

Limitations to the manipulation of growth

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Many areas of science become associated with both a particular centre and with the scientists who staff it, and there is no more famous trilogy than growth, Cambridge and the Hammond School. It is therefore difficult to see how the contributions of this distinguished group of workers and their numerous disciples can be incorporated into an original review which substantially supplements the many excellent summaries of growth in mammals which already exist. Perhaps the only justification is that for each true disciple of Hammond there are imitators. In no other area of animal production is it so easy, or so frequently practised, for marginal adjustments to the conclusions arising from experimental studies to be made and then, as a result of many such modifications, for the over-all interpretation to be so different from those of the original author.

The objective of this paper is to attempt to discuss those aspects of growth which can be generally accepted so that areas of ignorance, matters for debate or controversy can be identified. It is impossible to justify each statement in this paper with a comprehensive catalogue of references. The studies quoted should be considered merely as examples of specific features of growth rather than as either a comprehensive list of references or even the most important examples available since many of the experiments quoted are those in which the author had had some particular interest. It is accepted that this approach is subjective in terms of the material selected and others may reach very different conclusions by using different sources of information.

The greatest achievements of the Hammond School, probably best summarized by Palsson (1955), were to provide data on the growth of farm livestock which had not previously been published, to provide a cadre of workers who were fascinated by growth and to provide a series of papers from which emerged principles concerned with growth and development. These papers resulted in a confidence that the manipulation of growth was possible and that such techniques could be usefully and profitably incorporated into the technology of animal production. The individual experiments, acting as catalysts for change, inaugurated a new interest in animal husbandry. In particular the experiments of Wallace (1948) and McMeekan (1940) provided evidence that the strategic use of nutrition could lead to the control of growth in early life and reduce mortality as well as enable the tailoring of the carcass to meet both the needs of the consumer and the farmer. It would be naïve to believe that such concepts were new, they were at least as old as Virgil, but the Hammond School and the world-wide sub-

schools which Hammond caused to appear, found comfort in an explanation of the serial changes in composition and conformation that the slaughter techniques inevitably produced. The verification of such basic principles by experimentation made them academically acceptable to teaching establishments so that the message was quickly conveyed to all sectors of medicine and agriculture. It was at this multiplication stage that many of the half-truths were born which eventually produced the confusion that still exists between research scientists, those that interpret the results of scientific papers and those who seek to apply the results of science in medicine or agriculture. The proliferation of experiments from 1950 onwards produced some doubt about the validity of some principles of growth because of the apparent lack of agreement between the results of individual experiments. A more positive and realistic view would have been that under a wide range of experimental conditions and using a wide range of species the experimental programmes produced very few results which were at variance with a central theme, particularly when the results of some experiments were transformed to make the comparisons more appropriate.

In essence, the major questions arising from this programme concerning the growth of birds and mammals can be stated simply.

1. Do animals increase in weight according to simple functions which allow a pattern of growth to be discernible in circumstances when environmental factors are not allowed to distort growth and development?

2. What are the changes in conformation, composition and function that accompany this increase in total mass and do these changes follow some predictable pattern?

3. In what way can this normal pattern of growth be modified by the environment?

4. Does modification of the growth at one stage have implications to growth and development at some other stage?

5. How do the modifications achievable by changes in the environment, largely a function of nutrition, relate to and compare with those attributable to variations in genotype, to differences between the sexes and those which arise as a result of the stage of maturity at which the animals are assessed?

One way of assessing these apparently simple questions is to attempt to answer them with equal simplicity, a technique that usually reveals a deficiency in our knowledge and understanding.

1. *Pattern of growth*

The shape of growth pattern of animals so brilliantly portrayed by Brody (1945) is not a matter of controversy. It is accepted that the growth of mammals and birds follows a sigmoid pattern, although some animals, notably man, extend some of the phases of the sigmoid pattern. The acceptance of this growth pattern is due to the unanimity which results from the pooling of a substantial body of data.

This general agreement should not, however, disguise the fact that if intensive

recording of the growth of small populations is undertaken, such as those that constitute the animals within an individual experiment, then the growth of the animals may substantially differ from the generalized sigmoid form. The explanation may well lie in the distortions caused by features of the management or the environment. It is not easy to identify all the features that cause such deviations although some can be distinguished.

The difference in function of the animal between the pre-natal phases is evident and hence it is not surprising that differences exist in metabolism and dynamics of growth of components of the body. Attempts to combine both phases of growth are, therefore, in philosophical terms inappropriate, although in some circumstances it is possible in mathematical terms. Features of carbohydrate metabolism of the foetus, the production of brown fat by the foetus, the changes in role of the vascular, digestive and locomotory systems from the foetal to the post-natal phase all support this view.

In post-natal life, the pattern of growth may not be apparent due to the selection of the phase of growth examined. Thus for the pig between 35 kg and 90 kg live weight the impression can be gained on an animal growing according to a linear function.

In other circumstances the degree of unilinearity of the growth determined may merely be a result of environmental factors which tend to heighten the sigmoid nature of the growth curve. For example, the generally accepted growth rate of pigs over the period 5 to 20 d of life as piglets suckling the sows may not reflect the true potential of the piglets for growth. Experiments by many workers (Braude & Newport, 1973) demonstrate that pigs artificially reared over this phase can grow at a much higher rate than previously thought possible, whilst Braude (1955) quotes a study in which piglets suckling alternatively on two lactating sows can achieve very high growth at a stage when it has been generally assumed that the potential for growth is limited. The view that the pigs cannot attain a high growth rate before 25 kg is often confounded with a check at weaning and with the lowered palatability and digestibility of feed and the incidence of intestinal disorders which is frequently associated with the phase immediately following weaning.

Likewise it is dangerous to assume that once pigs are growing in the post-weaning phase that the provision of feed *ad lib.* always allows the individual pigs to consume feed at their appetite level. For example, pigs may exhibit specific behavioural patterns when they are housed in groups (Ewbank, 1972) and their responses can be further complicated by the form in which the feed is presented.

These examples have been selected to demonstrate that management practices may themselves combine to accentuate the pattern of growth which is expected, and the fact that such a generalized sigmoid curve is produced may conceal the fact that the piglets are not exhibiting their true potential. Very few authorities would be willing to identify the maximum growth, and in particular the potential protein deposition, that any specified population of animals could achieve in the absence of environmental constraints.

2. *The composition and conformation changes with time*

As a result of the initial stimulation provided by the Hammond group of workers over the last forty years, there is now factual information on most farm livestock that allows the description of development changes. This body of information allows regression equations to predict with considerable accuracy (e.g. Reid *et al.*, 1968) (Table 1) the developmental and compositional changes so brilliantly described by Hammond and his co-workers (Palsson, 1955). Apart from the more precise quantification of these changes, it can be queried as to whether the information now available alters in any major way the philosophy of developmental physiology propounded by Hammond or alters the over-all use that agriculture or medicine makes of the data. In many instances the information is far more comprehensive (Davies, 1973, 1974*a*, 1974*b*), but in most instances such studies merely record the biochemical or metabolic changes that accompany the simple measurements recorded by Hammond.

Table 1. *Relationship between weights of chemical components and the body-weight of all sheep studied, irrespective of fat concentration or breed (from Reid et al. 1968)*

Component	Prediction equation*	Correlation coefficient	R ²	Coefficient of variation† (%)
Water	$Y=0.4067X+ 5.313$	0.963	0.927	7.69
Fat	$Y=0.4537X- 7.003$	0.945	0.893	25.34
Protein	$Y=0.1190X+ 1.199$	0.961	0.924	8.46
Energy	$Y=4.9235X-59.6920$	0.967	0.935	16.29

Relationship between weight of chemical components and the body-weight of sheep containing less than 31% fat

Component	Prediction equation*	Correlation coefficient	R ²	Coefficient of variation† (%)
Water	$Y=0.4776X+ 3.511$	0.982	0.964	5.23
Fat	$Y=0.3570X- 4.559$	0.943	0.889	21.31
Protein	$Y=0.1386X+ 0.705$	0.979	0.958	6.06
Energy	$Y=4.1146X-39.2214$	0.968	0.937	13.02

*Y=body component (kg) or energy (Mcal) and X=ingesta-free body weight (kg).

†Coefficient of variation (%) = $(S_{y,x}/\bar{Y}) \times 100$.

The allometric changes which describe the changing rates of deposition of the tissues according to function (Berg & Butterfield, 1976, Fowler, 1972, Hammond, 1932) are not in dispute. The profuence of the data on all species does, however, serve to emphasize two points. Firstly, the changes in conformation and composition, that occur over that portion of the growth curve that is most easily controlled by the agriculturist in the production of meat from farm livestock, are comparatively small in comparison with the gross increase in live weight. (Table 2, Richmond & Berg, 1971). Secondly, the incorporation of these allometric changes

into simple mathematical expressions is successful in a generalized way, but such expressions do not describe with any accuracy what occurs in a small population such as that which normally constitutes the group of animals in a single experiment.

Table 2. 'Standard muscle groups' as percentage of weight of total side muscle in 109 barrows and gilts of three breeds and slaughtered at four live weights (after Richmond & Berg, 1971)

Muscle group	Live weight (kg)			
	23	68	91	114
Proximal pelvic limb	26.56	28.40	28.25	28.67
Distal pelvic limb	3.99	3.96	3.84	3.87
Spinal	16.83	17.01	17.42	17.44
Abdominal	12.41	11.32	10.98	11.16
Proximal thoracic limb	12.35	12.29	12.05	11.79
Distal thoracic limb	2.15	1.94	1.89	1.85
Thorax to thoracic limb	7.35	7.56	7.64	7.38
Neck and thorax	9.28	9.39 a	10.02 b	9.76 ab
Scrap	4.69	3.21	3.06	3.08
Expensive Groups A	30.61	32.36	32.09	32.54
B	47.46	49.38	49.51	49.98
C	59.81	61.67	61.56	61.78

The presentation of the information concerning these dynamic changes in conformation or composition, in itself, presents problems. In a typical Hammond description the sequence with which the tissues attain their maximum growth rates were simply classified by a maturity index (Fig. 1).

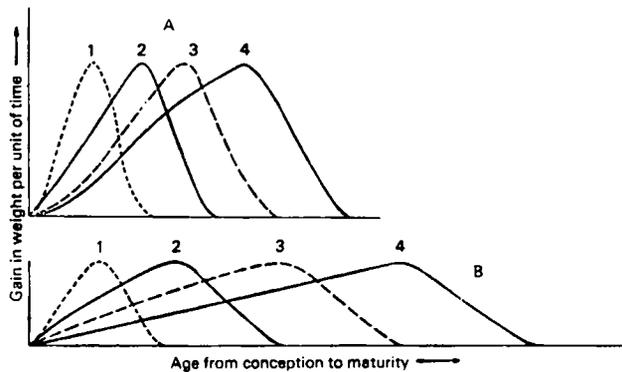


Fig. 1. The rate of increase in weight, showing the order of development of the different parts and tissues of the body and the way in which the changes in shape and body proportions are affected by early and late maturity and/or the level of nutrition. A, early maturity or high plane of nutrition, B, late maturity or low plane of nutrition. Curves: 1, head, brain, cannon, kidney fat; 2, neck, bone, tibia-fibula, intermuscular fat; 3, thorax, muscle, femur, subcutaneous fat; 4, loin, fat, pelvis, marbling fat. (From Palsson, 1955).

This graph which so brilliantly summarizes these important changes can also lead the casual reader into an entirely false premise. One interpretation would be that all the tissues respond independently of each other and that the order with which they attain maximum rates of deposition is immutable. This is not always the case particularly with regard to the deposition of fat. Using the pig again as the example, the rate of fat deposition can exceed any of the other tissues in the immediate post-natal period up to 5 d of age and the deposition of fat and protein can be identical for much of the period up to 8 weeks of age (Whitelaw, Elsley, Jones & Boyne, 1966).

The recent work of Lister and his colleagues using data available at the Meat Research Institute also questions the generality of Hammond's view of the maturity of the different sites of fat deposition (Lister, 1976). 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 rate of tissues. The need for caution in the use of these terms is best shown by comparing the relative rates of growth of tissues in the pre-natal and post-natal phase of growth where, for example, the relative growth of bones of the limbs can be transposed from 'late' maturity in the middle of the foetal phase to 'early' maturity in the immediate post-natal phase.

Table 3. *Growth coefficients of the logarithms of bone, muscle and fat in the side on the logarithms of different independent variables (from Cole, White, Hardy & Carr, 1976)*

	Independent variable	Growth coefficient $b \pm (t_{0.05} \times SE)$	Residual sd
Muscle	bone	1.30 ± 0.090	0.035
Fat	muscle	1.14 ± 0.181	0.094
Bone	total side	0.69 ± 0.046	0.025
Muscle	total side	0.95 ± 0.065	0.025
Fat	total side	1.22 ± 0.121	0.065
Bone	muscle+bone	0.75 ± 0.048	0.023
Muscle	muscle+bone	1.04 ± 0.009	0.003
Fat	muscle+bone	1.20 ± 0.186	0.093

$$t_{0.05} = 1.998, n - 2 = 64.$$

The need to compare tissues against some independent variable, in order to measure how the dynamics of the growth of tissues relate to each other, is widely recognized. It is clearly desirable to use an independent variable that contains a component which is insensitive to manipulation of the environment, which could lead to anomalies when tissues are relatively compared. This view is supported by Wilson (1954), Wallace (1948), Elsley, Macdonald & Fowler (1964) who all identified that fat is such a variable of the carcasses of pigs, and to a lesser extent of sheep, and thus the relative growth of other tissue cannot be satisfactorily compared against an independent variable which contains high fat concentrations. Recently Cole, White, Hardy & Carr (1976) have reported that a number of growth coefficients, as calculated from the allometric equation, can be determined using

different independent variables (Table 3). Although the growth coefficients differ their efficiency at describing the relative dynamics of tissue growth are similar. The authors claim that there is good agreement between the coefficients and values reported elsewhere for cattle, sheep and pigs. In accepting this view, it is probably not productive to seek endlessly for a universally acceptable independent variable against which to relate growth of components of the body. For example, the use of muscle plus bone as the basis for comparing the growth of tissues by Elsley, Macdonald & Fowler (1964) is subject to limitations; for example when comparisons are being made of the relative development of skeletal tissue for animals receiving different levels of minerals in the diet. Rather the view should be accepted that the body contains components that are correlated to differing independent variables; for example, eye lens weight up to puberty is related to age, heart weight to the gross weight of animal, the weight of individual muscles to the total muscle weight relative to age, and the weight of subcutaneous fat to the live weight of animal or to the plane of nutrition or to both. In each instance it is therefore to select the appropriate independent variable. In many instances the fat-free weight is subject to fewer objections than many other possible bases for comparison. The development of multi-regressional analyses which allow a partition of effects due, for example, to age, weight, sex, are clearly a considerable advantage in the philosophic study of growth and in eliminating many of the anomalies outlined above (Whittemore, 1976).

Within each species there is very good agreement in the development of the animals during growth. Obvious exceptions can be quoted such as the short-legged sheep, double-muscled cattle, but it is noteworthy that it is necessary to seek such abnormal differences in genotype in order to identify deviations from the general rule. As reported by many workers, the main differences in genotype lies in the rate of growth of the animals relative to their target mature weight (Taylor, 1965). Any comparisons between animals with different physiological ages are meaningless in physiological terms unless the comparisons are made with a knowledge of their stage of development relative to this final weight. The implications of this statement will be discussed later in the paper.

3. Manipulation of growth

Having established the 'normality' of growth of animals and the components that make up the increase in weight, it is important to establish if and how the 'normality' can be affected by changes in the environment. It was this concept of 'growth engineering' that caught the imagination of the animal productionists as a result of the experiments reported in the 1930s and 1940s largely by the Hammond School.

The animal productionist has a number of objectives in attempting to manipulate growth. It would be attractive if: (a) the proportion of the carcass which is edible could be increased by changing the amount of lean relative to other tissues; (b) the proportion of high priced joints relative to lower priced joints could be increased; (c) feed costs could be reduced largely by the avoidance of the high

cost of deposition of lipid; (d) these objectives could be achieved without too great a reduction in the growth rate.

The concept of waves of growth, with tissues reaching their maximum rates of growth at different stages of maturity gave hope that growth engineering could be achieved by inhibiting the growth of an undesirable component of the body at its most dynamic phase of growth. This view is most clearly stated by Palsson (1955). Since the gross feed intake is the most important factor controlling over-all increase in live weight of animals, research workers and the agricultural industry were interested in the effect of controlling feed intake upon the development of individual tissues. Perhaps more emphasis should have been directed to the relatively high correlation between growth rate and the feed intake after adjustment had been made for maintenance needs, before developing the hypothesis that there is differential sensitivity with which tissue respond to changes in feed intakes depending on the point of maturity at which the change is made.

The success of McMeekan's high-low group in restricting the deposition of late-maturing fat tissue, that is, severe restriction from 25 lb as compared with low-high group of *ad lib.* intake from 45 lb live weight, encouraged people to extrapolate the hypothesis to cover the prediction of an effect depending on whether the growth of the pigs was inhibited before birth, in early life up to 8 weeks, or between 50 and 100 lb live weight. Since the pig has the capacity to consume large amounts of digestible feed relative to its live weight and is clearly capable of manipulating its fat deposition, the pig is a useful animal against which to test these theories.

Manipulation of the growth in the pig

Since the experiment of McMeekan (1940) the pig has been studied in detail with respect to the effect of the environment upon growth and development. This interest is due to the fact that the appetite of pigs is high in relation to the maximum daily protein deposition of which it is genetically capable. This has led to a whole family of strategies which seek to maximize lean deposition whilst limiting fat deposition (Whittemore, 1976).

The response of the pig to simple manipulation of energetic intake has been frequently described. The subject was reviewed by Kielanowski (1972) and the over-all response to changes in intake pictorially represented by Whittemore & Elsley (1976) (Fig. 2).

Although the pig data are only most generally described by the equations of Parkes (1975) which is based on many species, a sensible summary to changes in intake in the period from 25 kg to 90 kg emerges from the publication of Davies & Lucas (1972), and such a response is in good agreement with the estimated results based on a biochemically based model (Whittemore & Fawcett, 1974). Similar response situations have been discussed for pregnant sows where a clear relationship exists between intake in pregnancy and the growth of individual foetuses (Lodge, 1972), between feed intake of lactating sows and the growth of

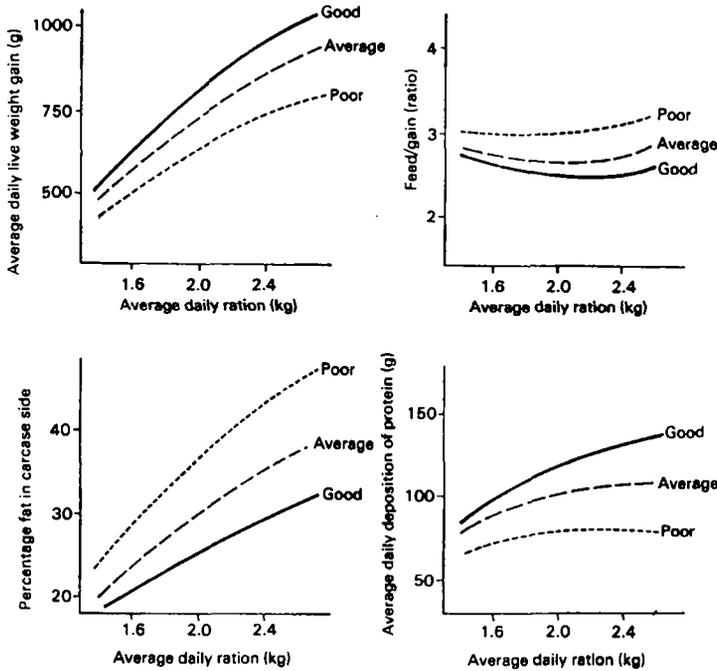


Fig. 2. The response of pigs to varying levels of nutrition. (From Whittemore & Elsley, 1976).

suckling pigs to 6 weeks of age Elsley (1972) and the growth of pigs weaned from the sows at early stages (Elsley (1961), Fowler (1964)).

From these and other studies there is clear evidence as to how pigs quantitatively respond to changes in intake.

Table 4. Weight of dissected fat and chemical lipid (predicted values) (from Fowler, 1972)

Dependent variate	Independent variate with selected value (kg)	Sex	H, HP*	H, LP*	L, HP*	Approx. LSR*	Over-all significance of treatments
Subcutaneous fat plus skin (kg)	carcass weight 80	M	19.9	26.3	13.5	1.14	$P < 0.001$
		M	20.0	26.9	16.8		
		F	22.5	28.4	15.2		
Perirenal fat (kg)	basic animal 50	M	1.08	2.42	1.49	1.51	$P < 0.001$
		M	1.06	3.07	1.00		
		F	1.28	3.56	0.67		
Chemical lipid in basic animal (kg)	Fat-free basic animal 42	M	5.7	10.1	3.9	1.30	$P < 0.001$
		M	7.0	14.1	5.7		
		F	5.8	12.4	4.8		
Intramuscular lipid (g)	Fat-free selected muscle 13	M	689	1235	521	1.34	$P < 0.001$
		M	763	1686	633		
		F	810	1483	546		

*H, HP high energy, high protein; H, LP high energy, low protein; L, HP low energy, high protein; LSR least significant ratio.

It is therefore useful to study to what extent changes in nutrition at different stages of growth can influence the conformation and composition of the tissues and components during these phases. Some of the likely results of individual experiments can be predicted from the results of the classical experiments undertaken by the Hammond School and by McCance and his co-workers. Although some controversy still exists there is now general agreement with the interpretation placed on the results obtained by McMeekan (1940) and Elsley & Macdonald & Fowler (1964). These views, substantiated by further experimentation by Fowler (1972), demonstrate that variation in fat is affected by level of nutrition but that the growth of the other tissues, relative to each other, are remarkably homoeostatic after allowance is made for the stage of development at which the comparisons are made (Table 4). Fowler (1972) argues that to suggest otherwise would be to postulate that the relative growth of the tissues is independent of function, a view that is contrary to the view of D'Arcy Thomson (1917). If 'form follows function' then one can readily accept the views of Berg & Butterfield (1976) who summarize data of cattle and reach the same simple but powerful conclusions. It could be argued that McMeekan (1940) and Fowler (1972) examined the plasticity of growth in a phase when little manipulation of composition other than fat would be probable. The classic and effective experiments of McCance and his co-workers most clearly support the view that in the period from 4.5 kg live weight the metabolism, and in particular the protein metabolism, of the pig has the great capacity to be reflected by changes in growth rate, but not in composition, as a result of gross nutritional insults. In view of this the results of Elsley (1961) and Fowler (1964), which demonstrated the ability of the pig to lay down fat at an early stage, which belies its maturity rating, but to develop in other respects normally, are logical. There are phases when restriction of nutrient supply can influence growth, but a summary of a range of experiments which sought to demonstrate the effect of nutrition of the pregnant dam upon the composition of foetal growth (Jones & Elsley, 1966) revealed no clear response apart from a restriction of over-all growth rate achieved as a result of reducing feed intake by factors of up to 50% of conventional nutritional regimes.

It is suggested that the results of the 179 experiments concluded since 1945 which sought to achieve composition changes as a result of gross nutritional manipulation including both changes in energetic and protein intake support the naïve view that the composition of the fat-free mass is largely immutable. It should be pointed out, however, that in some experiments the shape of bones have been effected by the pattern of nutritional regimes imposed, and that after puberty their constancy of composition can be affected by the burden of reproduction which competes for the nutrients available for the growth process. Elsley (unpublished results) found that under these conditions the bone development of immature sows subject to a range of nutritional treatments in lactation were unaffected by the treatment being positively correlated to the age of the sows whilst both the fat and muscle components were subject to considerable reduction in rate of deposition and eventually were mobilized.

This view of growth in the pig is supported and substantiated by the views of Berg & Butterfield (1976) who present a range of data concerned with cattle. It is not inconsistent with the published work on growth of the lamb and in particular, results from the substantial experimental programme of Jackson at Edinburgh (Jackson, unpublished results).

4. *The interaction between different phases of growth*

The above section has concentrated on the effects of manipulation of growth upon the composition of the animal at the completion of growth.

It is intriguing to postulate that growth at one phase can have an influence on growth in a subsequent period. The resolution of such a problem is important in relation to the view taken on the effects of malnutrition in an early phase upon the subsequent growth of children and upon the use that can be made of compensatory growth in farm livestock (Wilson & Osborne, 1961). To substantiate such effects it is necessary to postulate either: (i) a residual effect on feeding behaviour so that intake is very much higher, or lower than would be expected for an animal of a specified weight; or (ii) a residual effect on the efficiency of metabolism; or (iii) a permanent effect on either the potential for growth or the possibilities of the re-initiation of growth following a phase of growth of unusual severity.

Coey (1954) found clear relationships between growth at one phase with growth at other phases but most other workers have been surprised by the lack of 'carry-over' that can be detected even following large differences in nutrition. The results of, for example, Elsley (1961) who found that pigs grew from 8 weeks of age independently of the nutritional history up to 8 weeks of age, is not surprising when viewed against the growth of pigs which occurred during the realimentation phase of the McCance & Widdowson classical experiment. Lodge & Macdonald (1959) analysed the growth of pigs from birth to weaning taking into account birth weight, milk yield and creep consumption and concluded that quite large differences in birth weight reflecting large differences in physiological age at birth had little effect on subsequent growth. It would be ludicrous to suggest that there is no phase of growth of the pig where nutritional pattern cannot influence subsequent development.

When it is considered that in the pig the change in DNA to protein ratio which heralds a change in cell multiplication dynamics takes place between the 95th and 100th day of pregnancy it would be wrong to extrapolate from results from laboratory animals where this phase takes place much later than with farm livestock.

There must be a limit to the ability of the animal's metabolism, in particular the protein metabolism, to slow down, increase or stop. In pigs the behavioural effect on feed intake is not very noticeable although present for up to 20 d following realimentation. The changes in metabolic efficiency are in doubt, but the animals show considerable ability to accelerate or decelerate. In the ingenious experiment of Fowler & Livingstone (1971) the pigs ability to use, with identical efficiency, a standard quantity of feed provided according to a wide variety of feeding patterns,

as long as the pig fed at all times above maintenance, certainly indicates few 'carry-over' effects.

The question still remains as to whether, apart from feeding behaviour or metabolic efficiency, there is an absolute change in the ability of the animals to lay down tissue, particularly fat-free tissue. In particular, can animals which have been restricted lay down non-fat tissue with an efficiency that exceeds animals which have been subjected to no reduction in growth? It may well be that in some experimental circumstances the environment in the realimentation phase allows the animal to achieve its true genetic potential. This could be due to many factors and in specific circumstances this may result in an apparent increase in the productivity when compared with normally fed animals. However I remain to be convinced by scientific data that the potential for the rate of growth of non-fat tissues is increased as a result of a period of under-nutrition followed by feeding regimes designed to make use of 'compensatory growth' principle.

5. Influence of genotype, sex and stage of maturity upon the growth of animals

In attempting to manipulate the growth and the composition of animals by adjusting the environment in which animals are maintained, largely a factor of the nutritional environment, it should not be overlooked that the most effective way to manipulate growth is to change the genotype of the animals, to capitalize the differences between the sexes or to alter the stage of maturity at which the animals are slaughtered. In a range of papers Taylor has clearly indicated the correlation between the mature weight and the growth characteristics of cattle up to this point, and this concept has been used by Berg & Butterfield (1976) to explain a large proportion of the differences between the growth and development of different breeds of cattle. The interesting proposals of Lister and his co-workers at the Meat Research Institute clearly point to the important differences between breeds relating to method of fat deposition and hence to their carbohydrate metabolism but the fact remains that most important differences between genotypes are explained by differences in target mature weight. The percentage of variation attributable to mature weight greatly exceeds any variation in growth characteristics relating to the shape of growth curve or changes in the composition of growth.

The difference between the sexes in relation to growth and development is so well known that they require little elaboration. Surprisingly, in view of the differences in hormone balance which control the growth processes, reproduction function and secondary sexual characteristics, most of the differences between the sexes can be minimized by adjustments of the data to either equivalent feed intake or by transforming the carcass data so that differences in fat are eliminated (Fig. 3) (Berg & Butterfield, 1976). It is an intriguing prospect at the moment only partially achieved, that these differences attributable to sex could be simulated by the presence of synthetic steroid-like substances.

Finally it should not be forgotten that probably the most powerful way of manipulating growth and development of farm livestock is to alter the weight at

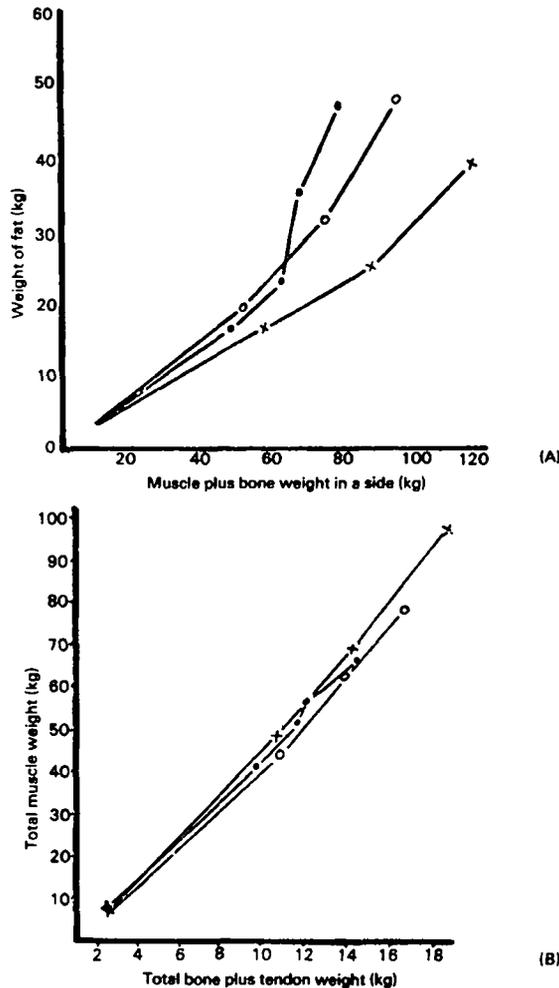


Fig. 3. Growth of tissues in heifers, steers and bulls. (A) Fat relative to muscle plus bone. (B) Muscle relative to bone. ●, Heifers; ○, Steers; ×, Bulls. (From Berg & Butterfield, 1976).

which they are slaughtered, relying on the clear differences in composition which occur as the animal develops which were originally demonstrated by the Hammond School and which have subsequently been substantiated by a whole range of workers (Table 5).

Table 5. Growth coefficients for various 'functional units' regressed on 'basic animal'

	♂	♀	
Head	0.70	0.71	Early maturing
Ribs plus intercostal tissue	0.92	0.90	
Forelimbs	0.98	0.97	
Hindlimbs	1.05	1.04	Late maturing
Abdominal wall	1.05	1.10	
Longissimus dorsi	1.23	1.20	

Conclusions

It is difficult to reach exact conclusions from an examination of the vast array of evidence on growth of animals of which only token reference has been made in this paper. It is important, however, to attempt to identify some conclusions so as to allow others a basis against which their own results can be compared.

1. The shape of the pattern of growth of most species is generally predictable although too little emphasis has been given to distinguishing the normal pattern of growth from the true potential for growth once environmental limitations have been excluded.

2. The pattern of the composition of growth of most domesticated species is well known and in most cases is closely related to function. Many of the apparent differences between different samples of any one species arise because of differences in the basis on which the results are compared.

3. The manipulation of over-all growth by adjustment in total intake, or by limiting the availability of individual nutrients is easy to achieve. The adjustments which arise out of nutritional manipulation in the shape of animals, their composition (other than in fat deposition) are not of sufficient magnitude to allow them to be important features of agricultural production.

4. The growth of animals at one phase can influence growth at another phase, but all mammals have considerable capacity to accelerate or decelerate growth with comparatively little effect on subsequent potential for growth and development. According to the stage and severity at which the nutritional treatment is imposed there may be 'carry-over' effects for a period in respect to feeding behaviour and short-term metabolic effects and longer term effects on target mature size. Evidence is awaited that will demonstrate a change in the capacity of protein deposition per se to be increased as a result of a phase of under-nutrition.

5. The manipulation that can be achieved by nutrition should be quantitatively compared with the effects attributable to genotype, sex or slaughter weight.

REFERENCES

- Berg, R. T. & Butterfield, R. M. (1976). *New concepts of cattle growth*. Sydney: Sydney University Press.
- Braude, R. (1955). In *Progress in the Physiology of Farm Animals* Vol. 1. London: Butterworths.
- Braude, R. & Newport, M. J. (1973). *Br. J. Nutr.* 29, 447.
- Brody, S. (1945). *Bioenergetics and Growth*. New York: Reinhold.
- Coey, W. E. (1954). *Agric. Prog.* 29, 60.
- Cole, D. J. A., White, M. R., Hardy, B. & Carr, J. R. (1976). *Anim. Prod.* 22, 341.
- Davies, A. S. (1972). *J. Anat.*, 113, 213.
- Davies, A. S. (1974a). *Anim. Prod.* 19, 367.
- Davies, A. S. (1974b). *Anim. Prod.* 19, 377.
- Davies, J. L. & Lucas, I. A. M. (1972). *Anim. Prod.*, 15, 127.
- Elsley, F. W. H. (1972). In *The Improvement of Sow Productivity*, Proc. Symp. Rowett Research Institute.
- Elsley, F. W. H. (1961). *J. Agric. Sci., Camb.* 61, 243.
- Elsley, F. W. H., McDonald, I. & Fowler, V. R. (1964). *Anim. Prod.* 6, 141.
- Ewbank, R. (1972). In *Pig Production* [D. G. A. Cole, editor]. London: Butterworths.
- Fowler, V. R. (1964). PhD Thesis, University of Leeds.

- Fowler, V. R. (1972). In *Pig Production*, [D. G. A. Cole, editor]. London: Butterworths.
- Fowler, V. R. & Livingstone, R. M. (1971). *Anim. Prod.* 13, 59.
- Hammond, J. (1932). *Growth and Development of Mutton Qualities in the Sheep*. Edinburgh: Oliver & Boyd.
- Jones, A. S. & Elsley, F. W. H. (1966). Annual Report of Studies in Animal Nutrition and Allied Sciences, Rowett Research Institute, 22, 97.
- Kielanowski, J. (1972). In *Pig Production* [D. J. A. Cole, editor]. London: Butterworths.
- Lister, D. (1976). *Proc. Nutr. Soc.* 35, 351.
- Lister, D. & McCance, R. A. (1967). *Br. J. Nutr.* 21, 787.
- Lodge, G. A. (1972). In *Pig Production* [D. J. A. Cole, editor]. London: Butterworths.
- Lodge, G. A. & McDonald, I. (1959). *Anim. Prod.* 1, 139.
- McMeekan, C. P. (1940). *J. agric. Sci., Camb.* 30, 276, 387, 511.
- Parkes, J. R. (1975). *J. theor. Biol.* 55, 381.
- Palsson, H. (1955). In *Progress in the Physiology of Farm Animals* Vol. 2. London: Butterworths.
- Reid, J. T., Bensadonn, A., Bull, L. S., Burton, J. H., Gleeson, P. A., Han, I. K., Joo, Y. D., Johnson, D. E., McManus, W. R., Paladines, O. L., Stroud, J. W., Tyrell, H. F., Van Biekerk, B. D. H. & Wellington, G. W. (1968). *Some Peculiarities in the Body Composition of Animals*. Washington: National Academy of Sciences.
- Richmond, R. J. & Berg, R. T. (1971). *Can. J. Anim. Sci.* 51, 41.
- Taylor, StC. S. (1965). *Anim. Prod.* 7, 203.
- Thompson, D'Arcy W. (1917). *On Growth and Form*. London: Cambridge University Press.
- Wallace, L. R. (1948). *J. agric. Sci., Camb.* 38, 367.
- Whitelaw, W. W., Elsley, F. W. H., Jones, A. S. & Boyne, A. W. (1966). *J. agric. Sci.* 66, 203.
- Whittemore, C. T. (1976). *Proc. Nutr. Soc.* 35, 383.
- Whittemore, C. T. & Elaley, F. W. H. (1976). *Practical Pig Nutrition*. Ipswich: Farming Press.
- Whittemore, C. T. & Fawcett, R. H. (1974). *Anim. Prod.* 19, 221.
- Wilson, P. N. (1954). *J. agric. Sci., Camb.* 45, 67.
- Wilson, P. N. & Osbourne, D. F. (1960). *Biol. Rev.* 35, 324.