus" and that therefore the proportion of the part to the whole remains unchanged.

As pointed out in the initial paper of Butterfield *et al.* (1983a) "The concept of examining growth of tissues in relation to their progress towards maturity as developed in this paper does not have to rely on the particular functional form (quadratic), statistical model (additive independent errors with homogeneous variances), or the consequent method of statistical analysis (unweighted least squares) adopted in this paper. Broadly similar conclusions would be obtained from alternative models with different functional form (e.g., allometric) and error structure, (e.g., multiplicative which would suggest a least squares analysis on the logarithm of the weights). The allometric analogue of the constrained quadratic $y = qx + (1-q)x^2$ is $y = x^b$. This is identical to the quadratic when $b = q = 1$, or when $b = 2$, $q = 0$. For q values over the range of 0 to 2 (which would encompass the likely range of most values for body tissues), appropriate values of 'b' can be chosen (or estimated from data) to describe a similar curve to the quadratic".

A further value of the maturity coefficient 'q' is that it is capable of describing the relative growth of parts of the body which achieve a weight greater than their mature weight and then decline, such as some parts of the intestinal tract. The maturing pattern of such a structure, which will have a 'q' value greater than 2.0, can be seen in Figures 1.f.5. and 1.f.7., p. 30. It is in the description of the growth of these structures that the maturity coefficient is unique as it can efficiently describe such phenomena with a single 'q', whereas this is not possible with allometric coefficients. Whereas Huxley's coefficient cannot describe such growth phenonomena, it can describe, for example, the pathway of relative growth of muscle:bone ratio, which is initially an increasing value which almost plateaus as shown in Figure 1.b.5., page 7.

Appendix 4 Figure 1 demonstrates the unsuitability of the coefficient 'q' to describe the pathway to maturity of muscle:bone ratio for, as will be obvious, the data points early in the growth all fall above the best fitting 'q' line whereas later points all fall below. In contrast, the best fitting line based on Huxley's 'b' value describes the pathway of the points quite accurately.

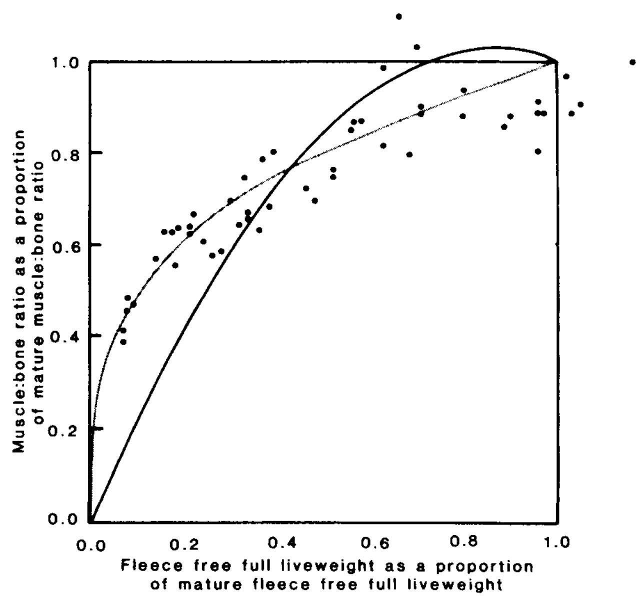


Figure 1
Progress to maturity of muscle:bone ratio of Merino ewes, demonstrating the poor fit of a quadratic based on Butterfield's 'q' (black) and the good fit of the line based on Huxley's 'b'. (Data from Thompson 1983.)

The use of maturity coefficients and maturing patterns in the estimation of composition at any given weight or any given stage of maturity

i. *Prediction of composition at any given weight*

The composition at any given weight can be predicted by using the formula of Butterfield *et al.* (1983a):

$I/T = q\ I_m/T_m + (1-q)\ (I_m/T_m{}^2)\ T.,$

where: I = weight of component,
T = weight of the whole,
I/T = proportional composition,
q = estimate of q,
I_m = mature weight of component,
T_m = mature weight of the whole,
and I_m/T_m = proportional composition at maturity.

Therefore, variation between two groups of animals in their composition at any given weight may be due to either:

a. different q values, or
b. different I_m and/or T_m or both.

The MAGNITUDE of the slope of this linear equation, i.e. $((1\text{-}q)(I_m/T^2))$ is a function of q, I_m and T_m, although the sign of the slope is determined solely by q, i.e, if q is greater than 1.0, then the slope of the equation is negative and the proportion of a component (I/T) will decrease as T increases.

Similarly, if q is less than 1.0, then the slope of the equation will be positive and the proportion of the component (I/T) will increase as T increases.

Further, if q is equal to 1.0 then the slope of equation will be zero and the proportion of the component will remain constant as T increases.

ii. *Prediction of composition at a given stage of maturity*

The composition at the given proportion of mature weight can be predicted by using the formula:

$I/T = q\ I_m/T_m + (1-q)(I_m/T_m)T/T_m$:
where: I = weight of component,
T = weight of the whole,
I/T = proportional composition,
q = estimate of q,
I_m = mature weight of the component,
T_m = mature weight of the whole,
I_m/T_m = proportional composition at maturity,
and T/T_m = given proportion of maturity.

The proportional composition at any given proportion of maturity will be influenced by 'q' and the mature size of the component (I_m) and/or the mature size of the whole (T_m).

Description of early postnatal growth

It was known that some structures, particularly individual muscles, had very different relative growth impetus in the early postnatal period to that adopted in later life (Lohse, 1971; Lohse *et al.*, 1971; Fourie, 1965), and it was for this reason that the maturity experiment of Butterfield *et al.* (1983a) did not embrace the early postnatal period. Therefore, to obtain the complete story of postnatal growth of Merino rams for this monograph, it was necessary to draw on the data of the rams in Lohse's study.

Simple plots were made of weight of a wide selection of structures, using data from both Lohse's ram lambs and those of Butterfield *et al.* to assess the continuity or otherwise of the patterns of growth from the periods before and after 20% mature. From these plots it was apparent that only in some structures did significant deviation occur during early postnatal life from the overall maturing pattern. These deviations, which were mainly intrinsic to the musculature, warranted the calculation of separate coefficients for this period. There was a marked deviation in fat, due to low plane nutrition of Lohse's pasture-reared lambs. A study of lambs on high plane of nutrition from birth, a rare state in Australian Merinos, is needed for the full fat story to be written.

The method of calculation of coefficients (designated "q*") in the period from birth, at about 4 kg liveweight up to 20% mature for the purpose of obtaining complete patterns for the structures of a 100 kg mature ram in Chapter 1, was as follows:

Using Lohse's data a 'q' value (q*) was calculated for a quadratic constrained to pass through (0,0) and the point on the original quadratic below which there was no data from the Butterfield *et al.* study. This was where liveweight and total muscle weight were approximately 20% mature ($T/T_m = 0.20$), i.e., at an x value (T/T_m), designated x_{PN}, equal to 0.20.

The value q* reflects the compositional change as the animal grows but relative to its composition when only partially mature rather than its composition at maturity. During this early postnatal growth phase a modified prediction formula may be used to estimate composition at a given stage of maturity:

$I/T = q^*\ I_m/T_m\ y_{PN}/x_{PN} + (1-q^*)\ y_{PN}/x^2_{PN}\ I_m/T_m \cdot T/T_m$

where y_{PN} is the proportional maturity (I/I_m) of the individual muscle corresponding to total muscle maturity of x_{PN}.

The relationship between 'q' and 'q*' is shown in Appendix 4 Figure 2.

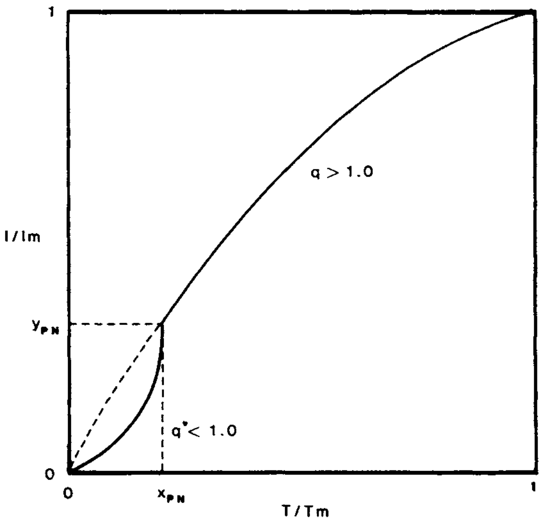


Figure 2
The method of determining a 'q*' value for the period covering birth to about 20% mature.

APPENDIX 5 – TABLE 1 The 'q*' values from birth to 20% mature for "Standard Muscle Groups" and the 'q' values from 20% mature to maturity for individual muscles of Merino rams of 100 kg mature liveweight with the weight and proportions of total muscle weight at birth, 20% of mature total muscle weight and at maturity

Muscle	0–20% maturity 'q*'	20–100% maturity 'q'	Weight (g) birth	Weight (g) 20% of mature total muscle weight	Weight (g) maturity	% of total muscle weight birth	% of total muscle weight 20% mature total muscle weight	% of total muscle weight maturity
GROUP 1. Muscles of the proximal hind limb								
M. tensor fasciae latae		1.51[a]	9.2	55.9	198.4	0.87	1.24	0.88
M. biceps femoris		1.31[a]	46.0	243.7	976.4	4.34	5.40	4.33
M. gluteus medius		1.16[a]	23.1	141.9	629.1	2.18	3.15	2.79
M. vastus lateralis		1.17[a]	24.7	116.8	514.1	2.33	2.59	2.28
M. gluteus accessorius		1.47[a]	5.1	27.3	99.2	0.48	0.61	0.44
M. rectus femoris		1.21[a]	23.6	112.7	482.6	2.23	2.50	2.14
M. semitendinosus		1.20[a]	16.3	93.1	401.4	1.54	2.06	1.78
M. gracilis		1.00	8.5	38.8	193.9	0.80	0.86	0.86
M. semimembranosus		1.17[a]	40.6	209.0	920.0	3.83	4.63	4.08
M. adductor femoris		1.29[a]	18.4	90.0	365.3	1.74	2.00	1.62
M. pectineus		1.21[a]	5.7	22.1	94.7	0.54	0.49	0.42
M. sartorius		0.95	2.9	7.8	40.6	0.27	0.17	0.18
M. quadratus femoris		1.54[a]	1.0	1.1	3.5	0.10	0.02	0.06
Mm. obturatorii externus et internus		1.55[a]	5.5	28.6	99.2	0.52	0.63	0.44
M. vastus medialis		1.15[a]	10.3	39.4	175.9	0.97	0.87	0.78
M. articularis genu		1.60[a]	-	6.7	22.6		0.15	0.10
M. iliacus		1.21[a]	6.8	31.6	135.3	0.64	0.70	0.60
M. gluteus profundus		1.45[a]	3.6	18.4	67.7	0.34	0.41	0.30
M. gemellus		1.71[a]		2.5	7.89		0.05	0.04
M. vastus intermedius		1.35[a]	23.1	43.3	169.1	2.18	0.96	0.75
Standard Muscle Group 1	0.77	1.23[a]	261.40	1330.0	5,617	24.66	29.49	24.91
GROUP 2. Muscles of the distal hind leg								
M. gastrocnemius et m. soleus		1.46[a]	24.7	91.3	333.74	2.33	2.02	1.48
Mm. extensors		1.10	8.7	32.6	151.09	0.82	0.72	0.67
M. peroneus longus		1.41[a]	2.5	9.3	34.95	0.24	0.21	0.16
M. extensor digitorum lateralis		1.91[a]	3.8	63.14	0.36	0.28		
M. tibialis cranialis		1.33[a]	2.8	8.6	33.83	0.26	0.19	0.15
M. tibialis caudalis		1.21[a]	1.3	6.9	29.32	0.12	0.15	0.13
M. popliteus		1.39[a]	4.5	13.6	51.84	0.42	0.30	0.23
M. flexor digitorum longus		0.78	1.9	4.8	29.32	0.18	0.11	0.13
M. flexor digitorum superficialis		1.70[a]	7.3	33.8	108.24	0.69	0.75	0.48
M. flexor hallucis longus		1.32[a]		36.3			0.80	
Standard Muscle Group 2	1.11	1.30[a]	64.6	258.4	980.93	6.09	5.73	4.35
GROUP 3. Muscles surrounding spinal column								
M. psoas major		1.45[a]	13.6	70.5	259.33	1.28	1.56	1.15
M. quadratus lumborum		1.01	2.9	17.3	85.69	0.27	0.38	0.38
M. iliocastalis thoracis		0.75[b]		20.9	130.79		0.46	0.58
M. longissimus thoracis et lumborum		1.19[a]	72.0	466.6	2024.99	7.03	10.34	8.98
M. multifidus thoracis et lumborum		1.67[a]	13.5	79.0	257.07	1.32	1.75	1.14
M. longissimus cervicis		0.74	3.5	20.4	128.54	0.33	0.45	0.57
M. spinalis cervicis et thoracis		0.75[b]		71.4	446.49		1.58	1.98
M. psoas minor		1.57[a]	5.6	32.2	110.50	0.53	0.71	0.49
Standard Muscle Group 3	0.72	1.15[a]	145.3	785.5	3506.53	13.71	17.42	15.55
GROUP 4. Muscles of the abdominal wall								
M. cutaneus trunci		0.75[b]	26.9	93.8	586.3	2.54	2.08	2.60
M. serratus dorsalis caudalis		0.94	1.3	9.0	47.36	0.12	0.20	0.21
M. obliquus externus abdominis		1.01	14.1	87.7	435.22	1.33	1.95	1.93
M. retractor costae		1.21		11.1	47.36		0.25	0.21
M. obliquus internus abdominis		0.87	8.2	52.9	295.41	0.77	1.17	1.31
M. transversus abdominis		0.84	11.5	66.5	381.10	1.08	1.47	1.69
M. rectus abdominis		0.87	15.0	101.8	568.26	1.41	2.26	2.52
Standard Muscle Group 4	0.58	0.92	76.9	445.4	2379.03	7.25	9.87	10.55

APPENDIX 5 – TABLE 1 (continued)

Muscle	0–20% maturity 'q*'	20–100% maturity 'q'	Weight (g)			% of total muscle weight		
			birth	20% of mature total muscle weight	maturity	birth	20% mature total muscle weight	maturity
GROUP 5. Muscles of the proximal forelimb								
M. deltoideus		0.86	5.5	21.6	121.77	0.52	0.48	0.54
M. infraspinatus		1.10	21.2	93.5	432.96	2.00	2.07	1.92
M. triceps brachii (Caput laterale)		1.19[a]	11.6	38.5	166.87	1.09	0.85	0.74
M. teres minor		0.64[b]	2.2	6.1	42.85	0.21	0.14	0.19
M. triceps brachii (Caput longum)		1.13	31.1	118.5	536.69	2.93	2.63	2.38
M. tensor fasciae antebrachii		0.69[b]	2.5	11.5	76.67	0.24	0.26	0.34
M. supraspinatus		1.15[a]	24.3	95.5	426.20	2.29	2.12	1.89
M. biceps brachii		0.84[b]	6.9	22.4	128.54	0.65	0.50	0.57
M. teres major		1.11	5.2	24.5	112.75	0.49	0.54	0.50
M. brachialis		1.44[a]	7.1	22.0	81.18	0.67	0.39	0.36
M. coracobrachialis		1.66[a]	2.2	11.0	36.08	0.21	0.24	0.16
		1.28[a]		8.8			0.20	
M. subscapularis		0.96	11.1	45.4	234.52	1.05	1.01	1.04
		1.42a						
M. triceps brachii (Caput mediale)		2.32[a]	4.03	40.59	62.7	0.38	1.39	0.18
		0.90		16.7			0.17	
Standard Muscle Group 5	1.14	1.10[a]	134.9	524.6	2428.68	12.73	11.63	10.77
GROUP 6. Muscles of the distal forelimb								
M. extensor carpi radialis		1.07	2.3	32.4	153.34	0.22	0.72	0.68
M. extensor digitorum tertii		1.52[a]	2.8	7.0	24.81	0.26	0.16	0.11
M. extensor digitorum communis		1.08	1.6	4.3	20.30	0.15	0.10	0.09
M. extensor digitorum lateralis		1.33[a]	3.8	5.7	22.50	0.36	0.13	0.10
M. ulnaris lateralis		1.29	5.8	19.5	78.92	0.55	0.43	0.35
M. abductor pollicis longus		0.82		0.8	4.51		0.02	0.02
M. flexor carpi radialis		1.01	14.31	5.0	24.81	1.35	0.11	0.11
M. flexor carpi ulnaris		1.00	3.9	11.3	56.38	0.37	0.25	0.25
M. flexor digitorum profundus		0.95	8.6	29.4	153.34	0.81	0.65	0.68
M. anconeus		1.59[a]	3.4	9.3	31.57	0.32	0.21	0.14
M. flexor digitorum sublimis		1.39[a]	4.1	14.2	54.12	0.39	0.31	0.24
		0.83		9.4			0.21	
Standard Muscle Group 6	1.73	1.11[a]	50.0	135.9	624.64	4.72	3.01	2.77
GROUP 7. Muscles connecting the thorax to the forelimb								
M. trapezius thoracis		0.51[b]	6.3	16.7	137.56	0.59	0.37	0.61
M. latissimus dorsi		1.12[a]	17.6	76.1	347.27	1.66	1.69	1.54
M. serratus ventralis thoracis		0.68[b]	43.3	65.1	437.47	4.08	1.44	1.94
M. pectoralis profundus		0.83[b]	30.3	122.4	708.07	2.86	2.71	3.14
Mm. pectoralis superficialis		0.94	11.5	51.1	299.92	1.08	1.27	1.33
Standard Muscle Group 7	0.58	0.85[b]	75.1	340.1	1932.54	7.08	7.54	8.57
GROUP 8. Muscles connecting the neck to the forelimb								
M. trapezius cervicalis		0.46[b]	5.4	14.9	130.79	0.51	0.33	0.58
M. omotransversarius		0.39[b]	3.1	19.9	193.93	0.29	0.44	0.86
M. rhomboideus		0.72[b]	8.2	28.4	182.66	0.77	0.63	0.81
M. serratus ventralis cervicis		0.60[b]	43.3	118.4	870.43	4.08	2.62	3.86
M. brachiocephalicus		0.58[b]	23.3	45.8	345.02	2.20	1.02	1.53
		0.95		66.2				
Standard Muscle Group 8	1.26	0.49[b]	67.7	204.3	1725.08	6.39	4.53	7.65
GROUP 9. Intrinsic muscles of the neck and thorax								
Mm. intercostales (externi et interni)		0.64[b]	37.8	125.2	879.45	3.52	2.78	3.90
M. serratus dorsalis cranialis		1.47	0.5	2.5	9.02	0.04	0.06	0.04
M. splenius		0.08[b]	3.9	7.3	139.81	0.37	0.16	0.62
M. intertransversarius longus		0.69[b]	3.5	28.8	191.68	0.33	0.64	0.85
M. longissimus capitis et atlantis		0.28[b]	4.9	15.5	182.66	0.46	0.34	0.81
M. intertransversarius cervicis (dorsalis et ventralis)		0.72[b]		26.3	169.13		0.58	0.75
M. complexus		0.55[b]	20.03	56.0	437.47	1.89	1.24	1.94
M. rectus capitis dorsalis major		0.63[b]	3.4	7.9	56.38	0.32	0.18	0.25
M. obliquus capitis caudalis		0.76[b]	5.8	20.0	124.03	0.55	0.44	0.55
M. cervicohyoideus		0.16[b]		0.9	13.53		0.02	0.06
		0.71[b]		2.1			0.05	
M. scalenus ventralis		0.56[b]	6.2	21.9	169.13	0.58	0.49	0.75
		1.07		35.7			0.79	
M. longus colli		0.54[b]	11.2	31.6	250.31	1.06	0.70	1.11
		1.09		53.7			1.19	
M. multifidus cervicus		1.22	8.2	39.3	166.87	0.77	0.87	0.74
		0.78		27.5			0.61	
M. transversus thoracis		0.97		10.1	51.87		0.22	0.23
Standard Muscle Group 9	1.34	0.64[b]	148.4	405.6	2848.07	4.00	8.99	12.63

APPENDIX 5 – TABLE 2 The composition of the musculature of mature rams of two strains of Merino rams of different total muscle weight (12,963.2 vs 10,338.0 grams) Data from Butterfield *et al* (1983b). Arranged in "Standard muscle groups"of Butterfield (1964b) Large strain N = 4; Small strain N = 6

	Weight				% Total Muscle Weight				Maturity Coefficients	
	LARGE		SMALL		LARGE		SMALL			
Muscle	(g)	S.E.	(g)	S.E.	%	S.E.	%	S.E.	q	±S.E.
GROUP 1. Muscles of the proximal hind limb										
M. tensor fasciae latae	110.0	3.0	93.1	4.7	0.86	0.02	0.90	0.03	1.51^{a*}	0.10
M. biceps femoris	559.7	8.8	447.0	25.1	4.32	0.07	4.33	0.20	1.31^{a}	0.06
M. gluteus medius	367.4	2.8	282.2	18.1	2.84	0.04	2.73	0.10	1.16^{a}	0.07
M. vastus lateralis	318.5	17.3	216.0	12.4	2.46	0.14	2.09	0.08	1.17^{a}	0.06
M. gluteus accessorius	58.5	5.8	44.6	3.5	0.45	0.05	0.43	0.03	1.47^{a}	0.14
M. rectus femoris	293.1	9.0	209.1	13.0	2.26	0.09	2.02	0.09	1.21^{a}	0.06
M. semitendinosus	225.1	4.3	188.2	11.0	1.74	0.05	1.82	0.07	1.20^{a}	0.06
M. gracilis	109.9	3.9	90.6	9.6	0.85	0.04	0.87	0.06	1.00	0.10
M. semimembranosus	558.6	20.5	397.6	21.6	4.31	0.16	3.84	0.13	1.17^{a}	0.07
M. adductor femoris	235.8	12.7	145.8	15.2	1.83	0.10	1.41	0.12	1.29^{a}	0.11
M. pectineus	51.5	3.9	45.1	3.1	0.40	0.02	0.43	0.02	1.21^{a}	0.08
M. sartorius	22.5	1.5	20.1	1.5	0.17	0.01	0.20	0.01	0.95	0.09
M. quadratus femoris	6.1	0.4	5.9	1.1	0.05	0.00	0.06	0.01	1.54^{a}	0.19
Mm. obturatorii externus et internus	55.8	2.9	46.2	1.9	0.43	0.02	0.45	0.02	1.55^{a}	0.08
M. vastus medialis	102.6	2.8	78.0	2.8	0.79	0.03	0.76	0.02	1.15^{a}	0.06
M. articularis genu	12.5	1.6	11.4	1.0	0.10	0.01	0.11	0.01	1.60^{a}	0.19
M. iliacus	74.1	2.4	64.8	4.5	0.57	0.02	0.63	0.04	1.21^{a}	0.09
M. gluteus profundus	36.3	3.8	33.2	2.0	0.28	0.03	0.32	0.01	L 1.45^{a}	0.13
									S 1.07	0.13
M. gemellus	4.0	0.3	4.0	0.2	0.03	0.00	0.04	0.00	L 2.75^{a}	0.26
									S 1.71^{a}	0.18
M. vastus intermedius	89.1	6.2	84.1	4.4	0.69	0.06	0.81	0.03	L 1.84^{a}	0.11
									S 1.35^{a}	0.11
Standard Muscle Group 1	3301.2	40.2	2515.5	123.4	25.48	0.48	24.33	0.52	1.23^{a}	0.04
GROUP 2. Muscles of the distal hind limb										
M. gastrocnemius et m. soleus	204.9	3.6	142.0	6.1	1.58	0.05	1.38	0.06	1.46^{a}	0.07
Mm. extensors	82.5	3.0	71.6	2.6	0.64	0.02	0.70	0.03	1.10	0.05
M. peroneus longus	19.1	0.6	16.8	1.3	0.15	0.01	0.16	0.01	1.41^{a}	0.12
M. extensor digitorum lateralis	36.4	2.2	27.9	0.9	0.28	0.02	0.27	0.01	1.91^{a}	0.09
M. tibialis cranialis	18.5	0.8	16.9	1.7	0.14	0.01	0.16	0.01	1.33^{a}	0.11
M. tibialis caudalis	17.7	0.4	11.6	0.7	0.14	0.00	0.11	0.01	1.21	0.13
M. popliteus	29.8	1.3	23.9	1.0	0.23	0.01	0.23	0.01	1.39^{a}	0.10
M. flexor digitorum longus	18.7	1.7	13.0	1.1	0.14	0.01	0.13	0.01	0.78	0.23
M. flexor digitorum superficialis	61.2	3.9	50.1	3.1	0.47	0.04	0.48	0.02	L 1.70^{a}	0.10
									S 1.20	0.10
M. flexor hallucis longus	88.7	4.2	62.4	2.9	0.68	0.03	0.60	0.01	L 0.91	0.08
									S 1.32^{a}	0.09
Standard Muscle Group 2	577.5	8.8	436.4	15.4	4.46	0.13	4.23	0.09	1.30^{a}	0.04
GROUP 3. Muscles surrounding the spinal column										
M. psoas major	148.9	7.4	119.4	7.4	1.15	0.05	1.15	0.02	1.45^{a}	0.07
M. quadratus lumborum	49.1	2.6	40.3	1.7	0.38	0.02	0.39	0.02	1.01	0.08
M. iliocostalis thoracis	75.0	4.2	58.0	2.2	0.58	0.04	0.57	0.03	0.75^{b}	0.11
M. longissimus thoracis et lumborum	1204.0	44.9	901.2	45.5	9.20	0.44	8.75	0.32	1.19^{a}	0.06
M. multifidus thoracis et lumborum	145.8	14.7	117.2	11.5	1.13	0.12	1.15	0.12	1.67^{a}	0.17
M. longissimus cervicis	70.3	13.4	61.9	3.8	0.54	0.10	0.60	0.03	0.74	0.15
M. spinalis cervicis et thoracis	240.0	23.2	220.5	25.4	1.84	0.15	2.11	0.17	0.75^{b}	0.10
M. psoas minor	63.5	6.3	51.3	3.5	0.49	0.05	0.49	0.02	L 1.57^{a}	0.14
									S 1.21^{a}	0.08
Standard Muscle Group 3	1999.3	30.3	1570.9	85.6	15.43	0.27	15.21	0.54	1.15^{a}	0.05
GROUP 4. Muscles of the abdominal wall										
M. cutaneus trunci	334.3	28.3	270.5	15.4	2.58	0.23	2.61	0.07	0.75^{b}	0.09
M. serratus dorsalis caudalis	21.7	0.2	24.5	1.0	0.17	0.00	0.24	0.01	0.94	0.10
M. obliquus externus abdominis	241.6	12.4	204.6	11.9	1.86	0.10	1.99	0.11	1.01	0.08
M. retractor costae	24.7	5.2	23.8	1.7	0.19	0.04	0.23	0.02	1.21	0.21
M. obliquus internus abdominis	172.1	7.1	132.8	8.0	1.33	0.07	1.28	0.04	0.87	0.09
M. transversus abdominis	210.4	13.3	181.3	6.8	1.62	0.10	1.76	0.06	0.84	0.08
M. rectus abdominis	318.3	20.0	267.1	23.2	2.46	0.16	2.57	0.14	0.87	0.08
Standard Muscle Group 4	1338.3	56.5	1111.97	55.0	10.33	0.46	10.76	0.24	0.92	0.05
GROUP 5. Muscles of the proximal forelimb										
M. deltoideus	64.6	3.6	60.4	6.1	0.50	0.03	0.58	0.04	0.86	0.10
M. infraspinatus	261.0	7.8	187.2	14.4	2.01	0.04	1.82	0.13	1.10	0.07
M. triceps brachii (Caput laterale)	94.8	3.9	76.9	5.4	0.73	0.03	0.74	0.02	1.19^{a}	0.06
M. teres minor	24.2	2.0	19.0	2.2	0.19	0.01	0.18	0.01	0.64^{b}	0.10
M. triceps brachii (Caput longum)	308.9	9.5	249.7	28.9	2.38	0.06	2.38	0.18	1.13	0.08
M. tensor fasciae antebrachii	36.5	3.6	40.3	3.6	0.28	0.03	0.39	0.02	0.69^{b}	0.10
M. supraspinatus	244.5	11.5	197.3	19.3	1.88	0.07	1.90	0.12	1.15^{a}	0.07

APPENDIX 5 - TABLE 2 (Continued)

	Weight				% Total Muscle Weight				Maturity	
	LARGE		SMALL		LARGE		SMALL		Coefficients	
Muscle	(g)	S.E.	(g)	S.E.	%	S.E.	%	S.E.	q	±S.E.
M. biceps brachii	75.2	3.0	57.2	5.0	0.58	0.03	0.55	0.02	0.84^{b}	0.08
M. teres major	64.3	3.0	51.4	4.6	0.50	0.02	0.49	0.02	1.11	0.07
M. brachialis	47.5	1.9	36.0	1.6	0.37	0.01	0.35	0.01	1.44^{a}	0.07
M. coracobrachialis	18.5	1.0	17.5	1.0	0.14	0.01	0.17	0.00	L 1.66^{a}	0.12
									S 1.28^{a}	0.11
M. subscapularis	143.7	6.5	100.5	8.4	1.11	0.05	0.97	0.06	L 0.96	0.08
									S 1.42^{a}	0.13
M. triceps brachii (Caput mediale)	18.9	1.1	20.7	2.2	0.15	0.01	0.20	0.01	L 2.32^{a}	0.15
									S 0.90	0.15
Standard Muscle Group 5	1403.2	39.9	1114.2	83.0	10.82	0.22	10.71	0.32	1.10^{a}	0.04
GROUP 6. Muscles of the distal forelimb										
M. extensor carpi radialis	84.7	1.7	73.0	5.3	0.65	0.02	0.70	0.02	1.07	0.05
M. extensor digitorum tertii	13.4	0.8	11.1	0.5	0.10	0.01	0.11	0.00	1.52^{a}	0.09
M. extensor digitorum communis	10.0	0.4	10.1	1.4	0.08	0.00	0.10	0.01	1.08	0.14
M. extensor digitorum lateralis	13.3	0.5	10.7	0.7	0.10	0.00	0.10	0.00	1.33^{a}	0.10
M. ulnaris lateralis	50.0	2.3	31.9	5.2	0.39	0.02	0.31	0.05	1.29	0.16
M. abductor pollicis longus	2.5	0.2	2.3	0.3	0.02	0.00	0.02	0.00	0.82	0.17
M. flexor carpi radialis	14.8	0.7	12.5	1.5	0.11	0.01	0.12	0.01	1.01	0.09
M. flexor carpi ulnaris	32.6	1.5	26.5	2.3	0.25	0.02	0.25	0.01	1.00	0.08
M. flexor digitorum profundus	85.0	5.9	72.6	11.2	0.66	0.04	0.69	0.08	0.95	0.13
M. anconeus	17.5	0.3	15.0	1.1	0.13	0.00	0.15	0.01	1.59^{a}	0.10
M. flexor digitorum sublimis	27.6	1.3	27.4	2.1	0.21	0.01	0.26	0.01	L 1.39^{a}	0.10
									S 0.83	0.13
Standard Muscle Group 6	351.6	10.3	293.2	21.4	2.71	0.09	2.82	0.09	1.11^{a}	0.05
GROUP 7. Muscles connecting the thorax to the forelimb										
M. trapezius thoracis	77.5	6.8	64.6	6.5	0.60	0.05	0.62	0.05	0.51^{b}	0.12
M. latissimus dorsi	198.3	5.0	161.1	13.3	1.53	0.02	1.55	0.06	1.12^{a}	0.06
M. serratus ventralis thoracis	247.4	21.4	205.8	23.5	1.91	0.15	1.97	0.15	0.68^{b}	0.01
M. pectoralis profundus	407.3	6.5	325.1	17.5	3.15	0.08	3.14	0.06	0.83^{b}	0.04
Mm. pectoralis superficialis	178.8	11.3	133.3	10.0	1.38	0.09	1.28	0.04	0.94	0.06
Standard Muscle Group 7	1111.4	24.7	889.8	68.3	8.57	0.15	8.57	0.32	0.85^{b}	0.04
GROUP 8. Muscles connecting the neck to the forelimb										
M. trapezius cervicalis	67.7	6.0	65.7	4.6	0.52	0.04	0.64	0.05	0.46^{b}	0.11
M. omotransversarius	108.3	13.0	91.9	4.4	0.83	0.09	0.89	0.03	0.39^{b}	0.12
M. rhomboideus	106.6	19.3	83.1	7.0	0.82	0.14	0.80	0.05	0.72^{b}	0.11
M. serratus ventralis cervicis	500.6	15.4	396.9	18.2	3.86	0.07	3.85	0.13	0.60^{b}	0.06
M. brachiocephalicus	200.2	9.8	156.4	9.8	1.54	0.07	1.52	0.10	L 0.58^{b}	0.08
									S 0.95	0.14
Standard Muscle Group 8	983.4	42.9	794.0	32.3	7.58	0.21	7.71	0.24	L 0.49^{b}	0.05
									S 0.73^{b}	0.09
GROUP 9. Intrinsic Muscles of the neck and thorax										
Mm. intercostales (externi et interni)	458.7	20.7	434.8	15.3	3.54	0.17	4.25	0.26	0.64^{b}	0.10
M. serratus dorsalis cranialis	3.6	0.5	4.6	0.3	0.03	0.00	0.04	0.00	1.47	0.30
M. splenius	77.3	13.9	66.7	4.8	0.60	0.10	0.64	0.02	0.08^{b}	0.16
M. intertransversarius longus	113.8	6.8	83.0	3.3	0.88	0.04	0.81	0.06	0.69^{b}	0.12
M. longissimus capitis et atlantis	99.3	7.7	88.0	5.2	0.77	0.06	0.85	0.04	0.28^{b}	0.14
M. intertransversarius cervicis (dorsalis et ventralis)	106.5	4.3	70.8	8.6	0.82	0.03	0.68	0.06	0.72^{b}	0.10
M. complexus	246.5	5.0	204.2	13.1	1.90	0.05	1.97	0.06	0.55^{b}	0.06
M. rectus capitis dorsalis major	30.6	1.9	25.9	1.5	0.24	0.02	0.25	0.02	0.63^{b}	0.15
M. obliquus capitis caudalis	69.8	3.6	58.2	7.6	0.54	0.03	0.56	0.05	0.76^{b}	0.10
M. cervicohyoideus	7.2	1.0	5.1	0.6	0.06	0.01	0.05	0.00	L 0.16^{b}	0.25
									S 0.71^{b}	0.32
M. scalenus ventralis	94.3	7.9	78.6	7.2	0.73	0.05	0.77	0.08	L 0.56^{b}	0.11
									S 1.07	0.23
M. longus colli	156.9	13.5	104.4	5.4	1.21	0.09	1.01	0.05	L 0.54^{b}	0.10
									S 1.09	0.13
M. multifidus cervicus	87.3	6.1	83.5	4.6	0.67	0.05	0.81	0.02	L 1.22	0.13
									S 0.78	0.14
M. transversus thoracis	25.4	3.9	26.1	0.7	0.20	0.03	0.25	0.01	0.97	0.14
Standard Muscle Group 9	1586.5	69.8	1340.2	51.1	12.24	0.47	13.02	0.42	0.64^{b}	0.07
Scrap muscle not included in a Standard Muscle Group	310.5	89.9	271.6	15.5	2.38	0.66	1.62	0.13		
Total Muscle Weight	12963.2	203.1	10338.0	471.7	100.00		100.00			

* a, b: q was significantly greater than and less than 1.0 respectively ($P < 0.05$).

APPENDIX 5 – TABLE 3 Impetus grouping of individual muscles of large and small mature size Merino rams from 20% mature to maturity

Muscle name	% of total muscle weight at maturity	'q'
(a) **Muscles with 'q' significantly less than 1.0**		
Merino—Large		
M. iliocostalis thoracis	0.58	0.75
M. spinalis cervicis et thoracis	1.84	0.75
M. cutaneus trunci	2.58	0.75
M. teres minor	0.19	0.64
M. tensor fasciae antebrachii	0.28	0.69
M. biceps brachii	0.58	0.84
M. trapezius thoracis	0.60	0.51
M. serratus ventralis thoracis	1.91	0.68
M. pectoralis profundis	3.15	0.83
M. trapezius cervicalis	0.52	0.46
M. omotransversarius	0.83	0.39
M. rhomboideus	0.82	0.72
M. serratus ventralis cervicis	3.86	0.60
M. brachiocephalicus	1.54	0.58
Mm. intercostales (externi et interni)	3.54	0.64
M. splenius	0.60	0.08
M. intertransversarius longus	0.88	0.69
M. longissimus capitis et atlantis	0.77	0.28
M. intertransversarius cervicis (dorsalis et ventralis)	0.82	0.72
M. complexus	1.90	0.55
M. rectus capitis dorsalis major	0.24	0.63
M. obliquus capitus caudalis	0.54	0.76
M. cervicohyoideus	0.06	0.16
M. scalenus ventralis	0.73	0.56
M. longus colli	1.21	0.54
Total	30.57	0.64
Merino—Small		
M. iliocostalis thoracis	0.57	0.75
M. spinalis cervicis et thoracis	2.11	0.75
M. cutaneous trunci	2.61	0.75
M. teres minor	0.18	0.64
M. tensor fasciae antebrachii	0.39	0.69
M. biceps brachii	0.55	0.84
M. trapezius thoracis	0.62	0.51
M. seratus ventralis thoracis	1.97	0.68
M. pectoralis profundus	3.14	0.83
M. trapezius cervicalis	0.64	0.46
M. omotransversarius	0.89	0.39
M. rhomboideus	0.80	0.72
M. serratus ventralia cervicis	3.85	0.60
Mm. intercostales (externi et interni)	4.25	0.64
M. splenius	0.64	0.08
M. intertransversarius longus	0.81	0.69
M. longissimus capitis et atlantis	0.85	0.28
M. intertransversarius cervicis (dorsalis et ventralis)	0.68	0.72
M. complexus	1.97	0.55
M. rectus capitis dorsalis major	0.25	0.63
M. obliquus capitis caudalis	0.56	0.76
M. cervicohyoideus	0.05	0.71
Total	28.38	0.65
(b) **Muscles with 'q' not different from 1.0**		
Merino Large		
M. gracilis	0.85	1.00
M. sartorius	0.17	0.95
Mm. extensors	0.64	1.10
M. tibialis caudalis	0.14	1.21
M. flexor digitorium longus	0.14	0.78
M. flexor hallucis longus	0.68	0.91
M. quadratus lumborum	0.38	1.01
M. longissimus cervicis	0.54	0.74
M. transversus thoracis	0.20	0.97
M. serratus dorsalis caudalis	0.17	0.94
M. obliquus externus abdominis	1.86	1.01
M. retractor costae	0.19	1.21
M. obliquus internus abdominis	1.33	0.87
M. transversus abdominis	1.67	0.84
M. rectus abdominis	2.46	0.87
M. deltoideus	0.50	0.86
M. infraspinatus	2.01	1.10

M. triceps brachii (caput longum)	2.38	1.13
M. teres major	0.50	1.11
M. subscapularis	1.11	0.96
M. extensor carpi radialis	0.65	1.07
M. extensor digitorum communis	0.08	1.08
M. ulnaris lateralis	0.39	1.29
M. abductor pollicis longus	0.02	0.82
M. flexor carpi radialis	0.11	1.01
M. carpi ulnaris	0.25	1.00
M. flexor digitorum profundus	0.66	0.95
Mm. pectoralis superficialis	1.38	0.94
M. serratus dorsalis cranialis	0.03	1.47
M. multifidus cervicis	0.67	1.22
Total	22.16	1.05
Merino Small		
M. gracilis	0.87	1.00
M. sartorius	0.20	0.95
M. gluteus profundus	0.32	1.07
Mm. extensors	0.70	1.10
M. tibialis caudalis	0.11	1.21
M. flexor digitorum longus	0.13	0.78
M. flexor digitorum superficialis	0.48	1.20
M. quadratus lumborum	0.39	1.01
M. longissimus cervicis	0.60	0.74
M. transversus thoracis	0.25	0.97
M. serratus dorsalis caudalis	0.24	0.94
M. obliquus externus abdominis	1.99	1.01
M. retractor costae	0.23	1.21
M. obliquus internus abdominis	1.28	0.87
M. transversus abdominis	1.76	0.84
M. rectus abdominis	2.57	0.87
M. deltoideus	0.58	0.86
M. infraspinatus	1.82	1.10
M. triceps brachii (caput longum)	2.38	1.13
M. teres major	0.49	1.11
M. triceps brachii (caput mediale)	0.20	0.90
M. extensor carpi radialis	0.70	1.07
M. extensor digitorum communis	0.10	1.08
M. ulnaris lateralis	0.31	1.29
M. abductor pollicis longus	0.02	0.82
M. flexor carpi radialis	0.12	1.01
M. flexor carpi ulnaris	0.25	1.00
M. flexor digitorum profundus	0.69	0.95
M. flexor digitorum sublimis	0.26	0.83
Mm. pectoralis superficialis	1.28	0.94
M. brachiocephalis	1.52	0.95
M. serratus dorsalis cranialis	0.04	1.47
M. scalenus ventralis	0.77	1.07
M. longus colli	1.01	1.09
M. multifidus cervicis	0.81	0.78
Total	25.47	0.99

(c) **Muscles with 'q' significantly greater than 1.0**

Merino Large		
M. tensor fasciae latae	0.86	1.51
M. biceps femoris	4.32	1.31
M. gluteus medius	2.84	1.16
M. vastus lateralis	2.46	1.17
M. gluteus accessorius	0.45	1.47
M. rectus femoris	2.26	1.21
M. semitendinosus	1.74	1.20
M. semimembranosus	4.31	1.17
M. abductor femoris	1.82	1.29
M. pectineus	0.40	1.21
M. quadratus femoris	0.05	1.54
Mm. obturatorii externus et internus	0.43	1.55
M. vastus medialis	0.79	1.15
M. articularis genu	0.10	1.60
M. iliacus	0.57	1.21
M. gluteus profundus	0.28	1.45
M. gemellus	0.03	2.75
M. vastus intermedius	0.69	1.84
M. gastrocnemius et M. soleus	1.58	1.46
M. peroneus longus	0.15	1.41
M. extensor digitorum lateralis	0.28	1.91
M. tibialis cranialis	0.14	1.33
M. popliteus	0.23	1.39
M. flexor digitorum superficialis	0.47	1.70
M. psoas major	1.15	1.45

M. longissimus thoracis et lumborum	9.30	1.19
M. multifidus thoracis et lumborum	1.13	1.67
M. psoas minor	0.49	1.57
M. triceps brachii (caput laterale)	0.73	1.19
M. supraspinatus	1.88	1.15
M. brachialis	0.37	1.44
M. coracobrachialis	0.14	1.66
M. triceps brachii (caput mediale)	0.15	2.32
M. extensor digitorum tertii	0.10	1.52
M. extensor digitorum lateralis	0.10	1.33
M. anconeus	0.13	1.59
M. flexor digitorum sublimis	0.21	1.39
M. latissimus dorsi	1.53	1.12
Total	44.66	1.28
Merino Small		
M. tensor fasciae latae	0.90	1.51
M. biceps femoris	4.33	1.31
M. gluteus medius	2.73	1.16
M. vastus lateralis	2.09	1.17
M. gluteus accessorius	0.43	1.47
M. rectus femoris	2.02	1.21
M. semitendinosus	1.82	1.20
M. semimembranosus	3.84	1.17
M. abductor femoris	1.41	1.29
M. pectineus	0.43	1.21
M. quadratus femoris	0.06	1.54
M. obturatorii externus et internus	0.45	1.55
M. vastus medialis	0.76	1.15
M. articularis genu	0.11	1.60
M. iliacus	0.63	1.21
M. gemellus	0.04	1.71
M. vastus intermedius	0.81	1.35
M. gastrocnemius et M. soleus	1.38	1.46
M. peroneus longus	0.16	1.41
M. extensor digitorum lateralis	0.27	1.91
M. tibialis cranialis	0.16	1.33
M. popliteus	0.23	1.39
M. flexor hallucis longus	0.60	1.32
M. psoas major	1.15	1.45
M. longissimus thoracis et lumborum	8.75	1.19
M. multifidus thoracis et lumborum	1.15	1.67
M. psoas minor	0.49	1.21
M. triceps brachii (caput laterale)	0.74	1.19
M. supraspinatus	1.90	1.15
M. brachialis	0.35	1.44
m. coracobrachialis	0.17	1.28
M. subscapularis	0.97	1.42
M. extensor digitorum tertii	0.11	1.52
M. extensor digitorum lateralis	0.10	1.33
M. anconeus	0.15	1.59
M. latissimus dorsi	1.55	1.12
Total	43.24	1.26

APPENDIX 5 – TABLE 4 The composition of the musculature and maturity coefficients of mature Dorset Horn rams and wethers whose total muscle weighed 24,650 g and 21,870 g respectively
Data from Butterfield *et al.* (1984a), arranged in "Standard Muscle Groups" of Butterfield (1964b)

	Weight				% Total Muscle Weight				Maturity Coefficients	
	Rams		Wethers		Rams		Wethers			
Muscle	(g)	S.E.	(g)	S.E.	%	S.E.	%	S.E.		S.E.
GROUP 1. Muscles of the proximal hind limb										
M. tensor fasciae latae	105.8	7.0	99.1	4.6	0.86	0.03	0.92	0.02	1.35^{a*}	0.07
M. biceps femoris	595.0	31.2	547.7	17.6	4.82	0.14	4.11	0.07	1.03	0.04
M. gluteus medius	386.2	7.0	357.3	13.7	3.14	0.08	3.34	0.08	1.20^{a}	0.05
M. vastus lateralis	286.2	11.4	270.3	10.2	2.33	0.09	2.53	0.08	1.14	0.07
M. gluteus accessorius	61.1	3.7	48.0	2.4	0.50	0.03	0.45	0.02	R 0.98	0.12
									W 1.36^{a}	0.14
M. rectus femoris	241.1	12.9	230.2	8.0	0.08	2.15	0.06	1.23^{a}	0.05	
M. semitendinosus	202.2	12.7	189.9	4.6	1.63	0.06	1.78	0.03	1.04	0.05
M. gracilis	111.2	3.9	102.2	2.8	0.90	0.02	0.96	0.02	0.98	0.05
M. semimembranosus	508.4	16.9	483.2	17.3	4.13	0.12	4.51	0.10	1.23^{a}	0.04
M. adductor femoris	210.2	5.4	203.4	5.9	1.71	0.05	1.91	0.06	1.30^{a}	0.06
M. pectineus	63.3	2.2	57.4	1.7	0.51	0.01	0.54	0.01	1.05	0.06
M. sartorius	24.2	2.5	21.3	1.4	0.20	0.02	0.20	0.01	0.70	0.15
M. quadratus femoris	5.7	0.8	4.7	0.3	0.05	0.01	0.04	0.00	1.46^{a}	0.16
Mm. obturatorii externus et internus	53.7	5.3	48.0	1.9	0.43	0.03	0.45	0.02	1.33^{a}	0.08
M. vastus medialis	101.9	4.7	90.4	3.8	0.83	0.04	0.84	0.03	0.13^{a}	0.06
M. articularis genu	13.2	0.9	12.0	0.4	0.11	0.01	0.11	0.00	1.18	0.12
M. iliacus	65.4	1.3	61.2	3.2	0.53	0.01	0.57	0.02	1.22^{a}	0.07
M. gluteus profundus	34.7	1.3	26.9	1.3	0.28	0.01	0.25	0.01	1.45^{a}	0.08
M. gemellus	4.7	0.3	2.4	0.2	0.04	0.00	0.04	0.00	1.78^{a}	0.12
M. vastus intermedius	86.2	6.2	71.8	4.0	0.70	0.06	0.67	0.03	1.24^{a}	0.10
Standard muscle group 1	3169.1	109.1	2937.6	76.7	25.73	0.50	27.44	0.27	1.16^{a}	0.02
Group 2. Muscles of the distal hind limb										
M. gastrocnemius et M. soleus	181.2	6.5	176.3	14.7	1.47	0.05	1.64	0.11	1.09	0.09
Mm. extensors	74.2	4.7	66.3	2.5	0.60	0.03	0.62	0.02	1.11	0.06
M. peroneus longus	18.8	1.6	18.2	0.9	0.15	0.01	0.17	0.01	1.31^{a}	0.10
M. extensor digitorum lateralis	24.0	2.2	22.8	0.9	0.19	0.01	0.21	0.01	1.45^{a}	0.08
M. tibialis cranialis	16.3	0.7	16.1	0.8	0.13	0.01	0.15	0.01	1.41^{a}	0.08
M. tibialis caudalis	14.4	1.1	11.3	0.7	0.12	0.01	0.11	0.01	R 0.69	0.16
									W 1.34	0.19
M. popliteus	33.7	1.9	28.8	0.9	0.27	0.01	0.27	0.01	1.34^{a}	0.07
M. flexor digitorum longus	12.1	1.2	12.1	0.6	0.10	0.01	0.11	0.01	1.46^{a}	0.12
M. flexor digitorum superficialis	66.2	3.9	57.5	2.3	0.54	0.02	0.54	0.02	1.22^{a}	0.06
M. flexor hallucis longus	57.7	4.0	49.8	2.3	0.47	0.04	0.46	0.01	1.34^{a}	0.07
Standard muscle group 2	498.8	21.1	459.2	20.6	4.05	0.13	4.28	0.14	1.19^{a}	0.05
Group 3. Muscles surrounding the spinal column										
M. psoas major	149.4	6.2	146.0	7.0	1.21	0.03	1.36	0.03	1.24^{a}	0.05
M. quadratus lumborum	39.1	2.8	38.6	2.2	0.32	0.01	0.36	0.02	1.09	0.08
M. iliocostalis thoracis	57.6	4.7	44.1	2.7	0.47	0.03	0.41	0.02	0.97	
M. longissimus thoracis et lumborum	1094.1	37.0	1006.9	39.8	8.88	0.17	3.39	0.21	1.25^{a}	0.06
M. multifidus thoracis et lumborum	145.4	3.2	124.0	9.5	1.21	0.06	1.115	0.07	1.47^{a}	0.01
M. longissimus cervicis	34.8	2.5	30.3	2.1	0.28	0.02	0.28	0.01	1.34^{a}	0.12
M. spinalis cervicis et thoracis	268.3	29.3	186.0	12.0	2.16	0.18	1.73	0.09	0.44^{b}	0.14
M. transversus thoracis	30.4	3.8	23.1	1.4	0.24	0.03	0.21	0.01	1.15	0.12
M. psoas minor	58.6	4.6	56.8	3.4	0.47	0.03	0.53	0.02	1.19^{a}	0.08
Standard muscle group 3	1880.7	80.3	1655.7	69.4	15.25	0.29	15.42	0.32	1.16^{a}	0.04
Group 4. Muscles of the abdominal wall										
M. cutaneus trunci	394.7	16.0	311.4	9.3	3.20	0.07	2.91	0.07	0.48^{b}	0.06
M. serratus dorsalis caudalis	27.5	3.1	27.7	1.5	0.22	0.02	0.26	0.02	1.01	0.16
M. obliquus externus abdominis	348.4	27.8	309.8	13.8	2.82	0.19	2.90	0.14	0.33^{b}	0.11
M. retractor costae	31.1	2.0	29.4	4.0	0.25	0.02	0.27	0.03	0.74	0.19
M. obliquus internus abdominis	216.0	15.1	208.8	14.0	1.75	0.08	1.95	0.11	0.50^{b}	0.10
M. transversus abdominis	321.2	24.4	266.5	11.2	2.60	0.14	2.50	0.13	0.54^{b}	0.10
M. rectus abdominis	368.6	25.3	369.1	26.6	2.98	0.13	3.43	0.18	R 0.76^{b}	0.09
									W 0.43^{b}	0.13
Standard muscle group 4	1707.4	103.2	1522.8	61.3	13.82	0.51	14.22	0.43	0.52^{a}	0.06
GROUP 5. Muscles of the proximal forelimb										
M. deltoideus	67.6	5.5	53.4	3.3	0.55	0.04	0.50	0.03	0.96	0.10
M. infraspinatus	244.9	13.6	222.6	7.5	1.99	0.09	2.08	0.03	0.95	0.05
M. triceps brachii (Caput laterale)	67.5	2.6	74.7	3.0	0.55	0.02	0.70	0.02	R 1.89^{a}	0.16
									W 1.21^{a}	0.09
M. teres minor	21.1	1.9	16.7	1.0	0.17	0.01	0.16	0.01	1.11	0.10
M. triceps brachii (Caput longum)	284.3	12.4	260.3	10.0	2.31	0.09	2.43	0.06	1.20^{a}	0.08
M. tensor fasciae antebrachii	50.9	5.2	32.8	1.8	0.41	0.03	0.31	0.01	R 0.23^{b}	0.15
									W 0.75	0.16
M. supraspinatus	218.7	4.3	206.6	5.3	1.78	0.03	1.93	0.03	1.23^{a}	0.05

APPENDIX 5 – TABLE 4 (Continued)

	Weight				% Total Muscle Weight				Maturity	
	Rams		Wethers		Rams		Wethers		Coefficients	
Muscle	(g)	S.E.	(g)	S.E.	%	S.E.	%	S.E.		S.E.
M. biceps brachii	69.2	3.6	65.0	2.7	0.56	0.02	0.61	0.02	R 1.08 W 0.86	0.06 0.07
M. teres major	70.9	5.2	61.9	2.8	0.58	0.04	0.58	0.02	0.94	0.08
M. brachialis	39.4	3.2	33.2	1.2	0.32	0.02	0.31	0.01	1.36^{a}	0.08
M. coracobrachialis	20.9	1.3	18.8	0.5	0.17	0.01	0.18	0.01	1.29^{a}	0.08
M. subscapularis	107.5	4.3	95.0	3.5	0.87	0.04	3.48	0.89	1.56^{a}	0.14
M. triceps brachii (Caput mediale)	16.1	0.6	15.4	0.9	0.13	0.01	0.14	0.01	2.01^{a}	0.12
Standard muscle group 5	1278.9	46.2	1156.5	35.0	10.38	0.24	10.80	0.16	1.16^{a}	0.04
Group 6. Muscles of the distal forelimb										
M. extensor carpi radialis	82.4	4.9	77.0	3.2	0.67	0.02	0.72	0.02	0.96	0.07
M. extensor digitorum tertii	12.3	1.1	11.1	0.5	0.10	0.01	0.10	0.00	1.35^{a}	0.09
M. extensor digitorum communis	9.6	0.7	8.8	0.4	0.08	0.01	0.08	0.00	1.09	0.08
M. extensor digitorum lateralis	13.0	1.2	10.8	0.7	0.11	0.01	0.10	0.00	1.41^{a}	0.11
M. ulnaris lateralis	40.1	2.1	33.6	2.0	0.33	0.02	0.31	0.02	1.33^{a}	0.12
M. abductor pollicis longus	1.7	0.3	1.3	0.2	0.01	0.00	0.01	0.00	1.27	0.29
M. flexor carpi radialis	11.9	0.4	11.5	0.6	0.10	0.00	0.11	0.00	R 1.23^{a} W 0.87	0.09 0.13
M. flexor carpi ulnaris	23.5	0.9	20.4	0.9	0.19	0.00	0.10	0.01	1.20^{a}	0.09
M. flexor digitorum profundus	56.3	5.6	54.1	3.7	0.46	0.04	0.51	0.03	1.32^{a}	0.13
M. anconeus	15.3	0.8	14.6	0.9	0.12	0.01	0.14	0.01	R 1.98^{a} W 1.35	0.13 0.18
M. flexor digitorum sublimis	21.2	2.4	19.6	1.6	0.17	0.02	0.18	0.01	1.36^{a}	0.13
Standard muscle group 6	287.3	13.0	262.8	9.4	2.33	0.08	2.45	0.05	1.22^{a}	0.05
Group 7. Muscles connecting the thorax to the forelimb										
M. trapezius thoracis	70.8	8.8	66.5	3.2	0.58	0.08	0.62	0.01	0.55^{b}	0.13
M. latissimus dorsi	255.3	14.9	214.6	9.3	2.07	0.12	2.01	0.09	0.77^{b}	0.09
M. serratus ventralis thoracis	314.6	31.5	242.0	13.3	2.55	0.25	2.26	0.09	0.19^{b}	0.11
M. pectoralis profundus	392.4	26.0	368.7	19.6	3.17	0.14	3.43	0.11	0.87	0.06
Mm. pectoralis superficialis	189.2	13.4	156.4	9.3	1.53	0.08	1.46	0.08	0.79	0.12
Standard muscle group 7	1222.3	50.3	1048.2	39.1	9.91	0.23	9.77	0.17	0.65^{b}	0.04
Group 8. Muscles connecting the neck to the forelimb										
M. trapezius cervicalis	54.1	6.6	42.6	2.0	0.44	0.06	0.40	0.01	0.67^{b}	0.13
M. omotransversarius	97.1	6.0	49.8	1.8	0.79	0.05	0.47	0.02	R 0.60^{b} W 1.01	0.12 0.14
M. rhomboideus	123.4	8.7	101.8	5.6	1.00	0.05	0.95	0.04	0.63^{b}	0.07
M. serratus ventralis cervicis	425.2	29.6	350.6	13.2	3.45	0.23	3.27	0.09	1.01	0.08
M. brachiocephalicus	174.1	7.6	126.6	6.8	1.41	0.05	1.18	0.05	0.92	0.08
Standard muscle group 8	873.8	38.9	671.5	26.4	7.10	0.30	6.27	0.16	0.89	0.06
Group 9. Intrinsic muscles of the neck and thorax										
Mm. intercostales (externi et interni)	400.2	11.2	343.2	14.0	3.25	0.07	3.20	0.07	0.98	0.04
M. serratus dorsalis cranialis	4.5	2.4	4.1	0.5	0.04	0.01	0.04	0.00	1.91^{a}	0.37
M. splenius	62.2	5.1	20.5	1.8	0.51	0.05	0.19	0.01	1.02	0.16
M. intertransversarius longus	95.3	4.7	53.0	2.7	0.77	0.04	0.49	0.02	0.94	0.10
M. longissimus capitis et atlantis	83.7	5.1	37.6	1.0	0.68	0.03	0.35	0.01	R 0.74 W 1.30^{a}	0.13 0.14
M. intertransversarius cervicis (dorsalis et ventralis)	62.0	4.3	52.9	2.6	0.50	0.02	0.49	0.01	1.05	0.08
M. complexus	179.2	9.6	117.9	6.4	1.45	0.05	1.10	0.04	R 0.69^{b} W 1.09	0.11 0.12
M. rectus capitis dorsalis major	14.9	1.4	10.1	0.8	0.12	0.01	0.10	0.01	0.63^{b}	0.15
M. obliquus capitis caudalis	52.4	3.0	41.5	1.3	0.42	0.02	0.39	0.01	1.30^{a}	0.10
M. cervicohyoideus	7.5	0.4	3.6	0.1	0.06	0.000	0.03	0.00	0.58^{b}	0.16
M. scalenus ventralis	73.6	7.3	46.3	1.4	0.60	0.05	0.43	0.01	R 0.90 W 1.37^{a}	0.17 0.12
M. longus colli	89.1	7.2	77.1	1.1	0.72	0.04	0.72	0.03	1.25^{a}	0.08
M. multifidus cervicus	67.1	3.0	53.6	2.1	0.55	0.02	0.50	0.01	1.22^{a}	0.10
Standard muscle group 9	1198.5	47.1	866.4	30.1	9.72	0.24	8.08	0.12	1.03	0.04
Scrap muscle not included in a standard muscle group	209.3	13.0	135.5	12.5	1.70	0.11	1.25	0.09		
Total Muscle weight	12,326.2	403.9	10,716.2	319.4	100.00		100.00			

* a, b; q was significantly greater than and less than 1.0 respectively ($P < 0.05$).
R, W; separate maturity coefficients for rams and wethers where a pooled coefficient was not appropriate.

APPENDIX 5 – TABLE 5 Impetus grouping of individual muscles of Dorset Horn rams and wethers from 20% mature to maturity

Muscle name	% of total muscle weight at maturity	'q'
(a) **Muscles with 'q' significantly less than 1.0**		
Dorset Horn Rams		
M. spinalis cervicis et thoracis	2.16	0.44
M. cutaneus trunci	3.20	0.48
M. obliquus externus abdominis	2.82	0.33
M. obliquus internus abdominis	1.75	0.50
M. transversus abdominis	2.60	0.54
M. rectus abdominis	2.98	0.76
M. tensor fasciae antebrachii	0.41	0.23
M. trapezius thoracis	0.58	0.55
M. latissimus dorsi	2.07	0.77
M. serratus ventralis thoracis	2.55	0.19
M. trapezius cerviculus	0.44	0.67
M. omotransversarius	0.79	0.60
M. rhomboideus	1.00	0.63
M. complexus	1.45	0.69
M. rectus capitis dorsalis major	0.12	0.63
M. cervicohyoides	0.06	0.58
Total	24.98	0.52
Dorset Horn Wethers		
M. spinalis cervicis et thoracis	1.73	0.44
M. cutaneus trunci	2.91	0.48
M. obliquus externus abdominis	2.90	0.33
M. obliquus internus abdominis	1.95	0.50
M. transversus abdominis	2.50	0.54
M. rectus abdominis	3.43	0.43
M. trapezius thoracis	0.62	0.55
M. latissimus dorsi	2.01	0.77
M. serratus ventralis thoracis	2.26	0.19
M. trapezius cervicalis	0.40	0.67
M. rhomboideus	0.95	0.63
M. rectus capitis dorsalis major	0.10	0.63
M. cervicohyoideus	0.03	0.58
Total	21.79	0.47
(b) **Muscles with q = 1.0**		
Dorset Horn Rams		
M. biceps femoris	4.82	1.03
M. vastus lateralis	2.33	1.14
M. gluteus accessorius	0.50	0.98
M. semitendinosus	1.63	1.04
M. gracilis	0.90	0.98
M. pectineus	0.51	1.05
M. sartorius	0.20	0.70
M. articularis genus	0.11	0.18
M. gastrocnemius et M. soleus	1.47	1.09
Mm. extensors	0.60	1.11
M. tibialis caudalis	0.12	0.69
M. quadratus lumborum	0.32	1.09
M. iliocostalis thoracis	0.47	0.97
M. transversus thoracis	0.24	1.15
M. serratus dorsalis caudalis	0.22	1.01
M. retractor costae	0.25	0.74
M. deltoideus	0.55	0.96
M. infraspinatus	1.99	0.95
M. teres minor	0.17	1.11
M. biceps brachii	0.56	1.08
M. teres major	0.58	0.94
M. extensor carpi radialis	0.67	0.96
M. extensor digitorum communis	0.08	1.09
M. abductor pollicis longus	0.01	1.27
M. pectoralis profundus	3.17	0.87
Mm. pectoralis superficialis	1.53	0.79
M. serratus ventralis cervicis	3.45	1.01
M. brachiocephalicus	1.41	0.92
M. intercostales (externi et interni)	3.25	0.98
M. splenius	0.51	1.02
M. intertransversarius longus	0.77	0.94
M. longissimus capitis et atlantis	0.68	0.74
M. intertransversarius cervicis (dorsalis et ventralis)	0.50	1.05
M. scalenus ventralis	0.60	0.90
Total	35.17	0.98

Dorset Horn Wethers		
M. biceps femoris	5.11	1.03
M. vastus lateralis	2.53	1.14
M. semitendinosus	1.78	1.04
M. gracilis	0.96	0.98
M. pectineus	0.54	1.05
M. sartorius	0.20	0.70
M. articularis genu	0.11	1.18
M. gastrocnemius et M. soleus	1.64	1.09
Mm. extensors	0.62	1.11
M. tibialis caudalis	0.11	1.34
M. quadratus lumborum	0.36	1.09
M. iliocostalis thoracis	0.41	0.97
M. transversus thoracis	0.21	1.15
M. serratus dorsalis caudalis	0.26	1.01
M. retractor costae	0.27	0.74
M. deltoideus	0.50	0.96
M. infraspinatus	2.08	0.95
M. teres minor	0.16	1.11
M. tensor fasciae antebrachii	0.31	0.75
M. biceps brachii	0.61	0.86
M. teres major	0.58	0.94
M. extensor carpi radialis	0.72	0.96
M. extensor digitorum communis	0.08	1.09
M. abductor pollicis longus	0.01	1.27
M. flexor carpi radialis	0.11	0.87
M. anconeus	0.14	1.35
M. pectoralis profundus	3.43	0.87
Mm. pectoralis superficialis	1.46	0.79
M. omotransversarius	0.47	1.01
M. serratus ventralis cervicis	3.27	1.01
M. brachiocephalicus	1.18	0.92
M. intercostalis (externi et interni)	3.20	0.98
M. splenius	0.19	1.02
M. intertransversarius longus	0.49	0.94
M. intertransversarius cervicis (dorsalis et ventralis)	0.49	1.05
M. complexus	1.10	1.09
Total	35.69	0.99

(c) **Muscles with 'q' significantly greater than 1.0**

Dorset Horn Rams		
M. tensor fasciae latae	0.86	1.35
M. gluteus medius	3.14	1.20
M. rectus femoris	1.96	1.23
M. semimembranosus	4.13	1.23
M. abductor femoris	1.71	1.30
M. quadratus femoris	0.05	1.46
Mm. obturatorii externus et internus	0.43	1.33
M. vastus medialis	0.83	1.30
M. iliacus	0.53	1.22
M. gluteus profundus	0.28	1.45
M. gemellus	0.04	1.78
M. vastus intermedius	0.70	1.24
M. peroneus longus	0.15	1.31
M. extensor digitorium lateralis	0.19	1.45
M. tibialis cranialis	0.13	1.41
M. popliteus	0.27	1.34
M. flexor digitorum longus	0.10	1.46
M. flexor digitorum superficialis	0.54	1.22
M. flexor hallucis longus	0.47	1.34
M. psoas major	1.21	1.24
M. longissimus thoracis et lumborum	8.88	1.25
M. multifidus thoracis et lumborum	1.21	1.47
M. longissimus cervicis	0.28	1.34
M. psoas minor	0.47	1.19
M. triceps brachii (caput laterale)	0.55	1.89
M. triceps brachii (caput longum)	2.31	1.20
M. supraspinatus	1.78	1.23
M. brachialis	0.32	1.36
M. coracobrachialis	0.17	1.29
M. subscapularis	0.87	1.56
M. triceps brachii (caput mediale)	0.13	2.01
M. extensor digitorum tertii	0.10	1.35
M. extensor digitorum lateralis	0.11	1.41
M. ulnaris lateralis	0.33	1.33
M. flexor carpi radialis	0.10	1.23
M. flexor carpi ulnaris	0.19	1.20
M. flexor digitorum profundus	0.46	1.32

M. anconeus	0.12	1.98
M. flexor digitorum sublimis	0.17	1.36
M. serratus dorsalis cranialis	0.04	1.91
M. obliquus capitis caudalis	0.42	1.30
M. longus colli	0.72	1.25
M. multifidus cervicis	0.55	1.22
Total	38.00	1.28
Dorset Horn Wethers		
M. tensor fasciae latae	0.92	1.35
M. gluteus medius	3.34	1.20
M. gluteus accessorius	0.45	1.36
M. rectus femoris	2.15	1.23
M. semimembranosus	4.51	1.23
M. abductor femoris	1.91	1.30
M. quadratus femoris	0.04	1.46
Mm. obturatorii externus et internus	0.45	1.33
M. vastus medialis	0.84	1.30
M. iliacus	0.57	1.22
M. gluteus profundus	0.25	1.45
M. gemellus	0.04	1.78
M. vastus intermedius	0.67	1.24
M. peroneus longus	0.17	1.31
M. extensor digitorium lateralis	0.21	1.45
M. tibialis cranialis	0.15	1.41
M. popliteus	0.27	1.34
M. flexor digitorium longus	0.11	1.46
M. flexor digitorium superficialis	0.54	1.22
M. flexor hallucis longus	0.46	1.34
M. psoas major	1.36	1.24
M. longissimus thoracis et lumborum	9.39	1.25
M. multifidus thoracis et lumborum	1.15	1.47
M. longissimus cervicis	0.28	1.34
M. psoas minor	0.53	1.19
M. triceps brachii (caput laterale)	0.70	1.21
M. triceps brachii (caput longum)	2.43	1.20
M. supraspinatus	1.93	1.23
M. brachialis	0.31	1.36
M. coracobrachialis	0.18	1.29
M. subscapularis	3.48	1.56
M. triceps brachii (caput mediale)	0.14	2.01
M. extensor digitorum tertii	0.10	1.35
M. extensor digitorum lateralis	0.10	1.41
M. ulnaris lateralis	0.31	1.33
M. flexor carpi ulnaris	0.19	1.20
M. flexor digitorum profundus	0.51	1.32
M. flexor digitorum sublimis	0.18	1.36
M. serratus dorsalis cranialis	0.04	1.91
M. longissimus capitis et atlantis	0.35	1.30
M. obliquus capitis caudalis	0.39	1.30
M. scalenus ventralis	0.43	1.37
M. longus colli	0.72	1.25
M. multifidus cervicis	0.50	1.22
Total	43.75	1.29

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