QUANTITATIVE ASPECTS OF RUMINANT DIGESTION AND METABOLISM

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GROWTH

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The word 'growth' implies a rate, an increase in size over time. This quantity can be measured in terms of weight, of the whole body, or of its component parts (organs and tissues). The increase in these components results from an increase in the number and/or the size of their constituent cells, the cells in turn being composed, mainly, of fat and protein, or in the case of bone, minerals. Potential body composition at maturity, and the optimum path by which to reach that composition, are defined by the animal's genes but in practice this potential is rarely achieved since intake is often constrained by properties of the feed (e.g. an imbalance of nutrients absorbed, or its physical bulk). Prediction of growth therefore needs to take account of the processes of ingestion, digestion and metabolism in addition to an adequate description of the animal.

Mathematical descriptions of the growth of the whole animal range from single equations which fit the recorded observations of weight change, to complex models which predict growth based on representation of the underlying biology. A number of models of varying complexity will be described in the third main section of this chapter, but before considering 'how' to represent growth, there is a need to consider 'what' to represent. Space is insufficient to review in detail the pattern of growth in ruminants, the theory behind it or up-to-date knowledge of the physiological regulation of growth – for more information on these subjects the reader is directed towards the pioneering work of Brody (1945), and the more recent texts by Parks (1982) and Buttery *et al.* (1992). The next section will summarize the present state of knowledge of the main processes which influence growth, giving particular emphasis to those which are still controversial. The final section will evaluate how far published models have been successful in describing and predicting growth.

Quantitative Aspects of Ruminant Digestion and Metabolism (eds J.M. Forbes & J. France)

THEORY – *WHAT* TO REPRESENT

The manner in which an animal grows is dependent on:

1. the animal's drive to achieve its inherent growth target;
2. any effects of the environment and management system which modify the nutrients required to meet this target;
3. the extent to which the nutrients that the animal can extract from its feed can satisfy its needs.

Details of some of the processes involved (e.g. consumption of feed, digestion) are described elsewhere in this book and therefore will only be mentioned briefly here. This chapter will concentrate on the implications of: differences between animals, environmental variation and feed quality on growth at the whole animal level.

The animal

In terms of weight, the main tissues of animals are adipose, muscle and bone. The fat content of the carcass is the most susceptible to change due to breed or nutritional effects, with the ratio of muscle : bone being fairly constant, at a given carcass weight (e.g. Berg & Butterfield, 1966). These observations reflect the theory of growth, whereby skeletal development precedes growth of muscle and fat. However, while this theory has general applicability, the inherent growth rates of the individual tissues obviously vary with characteristics such as species, breed and sex. Some of these influences will be discussed here, but since the majority of mathematical models of growth concentrate on fat and protein as the desired outputs, little attention will be given to bone.

Stage of maturity

Unconstrained increase in body weight with time follows a characteristic S-shaped curve, representing a slow rate at first, then increasing before a final phase of decreasing rate as the animal approaches maturity. Different parts of the body mature at varying rates and therefore the relative proportions change with age. Muscle is a faster developing tissue than fat (Elsley *et al.*, 1964). Thus the ratio of fat to protein in a carcass will depend on the stage of maturity of the animal at slaughter, with younger animals having a higher proportion of protein. Blaxter *et al.* (1966) reported a decrease in the proportion of energy retained as protein from 30% in young cattle, through 15% in mature ones to 10% in aged animals. This effect is mediated at the tissue level, with fractional synthetic rates for individual tissues decreasing with age (see Table 17.1 for values for lamb muscle). Since different organs mature at different ages, the rates of decline differ between parts of the body, but the overall effect is a decrease in whole-body fractional synthetic rate as animals mature (Waterlow *et al.*, 1978). This effect appears to be further magnified in terms of protein deposition,

Table 17.1. Summary of fractional synthetic rates (FSRs) of protein synthesis reported for muscle from lambs of different ages. (Data collated by Gill *et al.*, 1989a.)

FSR	Liveweight (kg)
0.223	5
0.188	4.7
0.048	12.9
0.042	17
0.039	31
0.019	45

since Lobley (1988), after reviewing experimental data, concluded that the ratio of protein deposition to protein synthesis also decreased with age.

Sex effects

Bulls exhibit a faster rate of growth than steers or heifers, with a higher protein content of the gain (see review by Galbraith & Topps, 1981). Feed conversion efficiency (FCE: g feed per g gain) is also improved (i.e. decreased) by castration, with the effect being more marked at ad lib compared to restricted levels of feeding. In interpreting the results of a comparison between steers and bulls which was conducted over a range of intakes, Andersen & Ingvartsen (1984) attributed the smaller difference in feed efficiency at low compared to high levels of feeding to a higher maintenance requirement of bulls as estimated by Webster *et al.* (1977). However, Turner & Taylor (1983) suggested caution in interpretation of Webster's results since they may be confounded by lag effects due to the higher previous rates of growth (see below). These authors also pointed out that maintenance costs do not differ with differing fat : protein ratios in the body. Thus the higher protein content of bulls could not explain a higher maintenance requirement.

Galbraith & Topps (1981) reported a difference between heifers and steers in carcass composition, with heifers having more fat. The effect of sex on rate of growth was less marked, with steers having a maximum of 5% higher growth. These and other data suggest that the weight of the mature, fat-free empty body would be greatest for intact males, least for females, and intermediate for castrates.

Breed comparisons

Large breed differences in growth rate and carcass composition have been observed. These differences can generally be grouped in relation to categories of breed size, where size is taken as referring to mature weight. Southgate *et al.*

(1982) reported a range in daily gain from 682 (Murray Grey) to 857 g d^{-1} (Simmental) when comparing 10 breeds and crosses, in two fattening systems. However, there was no difference in feed conversion efficiency.

The Agriculture Research Council (1980) also noted an effect of mature size on composition of gain. Smaller breeds contained less protein and more fat compared, at the same weight, to cattle of medium-sized breeds. These differences are to be expected, given the changes with stage of maturity discussed earlier. Animals of larger mature size will be at a lower proportion of maturity than those of smaller mature weight and therefore the former would be expected to have a higher proportion of protein.

The concept of maintenance

The preceding section has considered the factors which determine the nutrient requirements of animals for unconstrained growth, taking account of the animal's target growth in terms of both overall rate and composition. However, before the energy ingested can be used for the synthesis of new tissue, certain essential demands to maintain existing tissues must be met. This theory led to the development of feeding systems in which the energy demands for maintenance are calculated separately from those for production. These systems have assumed that maintenance costs are constant, relative to current animal weight, but this assumption is increasingly being questioned. Thus, before describing how environmental factors alter nutrient requirements, two main types of criticism of the maintenance concept will be considered. The first criticism suggests that basal energy costs are influenced by recent and current growth rates, i.e. not just liveweight, while the second takes the same theme further, by questioning the validity of separating energy requirements for maintenance from those for growth.

Maintenance as a function of production

Arguments relating to whether maintenance is solely a function of current state have been reviewed in detail by Turner & Taylor (1983). Briefly they are, first, that metabolic rate is unlikely to be a funciton solely of current weight (or weight$^{0.75}$ as used by ARC, 1980) since animals aiming for higher mature weights grow at faster rates. Thus, since both mature size and metabolism per kg body weight are determined genetically, a better prediction of maintenance could be obtained by including a term relating to mature weight. (Baldwin & Hanigan, 1990, summarize other methods for adjusting maintenance relative to potential growth rate.) The second concept which is criticized is the short time scale of many of the measurements used to estimate maintenance requirements. A re-examination of calorimetric data to exclude the results of short-term trials may be required. Turner & Taylor (1983) seem confident, however, that a dynamic model incorporating the concept of maintenance can be developed, which could represent feed utilization, and hence predict growth, more accurately than the Agricultural Research Council's (1980) system.

Table 17.2. Estimates of energy costs of various non-productive processes.

Physical functions:	
Standing[1]	13–25% basal energy expenditure
Exercise[2]	2.6 J kg^{-1} m horizontal
	28 J kg^{-1} m vertical
Ingestion:	
Eating[3]	20–400 kJ kg^{-1} DM min
Rumination[4]	9–16 J kg^{-1} LW min^{-1}
Service functions[5]:	
Circulation	9–11% basal energy expenditure
Respiration	6–7% basal energy expenditure
Kidney	6–7% basal energy expenditure
Liver	5–10% basal energy expenditure
Nervous	10–15% basal energy expenditure
Metabolism:	
Ion transport[6]	18–23% total heat production
Protein turnover[7]	15–25% basal energy expenditure
Fat turnover[8]	2–3% basal energy expenditure

[1] Summers *et al.* (1988).
[2] Agricultural Research Council (1980).
[3] Osuji *et al.* (1975).
[4] *Ku-Vera et al.* (1989).
[5] Baldwin *et al.* (1980).
[6] Gill *et al.* (1989b) (results of simulation).
[7] MacRae & Lobley (1986).
[8] Katz & Rognstad (1976).

The validity of maintenance

Other authors have less confidence in the validity of retaining the concept of an empirical value for maintenance, at least in the longer term (e.g. Milligan & Summers, 1986; Baldwin & Hanigan, 1990). They point out that the costs of some functions which are normally accounted for as maintenance, vary continuously from low to high planes of nutrition and therefore the division at zero energy balance is artificial. Example costs of some of these processes are presented in Table 17.2. For example, protein synthesis accounts for a relatively constant proportion of whole-body energy expenditure (Reeds *et al.*, 1985), in ruminants being around 20% (MacRae & Lobley, 1986). However, attempts to sum the costs of the individual processes have generally fallen short of total basal metabolic rate, even for individual tissues (Summers *et al.*, 1988).

The environment

Description of the animal enables calculation of the nutrients required to achieve potential growth rates, given no external influences. However, both exercise and ambient temperatures below the thermoneutral range will increase energy requirements through the need to maintain body temperature, and these effects and high ambient temperatures will affect the animal's willingness to consume feed and its ability to extract nutrients from it.

Exercise

Energy costs of exercise by ruminants can range from the energy required to raise the animal from a lying to a standing position (and maintaining its posture), to the energy associated with work. However, while estimates for the former costs exist, they vary from 1 to 26% of metabolic rate (see Summers *et al.*, 1988, for comparisons). These costs rise when ruminants are grazing, and Graham (1964) reported that total muscular work could account for 40% of daily energy expenditure at pasture in a sheep grazing a poor-quality pasture. For work, data from Lawrence (1991) suggested that under optimum conditions of feeding and management, oxen working for 5.5 h d^{-1} used energy equivalent to 1.7 times maintenance.

Heat stress

High ambient temperatures can have a negative effect on growth, but there has been adaptation within breeds. Morrison (1983) in a review of the effect of heat stress in ruminants quoted data showing adverse effects on growth for some breeds maintained at temperatures in the high twenties compared to temperatures of 10 or 20°C. However, F1 crosses of Brahman and Friesian breeds showed no response in intake or growth when comparing cattle at 38°C with those at 17°C. Pure-bred Friesians and Brahmans showed a significant drop in both intake and growth at the higher temperature. Morrison also quoted evidence for higher digestibility in response to the higher temperatures in crossbred cattle. With sheep, the effect of high temperatures on intake interacted with diet quality, the negative effect being more marked on high-roughage diets.

Cold stress

The effect of cold stress on ruminant production was reviewed by Young (1983). Data from feedlot steers exhibited marked seasonal effects with decreases of up to 20% in FCE during winter. Young concluded that animals adapt to the cold by increasing basal metabolic rate, combined with an increase in reticulorumen activity which results in feed being retained for less time in the rumen, leading to a decrease in the digestibility of fibrous feeds. The increase in basal metabolism (of up to 40% after prolonged cold exposure) also contributed to a decrease in FCE through partitioning of absorbed nutrients away from fat and protein synthesis, towards heat production.

The feed

The knowledge that different types of feed support different levels of growth was the basis of early rationing systems in which the 'values' of a range of feeds were related to a common index – 1 kg of barley or starch (see Blaxter, 1980, for review). However, assigning such values to feeds required the conduct of many feeding trials and was in time replaced by estimates of the ability of feeds to promote energy retention as fat or protein. This estimation requires knowledge not only of the ability of the feed to provide nutrients for absorption (the digestion process), but also of the efficiency with which these absorbed nutrients are converted to useful products.

Dietary effects on efficiency of energy use

The efficiency with which ingested energy is used for maintenance does tend to be lower with forage compared to concentrate diets (Agricultural Research Council, 1980), leading to higher net energy requirements for maintenance in the former. The efficiency of energy utilization for production is even more sensitive to diet, again being lower with forage diets. It had been demonstrated 50 years ago that the efficiency was negatively correlated with crude fibre content but there is still no generally accepted explanation of the mechanism(s) behind this relationship. While broad classifications of feeds are used in existing rationing systems, this approach is inadequate for more complex representations. Thus there is a need to consider the range of processes which have been implicated.

McClymont (1952) suggested that the higher heat losses observed with high-fibre diets might be attributed to the higher proportion of acetic acid in the energy absorbed in ruminants consuming concentrates, and this theory has received a lot of support (e.g. Blaxter, 1962). The biochemical basis of the hypothesis is that the synthesis of fatty acids from acetate requires NADPH, which is synthesized most efficiently through the pentose-phosphate pathway, from glucose. Thus when the absorption of propionate and amino acids is low, the lack of glucose precursors may lead to the generation of NADPH through the isocitrate dehydrogenase pathway. Black *et al.* (1987a,b) used a simulation model of growth in lambs to demonstrate that inefficiencies could indeed result from high proportions of acetate in the absorbed energy at high rates of absorption, but two other findings are of particular relevance to the present discussion.

Firstly, the inefficiency induced high rates of a reaction which represented 'substrate cycling', a phenomenon which is known to exist but whose quantitative importance is still unknown. This lack of data applies as much to the basal level of turnover as to the differential response between diets, particularly at the whole-animal level, since different substrate cycles attain different levels of importance in different tissues. For example, Rabkin & Blum (1985) reported that substrate cycles associated with glycolysis accounted for 23% of cellular ATP production in hepatocytes, while Lobley (1990) suggests levels of 5–8% in muscle.

The second relevant observation of Black *et al.* (1987b) was that when part of the acetate absorbed was replaced by amino acids, the increased efficiency of energy utilization could be attributed to changes in the relative rates of fat and protein deposition, rather than to the gluconeogenic nature of the amino acids. This effect of composition of the gain on efficiency is relevant to the discussion on the differences between forage and concentrates, given the tendency of higher fat : protein contents in the gain of forage-fed cattle as discussed by Thomas *et al.* (1988).

However, differences in composition of the gain and in the ratio of nutrients absorbed are not the only possible explanations for the differences in efficiency between forages and concentrates. Ørskov & McLeod (1990) examined the potential contribution of the cost of eating and ruminating to the different efficiencies, including the cost of longer time spent standing. They estimated that heat production could be increased by 5 MJ d^{-1} in steers consuming roughages.

In addition to observations by Ørskov & McLeod (1990) of a longer eating time for steers consuming roughage, different patterns of eating have been observed by Gill *et al.* (1987a), which could influence the pattern of absorption of nutrients; in turn this could influence the release of hormones, which are known to have effects on the uptake of nutrients by specific tissues and, indeed, on their metabolism.

Differences in the metabolic rate of different organs between diets may also be important. Reynolds & Tyrrell (1989) reported decreased oxygen utilization by the portal-drained viscera in heifers consuming concentrates relative to those consuming lucerne, a finding which may be of considerable importance given that the portal-drained viscera account for 20–25% of whole-body heat production (Webster, 1980).

A more recent hypothesis was proposed by Jessop & Leng (unpublished observations), who have suggested that the influence of acetate on transmembrane proton gradients may be influential in modifying sodium pump activity such that pump activity is enhanced when acetate is in excess. This would be consistent with the Reynolds & Tyrrell (1989) observations on O_2 uptake.

As with many controversies in animal science it is likely that there is no single explanation for the observed phenomenon; rather the differences are likely to be the combined result of variation in a number of processes. As more data become available, these can be incorporated into models to evaluate quantitatively the relative importance of individual processes in explaining differences in efficiency at the whole-animal level.

Dietary effects on efficiency of amino acid use

The effect of diet on the efficiency with which absorbed amino acids are retained as tissue protein has received considerably less attention than energy. It tends to be assumed that this efficiency is relatively constant; the Agricultural Research Council (1980), for example, quotes a value of 0.75 for apparent efficiency of utilization of absorbed amino acids. However, the few calculations which have been made for forage diets suggest much lower values: for example, Beever *et al.* (1990) calculated a 0.53 partial efficiency of use of extra amino acids supplied by fishmeal consumed by growing cattle as a supplement to grass silage. There is also some evidence (Wilton, 1989) that high levels of ammonia absorption, such as on silage diets, may increase the catabolism of amino acids in the liver. This work needs to be repeated, since if confirmed it could have a marked influence on the calculation of protein requirements and the prediction of the response to protein supplementation.

Care needs to be exercised, of course, in considering the efficiency of use of 'total amino acids'. If amino acids are not limiting for growth, then low efficiencies are to be expected. Similarly, if secondary functions of amino acids (e.g. gluconeogenesis) are quantitatively important, efficiency of amino acid use will be reduced – see, for example, the influence of glucose supply to the gut on amino acid utilization by gut tissue (Seal & Parker, 1991). Models of amino acid use must recognize the balance between supply of the first limiting amino acid (or ideal amino acid mixture) and demand. While these are generally recognized in models of amino acid use in pigs, less attention has been given to their importance in ruminant models.

Previous nutrition

The effect of previous nutrition in relation to the time needed for metabolism to re-stabilize at a new energy level has been discussed earlier, in relation to maintenance. In relation to growth, this adaptability of metabolism is the basis of compensatory gain, which occurs after periods of undernutrition as the animal tries to return to its genetically determined growth pattern (see review by O'Donovan, 1984, for details). True compensation would imply an acceleration of growth such that the animal would still achieve its 'target' composition within the same time-frame. Evidence that this is achievable is limited although the model is widely used (Jackson, 1990). More frequently, body tissue mass is achieved, with a loss of time, although even the ability to compensate to this extent depends on the physiological age of the animal at the time of undernutrition and on the severity and duration of restriction. For example, Allden (1968) found that restriction of lambs of less than 15 kg liveweight resulted in significantly lower liveweights at 3 years of age.

Consequences for mathematical representation

The appropriate degree of detail with which to represent the animal in mathematical models of growth will depend on the objective of the model, but since the proportions of fat and protein can vary independently, these tissues are generally represented. Bodyweight can then be calculated using ratios for water and bone relative to muscle, where these ratios depend on the age and weight of the animal. Constraints induced by environmental and feed factors also need to be included in a way which enables the interactions between factors to exert an influence. However, data on these interactions are often lacking, since in the reports of many nutrition experiments, the animal is frequently poorly defined, while details of the feed consumed may be limited in reports of genetic experiments. The development of models may help to unravel some of the apparent inconsistencies between experimental results, but efforts should also be made to record experimental conditions in more detail in future.

PRACTICE – *HOW* TO REPRESENT

The theories discussed in the preceding sections must, to varying degrees, be taken into account in all mathematical representations of growth. However, the degree of complexity with which different aspects are described will depend on the objectives of the specific model. Three broad types of model will be illustrated in this section: firstly, general equations which have been derived from consideration of the theories of growth; secondly, equations which are used as components of rationing systems to describe the growth of body components; and thirdly, models which have been developed to simulate the response of ruminants to different feeds.

Growth equations

The simplest expression of growth is weight (W) as a function (f) of time (t):

$$W = f(t) \tag{17.1}$$

As discussed on p. 384, the unconstrained growth curve is sigmoidal and thus f, if required to be representative of growth from birth to maturity, must generate a curve of this nature. Thus, growth is a rate and many growth functions are obtained by considering the rate of growth ($\mathrm{d}W/\mathrm{d}t$) as a function (h) of W:

$$\mathrm{d}W/\mathrm{d}t = h(W) \tag{17.2}$$

Many equations have been proposed and some of these are summarized in Table 17.3. Three types will be discussed briefly here; for more detailed reviews see Parks (1982) and France & Thornley (1984), in relation to the representation of bodyweight gain.

Table 17.3. Functions used to describe growth.

Name	Function (f): $W = f(t)$	Function (h): $\mathrm{d}W/\mathrm{d}t = h(W)$
Gompertz	$W_0 \exp[\mu_0(1 - e^{-Dt})/D]$	${}_{\mu 0}W[\ln(W_f/W)/\ln(W_f/W_0)]$
Logistic	$W_0 W_f/[W_0 + (W_f - W_0)e^{-\mu t}]$	$k'W(W_f - W)$
Richards	$W_0 W_f/[W_0^n + (W_f^n - W_0^n)e^{-kt}]^{1/n}$	$kW(W_f^n - W^n)/(nW_f^n)$

Where:
W_0 = initial weight (W) at time $t = 0$.
W_f = final weight as $t \to$ infinity.
μ = specific or relative growth rate.
D = decay in specific growth rate.
k, k' = constants.

Gompertz equation

The Gompertz equation can be derived by assuming that growth is again proportional to weight, but it assumes that substrate is non-limiting, and it is the fractional growth rate which decreases exponentially with time. The equation generates a sigmoidal curve, but non-symmetrical, with the inflection point occurring at 1/e times the final weight.

Logistic equation

The logistic equation assumes that growth is proportional to weight and to the amount of substrate available for growth, which is taken to decrease to zero at mature weight (W_f). Thus, $W_f - W_0$ can be substituted for the amount of substrate, giving the equation in Table 17.3, where μ is the (constant) fractional growth rate expressed relative to mature weight. This equation provides a curve with smooth sigmoid behaviour, with the point of inflection at half the final weight.

Richards equation

Both the Gompertz and the logistic equations are special cases of the family of curves described as the Richards equation, where the point of inflection can occur at any fraction of mature weight, depending on the value of n.

Composition of gain

Allometric equations

The general allometric equation:

$$P = aQ^b \qquad (17.3)$$

was used by Brody (1945) to estimate the weight of cattle (as P) from girth measurements (as Q), but allometric principles are now used more frequently to relate body composition to body weight. Different countries have derived different relationships in the development of standard feeding systems and four of these are described here.

United Kingdom (Agricultural Research Council, 1980; Agricultural and Food Research Council, 1991)
From consideration of the data available at the time, the Agricultural Research Council (1980) summarized 'average' patterns of weight and body constituent change for breeds defined as small, medium or large, according to sex. Thus, energy (E, MJ kg^{-1}) and protein (P, g kg^{-1}) contents of empty bodyweight change ($\mathrm{d}W/\mathrm{d}t$, kg d^{-1}) for cattle of weight W (kg) are:

$$E = (4.1 + 0.0332W - 0.000009W^2)/(1 - 0.1475\mathrm{d}W/\mathrm{d}t) \qquad (17.4)$$

$$P = (168.07 - 0.16869W + 0.0001633W^2)(1.12 - 0.1223\mathrm{d}W/\mathrm{d}t) \tag{17.5}$$

The equations imply that for an animal at a given weight, the energy content of gain rises and the protein content of gain falls as the rate of weight gain increases. This does not reflect the situation in practice, since dietary influences on the composition of gain are not included. For example, protein gain increases in response to protein supplementation of silage (Gill *et al.*, 1987b).

The effects of breed and sex in modifying this relationship are calculated by simple adjustment by factors in units of 10% (protein) or 15% (energy) between the reference animal and small (negative effects) and large (positive effects) breeds, intact males (positive protein, negative energy) and females (negative protein, positive energy). These crude adjustments are incongruous in conjunction with the precision to which the coefficients in the equation are given.

More recently (Agricultural and Food Research Council, 1991) Emmans and Whittemore have suggested that potential growth can be described by assuming that the Gompertz equation, i.e. fractional growth rate declining linearly with the logarithm of weight, can be applied to individual components of gain, with a slope which is the same for each component for a given type of animal. However, values for this slope still require estimation.

France (Institut National de la Recherche Agronomique, 1989)
For cattle, Geay and Micol have summarized a model of growth by Robelin from slaughter data on cattle from 150 to 850 kg. This combines allometric relationships for estimated body weight (from liveweight), body lipid (from empty body weight) and body protein (from lipid-free empty body weight) with relationships both for the composition of gain and growth rate. Liveweight over time is represented using a Gompertz form of description and the relevant parameters are tabulated. Rate of fattening ($\mathrm{d}L/\mathrm{d}t$, kg d^{-1}) is related to the change in empty body weight ($\mathrm{d}W/\mathrm{d}t$) according to:

$$\mathrm{d}L/\mathrm{d}t = c\,(\mathrm{d}W/\mathrm{d}t)^{1.8} \tag{17.6}$$

Where: c varies with the type of animal and its weight.

Daily rates of protein gain are estimated directly from fat-free body mass with the assumption that there is little variation in this ratio.

United States (National Research Council, 1984)
From compositional data of cattle the energy (E) and protein (P) contents of liveweight change are estimated from weight (W) and empty body gain ($\mathrm{d}E/\mathrm{d}t$) according to:

$$E = aW^{0.75}(\mathrm{d}E/\mathrm{d}t)^{1.087} \tag{17.7}$$

$$P = b - cE \tag{17.8}$$

where a, b and c are constants. Adjustments are made for sex and breed on a similar basis to that used by the Agricultural Research Council (1980), i.e. simple factorial adjustment.

It is interesting that for sheep (National Research Council, 1985) breed differences are dealt with in a quite different way: energy content of gain (scaled to empty body weight gain and empty body weight$^{0.75}$) is related to mature weight (estimated as yearling weight for a breed). Thus the energy content of gain (at a particular weight and rate of weight change) is less for breeds of large rather than smaller mature size. This fits reasonably with the genetic size scaling rules already referred to, although the approach is strictly empirical.

Australia (Commonwealth Scientific and Industrial Research Organization, 1990)

The recently published Australian recommendations on feeding standards for ruminants have adopted a 'Standard Reference Weight' (SRW) to allow for breed and sex differences in the estimation of growth. The concept is applied both to cattle and to sheep. SRW is the (approximate) weight achieved by an animal when skeletal development is complete and the empty body contains 250 g of fat kg^{-1}. This is quite an attractive concept, although the manner of use is rather complex. Thus the fat (*Le*) and protein (*Pe*) contents of the empty body gain (dE/dt), expressed as MJ kg^{-1}, are calculated as:

$$Le = (a + bR) + (c - bR)/[1 + \exp(-b(P - 0.4))] \qquad (17.9)$$

$$Pe = \qquad yR) - (z \quad yR)/[1 + \exp(\quad b(P - 0.4))] \qquad 7.10)$$

Where:
P is current weight as a proportion of SRW, *R* is an adjustment factor for rate of gain or loss, and *a*, *b*, *c*, *x*, *y*, *and* *z* are constants.

Use of SRW maintains a very large subjective element as the CSIRO approach uses two sets of equations – one for conventional breeds of sheep and cattle found in Australia and another for more exotic imported breeds. Adoption of this purely empirical approach therefore introduces an intricate mixture of descriptive statistical precision and crude proportionate adjustment.

Summary

These equations estimate the amount of energy and protein which is required at the tissue level, but need to be multiplied by efficiency factors to calculate the nutrients required in the feed. These efficiencies are empirical values derived from experimental data and do not take account of all the interactions between diet components and between animals, environment and diet. There is widespread recognition that generalized models of growth such as those in the feeding systems listed above are bound to have weaknesses when they are based on empiricism rather than theory. The data-sets which underlie these general descriptions define the boundaries of application for any particular model. Improvements can be made by widening the data-sets from which the equations are derived, but the improved accuracy relative to the costs of the experiments is likely to be marginal.

Prediction of responses

Support for an approach which predicts the responses of animals to feeds rather than the definition of feed requirements has grown over the last 20 years and is becoming accepted as the way forward for the future. In contrast to the prediction of requirements where a rate of gain is selected and output is given in terms of amounts of feed, in predicting growth responses the output is the rate of gain and its composition. The prediction depends on the simulation of the interaction between the absorbed nutrients and the animal's growth potential, through representation of intermediate metabolism. A large number of models to predict response have been published in the last 15 years and it is not possible to consider them all here. However, rather than consider a few models in detail, examples of a variety of ways in which different components have been represented will be given. Emphasis will also be given to models which have used a more theoretical understanding of the mechanisms involved to derive mathematical relationships.

Feed

Although the rumen confers benefits on the animals' abilities to utilize low-quality feeds, it creates problems in relation to describing the value of feeds ingested. A number of models of 'whole' ruminants have considered inputs in terms of metabolizable energy and absorbed protein (e.g. Graham *et al.*, 1976); other models of responses are based on the premise that metabolizable energy is an adequate predictor of growth. Such models (e.g. Gill *et al.*, 1984; Sainz & Wolff, 1990) represent the metabolism of the components of absorbed energy, and thus need to be driven by the outputs from a model of rumen fermentation. Such models are considered elsewhere in this book and will not be referred to here. The outputs of rumen models vary in terms of the number of nutrients which they represent but generally include amino acids, lipids, acetate and a pool representing C_3 metabolites, i.e. either glucose or propionate.

Intermediary metabolism

The step represented by calculation of efficiency in models of requirement is more complex in models which consider the components of metabolizable energy, since interactions can be considered. Metabolism models use the concentrations of metabolites generated within the model as parameters in the equations used to partition metabolites between fat and protein synthesis and heat production. Most of the models use modifications of the Michaelis–Menten equation to calculate the rate at which substrates are utilized (U, mol h^{-1}):

$$U = V_{max}/(1 + K_m/[S]) \qquad (17.11)$$

Where:
V_{max} is the maximum velocity of the reaction, K_m is the Michaelis constant, and [S] is the substrate concentration.

Protein synthesis, though, is viewed as the main equation representing the animal's growth potential and will be described in the next section, except to say that the equation generally includes a modifier dependent on amino acid concentration and, in some cases, energy concentration (e.g. France *et al.*, 1987).

It is also worth noting that, consequent on the lack of quantitative data to describe the individual processes which constitute maintenance requirements, most models of growth use an empirical equation to estimate the energy used for maintenance (e.g. Gill *et al.*, 1984). As part of the process of identifying 'gaps in knowledge' which prevent more mechanistic representation of maintenance, Gill *et al.* (1989b) developed a model to integrate knowledge on the costs of two of the main processes contributing to non-productive processes, protein turnover and ion transport, but could only account for 83% of the heat increment associated with higher levels of feeding.

The animal

The ability of a model to predict growth is highly dependent on the equation used to predict protein synthesis. Gill *et al.* (1984) used the equation of Black & Griffiths (1975):

$$\text{Max protein deposition} =$$
$$0.001(6.25/110)(2.017E_{\text{met}} - 0.401W_{\text{met}} - 0.106E_{\text{met}}W_{\text{met}} + 0.024W_{\text{met}}^2) \tag{17.12}$$

Where:
E_{met} is metabolizable energy intake (MJ d^{-1}) and W_{met} is the metabolic weight of the animal (kg) with no modification for differences in mature weight or previous nutrition.

Sainz & Wolff (1990) used a Michaelis–Menten basis to calculate the utilization of amino acids for protein synthesis, where the maximum velocity (V_{AaPb}) was calculated as:

$$V_{\text{AaPb}} = V'_{\text{AaPb}}\, Pb^{0.682}\, Db \tag{17.13}$$

Where:
V'_{AaPb} is a factor for calculation of V_{AaPb}, Pb is the quantity of protein in the carcass (mol of amino acid), and Db is the quantity of DNA in the carcass.

The equation to calculate DNA accretion is:

$$\mathrm{d}(Db)/\mathrm{d}t = k_{\text{Db}}(Db_{\max} - Db)H_{\text{A}} \tag{17.14}$$

Where:
Db is carcass DNA, k_{Db} is the rate constant for DNA accumulation, $Db_{\max}$ is maximum DNA content in the carcass, and H_{A} is a function of nutritional state.

The term for maximum DNA produces a decrease in growth rate as the animal approaches maturity. H_{A} allows hormonal effects on cell proliferation to be represented. These equations are similar to those used by Oltjen *et al.* (1986). France *et al.* (1987) also allowed for the decrease in growth rate as the animal matured with protein synthesis being represented by:

$$k_P P[1 - (P/P_{\max})^{\theta_P}]/(1 + K_{N,NP}/N + K_{C_2,NP}/C_2) \qquad (17.15)$$

Where:

k_P is the fractional rate of protein synthesis; P is the body protein pool (kg); $P_{\max}$ is the maximum weight of protein (kg) and is breed dependent; θ_P is a steepness parameter; $K_{N,NP}$ is a constant set relative to N, to limit synthesis when amino acid concentration is low; N is the amino acid metabolite pool (kg N m^{-3} blood); $K_{C_2,NP}$ is a constant set relative to C_2, to limit synthesis when C_2 is low; and C_2 is the concentration of acetate equivalents (kg carbon m^{-3} blood).

The differing degrees of complexity of these models represent the different objectives of their authors. The model of Gill *et al.* (1984) was developed to examine hypotheses regarding the relationships between absorbed nutrients, growth efficiency and body composition and was only used to simulate short time intervals. The model of France *et al.* (1987) aimed to simulate growth over a number of weeks and thus had to take account of the relative maturity of the animal, while the model of Sainz & Wolff (1990) was developed to look at the effect of growth promoters, hence the need for long-term simulations and the inclusion of a factor to simulate hormonal effects.

EVALUATION OF MATHEMATICAL REPRESENTATIONS OF GROWTH

When evaluating the many different models which have been developed to represent growth, it is important to bear in mind the objectives for which each model was developed. The ARC and NRC feed rationing systems were developed as tools to help advisers and farmers to recommend appropriate rations to meet production targets. This they have done, but as modern systems move further from the situations in which the original data used to derive the systems were collected, there will be an increasing number of examples of data which disagree with the ARC or NRC predictions.

Models which have been derived from theory, rather than derived purely statistically from experimental data, should be more robust and better able to adapt to changes in feed availability. However, this depends on accurate representation of the processes involved and the interactions between them. To date, evaluation of the type of metabolism model described in the preceding section has been hindered by lack of appropriate input data, but Arnold & Bennett (1991) recently compared four growth models using unpublished data of C.L. Ferrell. Of these, Notter *et al.* (1979) and Sanders & Cartwright (1979) used growth descriptions of the Brody form, Loewer *et al.* (1983) used a Gaussian function and Oltjen *et al.* (1986) related protein synthesis to the accumulation of DNA, relative to a maximum value. Taylor's size scaling rules (Taylor, 1980) were used to adjust for differences between cattle of different mature size.

Arnold & Bennett (1991) concluded that none of the models consistently predicted weight gain or composition, even where measured intakes were used as inputs. For some individual treatments the degree of mis-estimation was 20–25%. In general, empty body weight was predicted more accurately than composition, and fat less accurately than protein. They concluded that one possibility is that our understanding of growth and available data is as yet too limited for an accurate model to be developed. Some of the processes requiring further study have been mentioned above. The challenge is to maintain an objective view of the relevance of studying different processes and to integrate both the approaches adopted and the results obtained between laboratories.

However, the 'success' of mechanistic models should not be viewed only on the basis of their ability to predict growth accurately. Response models in particular may be developed with the objective of increasing understanding of the process of growth. Such models should be evaluated on the basis of their ability to aid in the interpretation of data to test hypotheses and to clarify objectives for further research.

CONCLUSIONS

Different mathematical approaches to predict liveweight gain and body composition of ruminants have been developed. Some have specific objectives, others are intended to be more general in nature. However, there are still many experimental observations which are not predicted by existing models. This is partly due to inadequate description of experimental conditions, thus precluding an evaluation of the effects of interactions between animal, feed and environment. Careful attention to selection of genotypes for particular studies is one way in which variation could be reduced. There is also a need to record not only the steady-state situation, but also the short-term changes which occur while animals are adapting to changing environments and diets. New technologies such as computed tomography and magnetic resonance spectroscopy may make this possible.

However, in parallel with the collection of new data, there is a continuing need to integrate existing data. In the past the development of national systems for the prediction of animal performance integrated large amounts of experimental data. In recent years, there has been a proliferation of mathematical models developed by groups of authors to meet specific objectives. Once published these objectives may be forgotten and the models used to predict performance in situations for which they were not designed. While the continued development of such models is a valid exercise, where it is used as a means of increasing our understanding of the processes involved, expectations of these models should be realistic.

There is a need for a more general mechanistic model of ruminant growth which takes into account animal, feed, external factors and their interactions, but whether there are yet sufficient data to develop a model which can provide accurate predictions will not be known until the exercise is under way. Finding the personnel and funding for such an undertaking is also a task of some magnitude. However, much new data have appeared since the recommendations of, for example, the Agricultural Research Council (1980) were published and there is a need to dissect that information, interpret the data with care and at least begin to reanalyse some of the controversies referred to above in preparation for more mechanistic developments at a later stage.

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