Understanding body composition and efficiency in ruminants: a non-linear approach

V.H. Oddy[1], A.J. Ball[2] and A.B. Pleasants[3]

[1] NSW Agriculture, Cattle and Beef Industry CRC, University of New England, Armidale NSW 2351 Australia
[2] Department of Animal Science, Cattle and Beef Industry CRC, University of New England, Armidale NSW 2351 Australia
[3] AgResearch, Whatawhata Research Station, Whatawhata, New Zealand

Summary

We present the ideas behind an approach we are working with to develop a system to understand and describe variation in body composition, growth and efficiency of nutrient use in ruminants. The mathematics and philosophy of non-linear dynamic systems are briefly presented and our rationale for using this approach are outlined. The following simplifying assumptions are employed. Protein mass is used as an index of cellularity, the dynamics of which arise from interaction between an unfolding of genetic message and the environment. Protein turnover is used as a proxy for tissue energy expenditure. Heat production arises from separate pools (viscera and muscle) with respectively high and low protein turnover per unit mass, but low and high protein mass. Fat deposition occurs from energy not used for protein turnover and deposition or lost as heat. Feed intake is regulated as a balance between energy intake, expenditure, and environmental losses and inputs. All the above interact. In this system, growth and efficiency of nutrient use arise from interactions between structural (inherited) and environmental (energy and amino acid supply) elements, rather than implicit mechanisms.

Several novel representations are incorporated. Rate of protein deposition behaves as if it is first order with respect to protein mass in unperturbed (normal or continuously grown) animals. In perturbed systems, the future trajectory of potential protein deposition is altered to target a potential protein mass which may differ from the original depending on timing and extent of deviation. Differences in feed composition alter efficiency of energy retention in ruminants through the effect of the feed on visceral mass and energy expenditure. Through this approach, the need to invoke variation in efficiency of energy use for maintenance and growth due to differences in substrate use is not required. Both the short term variation and long term stability seen in *ad libitum* feed intake of individual animals arises from the time scale of the dynamics of the interactions, rather than specific causes. The work is unfinished, and is presented in this early form to promote discussion.

Introduction

Important challenges that confront applied animal scientists are:

- to reduce cost of production through improvement in efficiency of nutrient use;

- to increase precision of estimation of the output of saleable product and the quality of that product; and

- reduce environmental impact of production through:
  - reduction in overall energy use
  - minimisation of waste products, for example, excreta and fat, and
  - minimise adverse consequences of production processes in, for example, food safety, animal welfare and environmental degradation.

Quantitative understanding of the factors which affect efficiency either in terms of monetary or nutrient use, and improvement in achieving market goals, is a pre-requisite to meeting these challenges. The efficiency of nutrient use for growth of individual animals is affected by:

- stage of maturity-less mature animals have a higher gross efficiency because their voluntary feed intake, as a multiple of maintenance, decreases with age;

- composition of gain-leaner animals are more efficient when expressed as g gain/MJ eaten (but perhaps not when expressed as MJ gain/MJ eaten);

- heat production due to:
  - activity-less activity less heat production;
  - relative size of visceral organs-visceral organs have a disproportionately high rate of energy utilisation compared to carcass tissues

(Ferrell, 1988) so animals with proportionately less visceral mass are more efficient,

- turnover of protein and ion transport processes-lower turnover relative to mass should be associated with reduced energy expenditure (Webster, 1984; Milligan and McBride, 1985; Knapp and Schrama, 1996); and

• pattern and amount of nutrients supplied by a feed (Webster, 1989).

These are influenced by both genetic and environmental factors (e.g. nutrition, disease, temperature, growth promotants).

Our challenge is to draw these aspects together at the individual animal level to predict growth of body components in response to feed and environmental factors in animals of diverse genotype. This paper describes our thinking about how growth and body composition, and in turn the efficiency of individual animals, can be predicted from simple assumptions using non-linear mathematical techniques. Our thinking is not complete, and this paper should be viewed as a statement of progress rather than a definitive document.

The nature of the problem

Previous growth rate (usually arising from nutritional treatment) affects finishing growth rate, retail meat yield, fat depth and intra–muscular fat content of beef cattle (Carstens, 1995; Oddy *et al.* 1997; Table 1) and lambs (Hegarty *et al.* 1994). Low growth rate of weaned ruminants pre-finishing may be accompanied by enhanced growth during finishing, and a greater proportion of lean and less fat in the finished carcass. On the other hand, low growth rate before weaning, or early in life may reduce subsequent growth, and increase fat deposition (Carstens, 1995; Oddy *et al.* 1997). Thus, prior nutrient restriction may affect body composition either by increasing or decreasing fat content at a given weight, depending on the age of the animal at the time of feed restriction and the extent of feed restriction at that time. The practical implication of these observations is that previous nutrition can alter subsequent body composition, but the magnitude and direction of change

is dependent on the stage of growth at which alteration of nutritional input occurs. This is not predictable by our present feeding systems.

There is a need for a feeding system for ruminants which predicts not only the weight gain of an animal, but also describes outputs of marketable body components and some meat quality attributes. Immediate inputs to such a system ideally should remain much the same as in present feeding systems and represent animal genotype, gender, feed quality and amount, and some elements of the thermal and disease environment. An additional input will be some description of the nature of prior growth, both with respect to time relative to developmental pattern, and extent relative to potential (for more details, see the companion paper, Ball *et al.* 1997). ,

Current feeding systems do not allow body composition to be adequately predicted. Only one, SCA (1990), attempts to do so by providing empirical relationships between rate of gain, current and potential weight, and composition. NRC (1996) use body condition score to adjust for previous nutrition. However, it is acknowledged that this does not adequately describe potential changes in body composition. The basic premise of current feeding systems for ruminants is to use a single term for efficiency of feed for weight gain which encompasses deposition of energy in both fat and protein. In the California net energy (NE) system and its derivatives (NRC, 1996) variation in efficiency of feed utilisation is seen as a property of the feed which is given an estimate of feed value for maintenance and another value for growth or yet another for lactation. In the metabolisable energy (ME) system, feed is described by a single energy value, and variation in efficiency of use is derived from a function describing the interaction between feed and animal. In both, there is no adjustment in efficiency of feed use for age, or composition of body gain. Present systems assume the current state of the animal is the major determinant of the animal component which responds to feed intake. Accordingly they cannot satisfactorily incorporate previous nutritional effects. Although SCA (1990) and NRC (1996) attempt to account for prior nutrition, they do so by linear adjustments to intake, rather than account for the changes in body composition which emerge in response to variation in feed regime. Inclusion of genotype,

Table 1   Effect of previous nutritional treatment on growth and carcass characters of feedlot cattle. Data shown are least square means for Angus and Shorthorn steers, grown from weaning (approx. 220 kg) to feedlot entry at 400 kg in three different pasture systems: low = improved pasture only, medium = pasture plus protein pellets during winter, high = pasture plus forage crop during winter. Cattle were finished in a feedlot for either 100 or 150 d to 280 kg or 330 kg carcass weight. Values shown are adjusted for sire, herd of origin, age, carcass weight and time of finish.

Background Treatment	Background growth rate (kg/d)	Fat thickness at feedlot entry (mm)	Feedlot growth rate (kg/d)	Fat thickness at feedlot exit (mm)	Retail yield (%)	Intramuscular fat (%)
Low	0.62	4.6	1.50	10.9	68.2	4.1
Medium	0.70	5.0	1.46	10.3	68.0	4.1
High	0.81	5.8	1.39	11.5	67.6	4.7

gender and growth promotant induced differences between animals in feeding systems are confounded within a size term (used as a proxy for both mature size and hence body composition) and are reflected in estimates of maintenance requirements, rather than in a description of body composition and hence as a contributor to variation in efficiency of gain. These and other shortcomings of current ruminant feeding systems are described by Ferrell(1995).

To be fair to the current feeding systems, they are limited by the realities of data collection and analysis, and the corresponding error structures which are implicit in the data, and the linear methods used for analysis. Moreover, they evolved fiom a time when feeding for liveweight and liveweight gain and milk production were the required production goals. Product description and meat quality was less well accepted as an important attribute of output from ruminants. With the success of the products of the intensive livestock industries in the marketplace, which arose predominantly from consistency of supply of relatively cheap high quality meat products, the technical needs of the ruminant production industries have to change to compete.

Our way of looking at the problem

Animals are self organising, structurally stable, systems, both 'open' or 'dissipative ' with regard to energy and matter (nutrient) flow, and 'closed' or 'conservative' with regard to information flow (in particular the expression of potential as contained within the genome). They operate far from equilibrium conditions. Indeed., in living systems, equilibrium is death. The mathematics required for dealing with such systems is that of non-linear rather than linear systems. This requires quite a different approach to that traditionally used in development of feeding systems. In particular it requires consideration of animals as 'self making' (autopoietic) entities, in which reinforcing interactions (feed back and feed forward) couple the internal and external environments of an animal.

With this view, we see variation in body composition as a result of interactions between internal information (genotype) and external inputs (the dissipative system) which arise from the environment, of which matter and energy (nutrition) are the major components. Those variations in growth and efficiency which are essentially expressed in the open domain arise, we believe, from the dynamics of the interaction between feed (energy and amino acid) intake, deposition of protein and fat (which give rise to changes in body composition) and heat production (Figure 1).

Combining components of both internal and external control directly confronts the research paradigm of the experimental animal scientist. In our experiments we generally observe states at a point in time, and not the evolution of the states through time. We experiment by attempting to hold factors other than the experimental variable constant, but in animal studies we know this is rarely true. Although the experimental and statistical techniques available to remove unwanted influences have become increasingly sophisticated (*i.e.* reduce variation to either random effects or include them in the error term) they constrain our capacity to appropriately incorporate variation arising from several sources simultaneously. Non-linear models do not obey superposition rules, so extracting effects assuming additivity is questionable. New mathematical techniques which can simultaneously consider non-linear interactions are emerging. This mathematics of non-linear dynamic systems requires us to think differently about the biology, but at the same time offers opportunities to deal with the complex problems of animal growth and efficiency in, perhaps, a more realistic way.

We outline here an initial attempt to develop the guidelines for a non-linear dynamic system to interpret and analyse factors which influence efficiency and body composition in animals. Although it is intended only to outline our ideas in a general sense, we have attempted to draw together the key components to illustrate the implications in the special case of compensatory gain. The ideas presented here comprise the major components that will be integrated in a framework which uses non-linear dynamics to predict body composition and efficiency of gain of sheep and cattle. We believe that a high degree of simplification is sufficient to capture most of the observed behaviour of animal growth, body composition and efficiency.
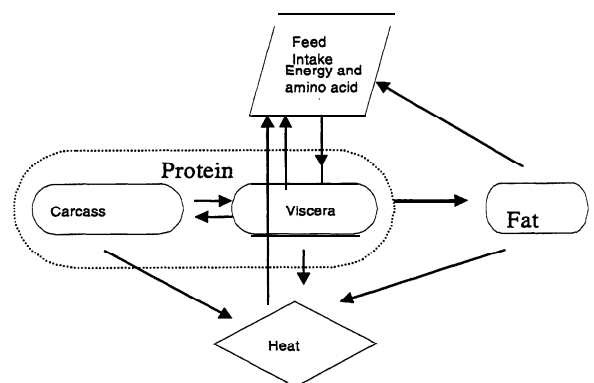
Figure 1 Schema for a minimal model describing the interactions between body protein and fat energy (and hence weight and body composition) and feed intake. Note that this is not meant to represent a compartmental model. The important elements are the arrows denoting matter and energy flow and interactions, and the boxes represent both capacity for pattern emergence and mass storage.

Past representations of the problem

Growth is a change in weight of the organism. It is a summation of a number of components which are developing at different rates, and which interact within themselves and externally with the environment. Current models of animal growth work from either one of two premises. Growth is either pulled through time by some notion of maturity (e.g. weight (Brody, 1945), DNA (Baldwin and Black, 1979), ash (as a proxy for bone growth, France *et al.* 1987), protein (Whittemore, 1986)), or is pushed through time by ingestion of nutrients (e.g. food intake (Parkes, 1982); energy intake (Blaxter and Boyne, 1976); energy intake and amino acid supply (Graham *et al.* 1976)).

The approach which we believe has come closest to prediction of body composition (and through that carcass yield) is that of Keele *et al.* (1992) and Williams *et al.* (1992). These workers have constructed a model of cattle growth and body composition based on the assumption that faster rates of growth contain more fat, and that the allometric relationship between body components holds. Using these simple assumptions the model they have developed is able to predict the direction of changes in body composition associated with changes in growth rate, but not where the composition of the diet induces changes in body composition. Unfortunately, it does not adequately predict where previous nutritional effects are substantial, such as seem to occur with nutrient restriction in pastoral conditions in Australia. In these circumstances, we have found that faster growth during compensatory growth is associated with higher rates of protein (and water) deposition, but that rate of fat deposition may not increase (Oddy *et al.* 1994 and Table 1). The nutritional inputs used in the model of Keele *et al.* (1992) preclude use of the model to predict effects of diet on body composition.

Although other attempts have been made to incorporate interactions between growth 'potential' and feed intake (for example, Oltjen *et al.* 1986; Baldwin, 1995; Schinckel and de Lange, 1996), these are usually constrained by the number and functional form of the equations used, and the manner in which they interact. In particular the form, and number, of the equations chosen constrains the dynamics of the system, yet there is little recognition of this mathematical impasse.

Our approach

We are trying to distil from our understanding of biochemistry and physiology simple mechanisms that capture the main elements of the animals 'emergent properties', and evaluate the mathematical consequences of the simplifications.

The problem we are trying to resolve is how to represent an animal, as a simplified or model system, realistically in terms of growth of the major components of the body given genetic and nutritional inputs and

> Emergent properties refer to the observation that phenomena exhibit properties which did not exist at the lower level. Perhaps the most powerful example of an emergent property is life, the existence and development of which cannot be predicted from a knowledge only of physics and chemistry. In the present context we mean that we are dealing with the consequences of biochemistry and physiology at the level of two major components of the animal, protein and fat. Sometimes a higher level property or process is considered emergent when the variance associated with its expression is less than the variance of the parts that make it up. Consider muscle, the structure in which protein is predominantly held in animals, as an example. Although the biochemical processes within a muscle are generally conserved, the variation in rate and pathways of the biochemical reactions within the muscle is much greater than in the function and morphology of the muscle structure.

appropriate environmental constraints. The first task is to construct a minimal model that can describe the behaviour of the system. Our current attempt is shown in Figure 1. The choice of level of abstraction to represent the system as simply and as completely as possible is not arbitrary. The rigorous process of system development will both require and provide fundamental information about the constructs incorporated.

The minimal components we wish to describe are temporal development of:

I   mass of protein in the carcass, and non-carcass (viscera);

II   mass of fat; and

III   their summation to body weight and liveweight.

The units used for the model are energy (MJ). Transformations to mass are made on the basis of 24, and 39 MJ/kg for protein and fat respectively.

The assumptions included in our simple model are:

I   the **animal** is attracted to some future protein mass;

II   heat production is a function of feed intake and protein mass of the animal;

III   the animal is homeothermic, i.e. regulates its body temperature within narrow limits

IV   feed intake is simultaneously attracted to an amino acid and energy 'target' consistent with assumption i) above, and constrained by heat production (body temperature, assumption iii) and overall level of body fat;

> The state towards which a dynamical system evolves is called the attracting state, or the attractor. When in this state the system is unchanging or in equilibrium. Note, however, that this equilibrium can be dynamic, *i.e.* dependent on the addition of, for example, energy to the sytem to continuously maintain equilibrium.

V fat deposition is the difference between energy intake, energy deposited in protein and heat production;

VI other body components (water, ash) can be predicted from their relationship with protein.

The key elements of our approach are to bring together relationships between feed intake and heat production through protein mass and gain in viscera (viscera being a high turnover, low mass component) and in the carcass (low turnover, high mass).

The purpose of including protein rather than animal weight as the attractor is to capture some image of the growth of cell number and size (and hence phenotype) in animals. This thinking is a simplification of the DNA size concept introduced by Baldwin and Black (1979), but overcomes the confounding introduced by between tissue variation in protein/DNA, particularly in muscle (Di Marco *et al*, 1987). This approach is consistent with both measurement capabilities and the level of abstraction of the model.

The approach to estimation of efficiency differs to previous feeding systems. Traditional feeding systems utilise empirically derived linear (additive) relationships between feed, weight (and through weight, body composition) and heat production. Our approach uses empirically derived dynamic relationships which encompass simultaneous interactions between feed intake, body components (protein and fat and hence weight), and heat production. In this construction, efficiency of energy use for maintenance and growth is an outcome rather than an input.

The system we are working with can be described by the following five coupled non-linear differential equations written here in general form:

$$v' = fn(v,m,I) + h$$

$$m' = fn(m,v,I) + h$$

$$h' = fn(v,m,I,f)$$

$$f' = fn(I,h) + h$$

$$I' = fn(v,m,I,h,f)$$

where

   v = viscera (including liver, intestines, heart, lungs, head, skin, blood)

   m = muscle (all carcass lean)

   f = fat (carcass and non carcass)

   h = heat

   I = intake

and the prime notation signifies the differential with respect to time (*e.g.* v' = dv/dt).

Each equation contains functions of terms from other coupled equations. Unlike models derived directly from experimental data, the equations are built from behavioural analysis of the system of equations to ensure that they have properties that include and mimic the observed (experimental) behaviours of the system. This is an iterative process between the mathematicians and biologists and takes place before any numerical solutions are derived. Our simple notions of cause and effect have come under close scrutiny during this process, including the idea that complex behaviours can arise from simple laws.

The first step in the model building process is to look at the behaviour of the components of the system that the model will ultimately capture. The difference in approach to that used in development of previous feeding systems is that a qualitative analysis of the system's behaviour is conducted before numerical solutions are sought. This is to ensure that the equations will generate realistic solutions.

Some of the qualitative and quantitative characteristics that influence our thinking about the form of the separate equations for protein (muscle and viscera), fat, heat production and feed intake are shown below.

Protein deposition

We have recently shown that rate of protein deposition in well (continuously) grown animals can be described by a simple first order relationship between fractional accretion rate of protein and protein mass. This seems to hold in different genotypes of sheep and cattle (Dobos and Oddy, 1994) and pigs (data from Thompson *et al.* 1997). The intercept at zero protein mass is the same for animals of different potential protein mass, and in continuously grown animals only one parameter is required to define different genotypes. However, when protein deposition has been perturbed from the pattern of the well grown animal, the behaviour of protein gain during return to normal protein mass is complex and appears to follow a pattern resembling a damped oscillation (Figure 2). The pattern of return to normal growth state seems to be symmetrical. Perturbations in rate of protein gain to less than expected for protein mass result in subsequent higher rate of protein gain when conditions allow. Return from higher than expected rates of protein gain for protein mass (such as occur during nutrient infusion) results in less than expected rates of protein gain (Ørskov *et al.* 1976; Oddy, unpublished).

The kinetics of protein gain in muscle with respect to feed intake appear to follow an exponentially

a)

b)
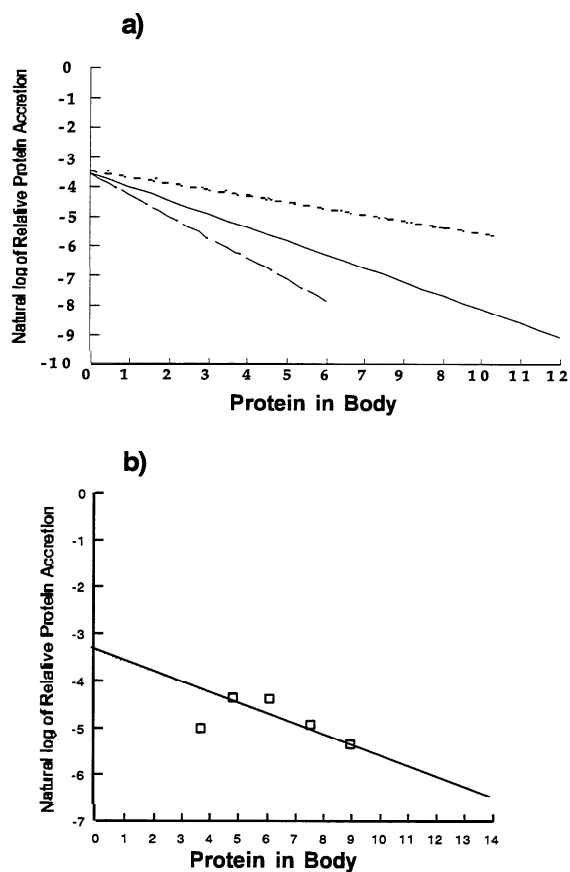
Figure 2

a Relationships between natural log of relative rate of protein accretion (ln(dP/dt)/P) and protein in the body (kg) for constantly grown sheep. Searle *et al.* (1972) (*ad lib* —; 50% *ad lib* – – –) and Orskov *et al.* (1976) (HP - -).

b Relationship between natural log of relative protein accretion and protein mass in the body for normal 'well grown' sheep (HP) and sheep that are compensating (LHP o). Data from Orskov *et al.* (1976).
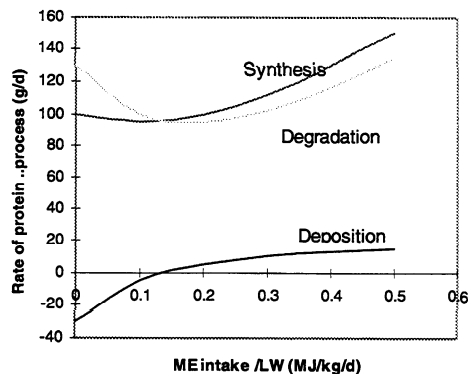
Figure 3   Relationship between metabolisable energy intake and net protein deposition, and protein synthesis and degradation in hind limb muscle of **wether** lambs of similar weight and age. From data presented in Oddy, 1993.

decreasing form (Oddy, 1993; Figure 3). In viscera the kinetics of protein gain with respect to intake are less clearly described, but limited data for small intestine (Neutze *et al.* 1997) suggest a similar form of relationship between intake and protein gain as in muscle, although the parameters would be expected to differ.

Protein depositon is the balance between two energy requiring (heat producing) processes, protein synthesis and degradation. The form of the relationship between rate of protein deposition, rate of protein synthesis and degradation is shown in Figure 3. This general form applies at least in muscle (Oddy, 1986) and small intestine (Neutze *et al.* 1997). The form of the relationship between protein synthesis and degradation differs between tissues only by the amount of synthesis relative to deposition. In muscle, where synthesis exceeds deposition by perhaps 5 to 1, the relationship between feed intake and protein degradation is as shown in Figure 3, but, in viscera, where protein synthesis exceeds deposition by perhaps 20 to 1, 1protein degradation and synthesis have almost the same form. This arises from the equality, protein deposition = synthesis-degradation (which also means that only two components need be described to specify the relationship).

The relationships between protein deposition, synthesis and degradation are confounded not only because of the equality above, but also because variation in these parameters is induced by variation in feed energy (and amino acid) intake and between animal variation from both genotype and previous growth history. It is notable that the form of the relationship between feed intake and protein synthesis is the same as that between feed intake and heat production (Figure 8).

We have shown that, at least in muscle, genotype affects the form of the relationship between protein deposition and feed energy intake through alteration in the rate of protein degradation (and hence protein synthesis) with respect to feed intake (Figure 4). Thus genetic and history effects do not change the form, but alter the position of the relationships between energy (and amino acid) intake and protein synthesis, degradation and deposition as shown in Figure 4.

The information contained in these diagrams is drawn not from a single experiment but an overview of many. The diagrams tell us about the form of the equations needed to describe protein deposition generally in muscle and viscera, the manner in which they change relative to each other, immediate and past feed intake and in genetically different animals.

Figure 3 indicates that the relationships between feed intake and protein deposition are cubic in form for muscle. It is important to determine if protein deposition in muscle and viscera follow the same trajectory with respect to feed intake during periods of increased and decreased intake. Figure 5 suggests that viscera at least does not follow the same relationship during periods of reduced feed intake as during increased intake. This suggests that there is a bifurcation in the viscera, and

possibly muscle, response to feed intake. The form of equations used to describe protein gain in both muscle and viscera was set to correspond to the implications of Figure 3 and Figure 5 (*i.e.* cubic in form with a single bifurcation node). The equations are :

$$m' = a(v)I - b(v)m + c(v)m^2 - d(v)m^3 \quad (= f_1(v,m))$$

$$v' = \alpha(m)I - \beta(m)v + \gamma(m)v^2 - \delta(m)v^3 \quad (= f_2(v,m))$$

where m' = dm/dt, v' = dv/dt, and I = dI/dt are rate of energy gain in muscle, viscera and feed intake (MJ/d) respectively; a, b, c, d, a, β, γ, δ are parameters (which may be either constants or functions). By equating b =, and c =, a potential (a Lyapunov function) is derived such that $df_1 / dm = df_2 / dv$ defmes an attractor in m,v space. The field approaching this attractor is the potential. The potential formulation is dynamically identical with the dynamic system (gradient) equations but can be resolved with approximately 2/3 the number of parameters.
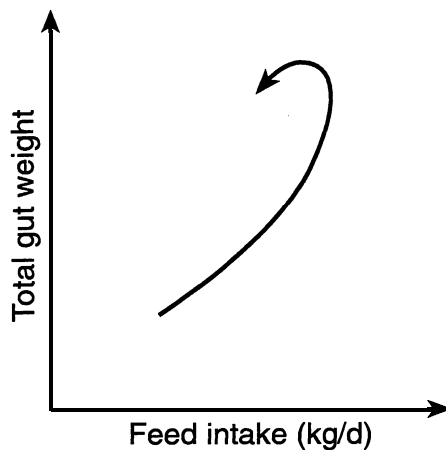
The bifurcation diagram for muscle, viscera and intake is shown in Figure 6. The actual state (growth trajectory) tracks between two stable basins of attraction, such that as intake increases above a certain value the preferred attractor is high protein gain, and as intake falls below a particular value the preferred attractor is is low protein gain (or loss). The distance between the attractors (the cusp distance) may vary, and at times be quite small.

That is as far as we have progressed to date with development of the equations. There are several areas in which we plan to incorporate genotype into the protein system. The most obvious is in the rate of approach to a 'mature or potential' protein pool to capture the simplicity shown in Figure 2. The others are in the area of variation in feed intake with regard to protein mass and heat production (derived from protein synthesis as proxy) which will be discussed next.
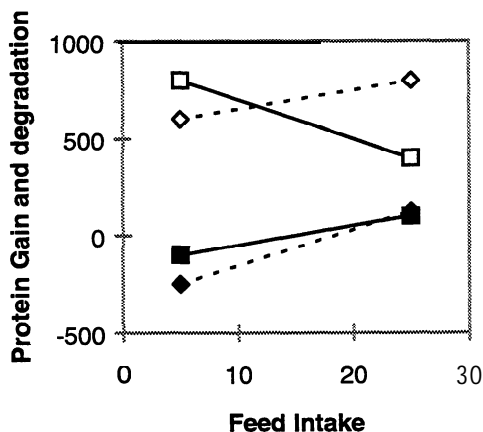
Figure 4 Response of protein gain and degradation in hind limb muscle to feed intake (g/ kg LW) in sheep selected for (W+) and against (W–) rate of gain to weaning. Symbols are respectively W+ protein gain and degradation (■___■, □__□) and W–protein gain and degradation (◆--◆, ◇---◇). Units for protein kinetics are nmol phenylalanine /kg hind limb/ min. (from Oddy *et al.* 1995).

What is a bifurcation? A non-linear dynamical system may have several attractors. When the system changes from moving towards one attractor to moving to a different attractor (because, for example, energy intake has changed) this can result in the system exhibiting qualitatively different features. For example, a grazing system can move from being in a stat e of equilibrium to collapse as a parameter, stocking rate, increases. The type of change is called a bifurcation. The evidence suggests that the relationship between muscle and viscera can exist in two different states of equilibria, the particular state depending on the energy intake and the previous nutritional history. As the bifurcation parameter, in this case energy intake, changes, the equilibrium of the muscle viscera relationship may change once the energy intake passes a certain value. If this phenomena occurs then such a bifurcation would explain many of the aspects of compensatory growth in animals. That is, compensatory growth arises from a qualitative change in system behaviour arising from a change in the attractor which the system is obeying.

Figure 5 Relationship between weight of gut (rumen plus small and large intestine tissues) and feed intake in Merino rams. Data from Butterfield (1983).
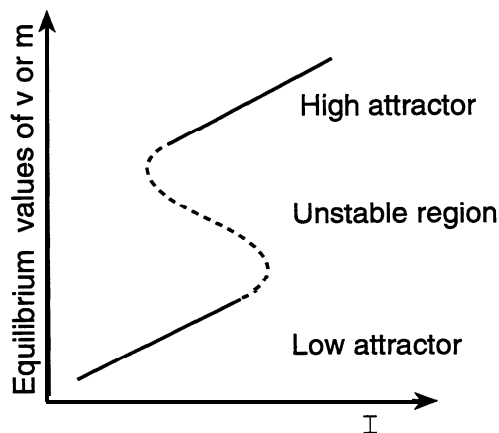
Figure 6 Bifurcation diagram for viscera (v) and muscle (m) mass versus feed intake (I).

Heat production

Lean body mass is more closely related to heat production than is total body mass (Graham, 1967; Waterlow *et al.* 1976; Webster, 1980; Baker *et al.* 199 1). Viscera has a substantially higher specific rate of heat production (i.e. heat production per unit mass) than does muscle, as measured by oxygen consumption (Eisemann *et al.* 1996). Muscle has a higher rate of heat production than fat. This suggests that the proportion of the highly metabolically active visceral tissues relative to muscle weight will affect the heat production of the animal.

Two mechanisms link lean body (protein) mass to heat production: turnover of protein, of which protein synthesis is the major energy utilising process; and ion transport--i. *e.* maintenance of intracellular integrity—which in itself seems to be related to protein synthesis (Milligan and McBride, 1985; Webster, 1980). Protein synthesis per unit of protein mass generally declines with age (growth) as does utilisation of energy for maintenance relative to protein mass. An approach which deals with the contribution of protein synthesis to heat production, and hence maintenance requirements, has recently been suggested by Knapp and Schrama (1996). These authors propose that a dynamic maintenance requirement can be calculated from different energy costs for synthesis of newly deposited protein and existing protein in different body pools. Although sound theoretically, such an approach is difficult to quantify because current methods for measurement of protein synthesis in animals are unable to distinguish between peptide bonds formed in 'new' or 'old' proteins. The contribution of protein synthesis to heat production (calculated on the basis that 1 g protein synthesised requires a minimum of 4.5 kJ for peptide bond formation) suggests that whole body protein synthesis may contribute from 15 to 30% of heat production. The close relationship between protein synthesis and heat production summarised by Webster (1980) suggests that protein synthesis is quantitatively entrained with other energy utilising processes, and provides at least a convenient proxy by which dynamics of heat production can be estimated and investigated.

As shown in Table 2, the relative contribution of protein synthesis to oxygen utilisation varies between tissues. The highest rate of protein synthesis and oxygen utilisation is in visceral organs. It is for this

reason, and their higher specific energy utilisation, (Ortigues and Doreau, 1995), that we have chosen to describe the viscera separately from the more slowly turning over, and hence less energy demanding, carcass proteins in our description of protein deposition and heat production.

We are accustomed to comparing energy retention with respect to intake. Such ideas are the basis of the metabolisable (ME) and net energy (NE) feeding systems. In general the relationship is of the form shown in Figure 7.

This implies that the relationship between ME intake (MEI) and heat production has a curvilinear form (Figure 8) which is the same shape as the relationship between protein synthesis and MEI (Figure 3). We
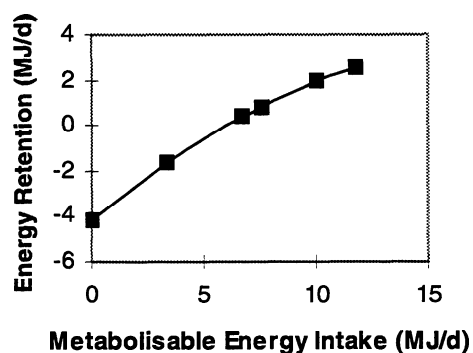
Figure 7   An example of the relationship between metabolisable energy intake and energy retention in sheep (data from Corbett *et al. 1966).*
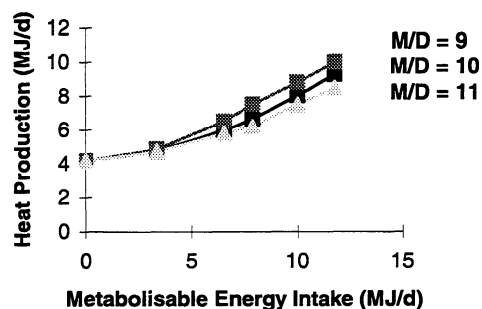
Figure 8   Relationship between heat production and ME intake. The different lines show the general effect of change in energy density of the feed.

Table 2   Oxygen uptake in tissues and the minimal proportion of tissue and whole body oxygen consumption due to protein synthesis.

Tissue	Contribution to whole body energy use (%)	Minimal proportion of O_2 uptake used by protein synthesis (%)	Proportion of whole body protein synthesis (%)
Liver	20	25–50	20
Small Intestine	15	30–60	25
Muscle	25	12–20	25

propose that variation in slope of the relationship between MEI and heat production, and by definition, energy retention, arises from variation in heat production in muscle and viscera because of changes in protein turnover and mass of protein in these different pools (Knapp and Schrama, 1996).

The effect of feeds of different energy density (MJ ME / kg feed dry matter, M/D) on heat production has been both a cornerstone and a source of controversy in the field of ruminant nutrition. Our view is that these effects are mediated through affects on visceral mass (Ferrell *et al.* 1986) and protein turnover and hence energy expenditure (Neutze *et al.* 1997), and to a lesser extent on muscular energy expenditure (Ortigues and Doreau, 1995). This proposal is consistent with the suggestion of Sainz (199 1) that heat production in lambs eating different diets was better related to visceral mass and an undefined function of energy intake, than visceral mass alone. Sainz speculated that the undefined function of energy intake consisted of changes in ion–transport or substrate cycling (Sainz, 199 1).

There have been previous attempts to quantify relationships between visceral oxygen consumption and heat increment of feeding, (Webster *et al.* 1975) but these workers were unable to gather sufficient evidence at that time to convincingly quantify the importance of visceral mass and metabolism on heat production.

Subsequently the case for differences in heat production driven by differences in substrates arising from feeds of different M/D intensified and dominated thinking despite lack of clear evidence (contrast Blaxter, 1962 and Black *et al.* 1987; with Orskov *et al.* 1979 & 199 1).

Clearly heat production and nutrient deposition are connected in that the composition of tissue deposition depends on the relative amounts of protein and fat deposited, and heat production is related to protein mass (and deposition) and turnover. Thus, energy density (different feeds) would be expected to influence composition of gain.

For example, Tudor (1992 and unpublished) and Sainz *et al* (1995) (Table 3a and 3b) demonstrated that at the same rate of gain, composition of gain can vary depending on the M/D of the diet. The discrepancy in body energy gain of cattle fed a high M/D (concentrate limit fed, CL) diet and low M/D diet (*ad libitum* forage, FA) when metabolisable energy intake was equal was 3.08 MJ/d. Efficiency of use of MEI was less on the FA than the CL diet, an idea consistent with our expectations that animals have higher heat production when eating roughage compared to concentrate diets (and with the idea that pattern of substrate supply influences heat production). Sainz and Bentley (1997) have since reported the masses of internal organs in cattle fed the same MEI as forage or concentrate in Sainz *et al.* (1995).

Table 3a Body composition changes in cattle fed a forage based diet *ad libitum* (FA) or limit fed a concentrate based diet (CL) in pens (Intermediate slaughter group, Sainz *et a/.* 1995). The period between slaughter of initial and treatment groups was 110 d.

	Initial	FA	CL
Empty Body Weight (kg)	214	283	292
Hot Carcass Weight (kg)	140	188	195
Fat (kg)	25.2	33.2	41.9
Protein (kg)	39.1	53.9	52.3
Fat gain (g/d)		72	152
Protein gain (g/d)		135	120

Table 3b Comparison of grass vs grain feeding on composition of gain in animals growing at the same growth rate (from Tudor 1992 and unpublished). Animals were Hereford steers (12-l 5 months old at the start of the experiment), and were limit fed a grain based diet to achieve the same rate of gain (-0.8 kg/d) as the group with *ad libitum* access to high quality grass pasture. Grain diets consisted of both sorghum and barley plus minerals and urea (80%) and chaff (20%). The period between slaughter of initial and treatment groups was 240 d. Values are means ± sd.

	Initial	Grass	Sorghum	Barley
Empty Body weight (kg)	160.5 ± 10.9	347.3 ±6.3	344.0 ± 6.4	335.9 ± 5.5
Hot Carcass weight (kg)	99.2 ± 6.8	228.8 ± 2.9	229.1 ± 5.3	221.3 ± 4.23
Fat (kg)	21.4 ± 1.27	74.7 ± 6.60	88.7 ± 8.60	82.9 ± 8.05
Protein (kg)	30.2 ± 2.54	62.4 ± 3.71	57.4 ± 1.65	56.9 ± 1.71
Ash (kg)	6.7 ± 0.87	14.0 ± 0.65	12.2 ± 0.76	11.7 ± 0.97
Fat gain (g/d)		220	280	256
Protein gain (g/d)		134	113	111
Ash gain (g/d)		30	23	21

It can be seen from Sainz's data (Table 4a) that intestinal and liver growth on the low M/D diet was greater than the high M/D diet. The difference in energy content of protein gain between ad lib forage (FA) and restricted concentrate diet (CL) (0.16–0.07 = 0.09 MJ/d), and the extra energy used by the liver and portal drained viscera (PDV) (25.02–21.64 = 3.38 MJ/d) was sufficient to account for the difference in fat deposition between high and low M/D diets (Table 4a). The same trend is apparent in data from Tudor (Table 4b). This suggests that it is possible to explain the differences in body composition arising when animals eat different diets from change in mass of organs with high metabolic rate without the need to invoke a separate substrate driven mechanism.

Differences in energy expenditure because of eating and ruminating are partially incorporated in the measures of PDV energy expenditure utilised above, but energy expenditure associated with muscular activity such as chewing and exercise is not. In small yards or pens (e.g. study of Sainz et *al.* 1995) energy expended on walking and postural change is small. However, walking and postural change in grazing animals may contribute significantly to energy expenditure (SCA, 1990). On this basis it would be expected that differences in exercise could influence body composition by a) stimulation of muscular growth and b) associated decreased availability of energy for fat deposition. Nonetheless, differences in visceral mass, the components of which were not as well defined as by Sainz and Bentley (1997), account for the greatest part of the difference in body composition between grass and grain fed cattle growing at the same rate (Tudor, 1992; Tables 3b and 4b). These observations are consistent with observations in lambs fed diets of different energy density or amount (Ferrell et *al.* 1986; Oddy, 1994; Ortigues and Doreau, 1995; Fluharty and McClure, 1997).

Fat deposition

At the turn of the century **Armsby** and Attwater reasoned that the energy deposited in fat was equal to the difference between energy intake, protein deposition and heat loss. There has been no subsequent evidence to disagree with this hypothesis. Our own recent experiments have shown that fat mass may increase at

Table 4a   Mass, and protein content (in parentheses) of liver, forestomachs, intestines and pluck (heart, lungs and spleen), and the implications for energy expenditure and fat deposition of cattle described in Table 3. Data from Sainz and Bentley (1997; Table 3a). Protein content of pluck was assumed to be the same as mean of other internal organs (0.123). Energy content of protein was assumed to be 24 kJ/g, energy expenditure in viscera was derived from similar weights of cattle (Phase I of Eisemann et a/. 1996). Energy expenditure (heat production) values were calculated from oxygen consumption as described by Webster 1980; and were liver 3.16 MJ/kg/d , portal drained viscera (forestomach + intestines) 0.45 MJ/kg/d , values for pluck were assumed to be 50% of PDV (vis 0.225 MJ/kg/d).

	Initial	FA	CL
Liver	3.36 (0.608)	4.33 (0.791)	3.80 (0.640)
Forestomachs	8.21 (1.02)	12.1 (1.36)	9.08 (1.09)
Intestines	7.84 (1.00)	9.91 (1.10)	8.85 (1.04)
Pluck	5.53	6.48	7.03
Protein gain in above (g/d)		6.75	2.98
Energy retained as protein (MJ/d)		0.162	0.072
Additional energy expenditure in visceral organs to support additional mass (MJ/d)		25.02	21.64

Table 4b   Changes in mass of viscera in cattle growing at the same rate, either grazing pasture or fed diets containing 80% sorghum or barley grain (as described in table **3b**, unpublished data of G. Tudor). Energy expenditure in viscera were calculated as described above, on the assumption that the proportional contribution of liver and portal drained viscera were similar.

	Grass	Sorghum	Barley
Visceral mass (kg)	49.9	46.6	47.3
Estimated * mass (kg) of:			
Liver	6.5	6.1	6.2
Forestomach / intestines	33.4	29.1	29.6
Pluck	10	11.4	11.6
Estimated energy expenditure in viscera (MJ/d)	37.80	34.70	35.30
Gain in fat in carcass (MJ/d)	8.58	10.92	9.98

the expense of lean tissue in animals that experience some form of nutritional manipulation (Ball *et al.* 1997). There is a suggestion that deposition of fat has an upper bound (shown as constancy in slope of fat deposition with respect to body mass) in sheep (Searle *et al.* 1972) and cattle (Owens *et al.* 1995).

We suggest that an apparent upper limit to the rate of fat deposition arises only from the interaction between energy intake, deposition and expenditure. This accounts for possible feedback of fat on feed intake, through either physical action-for example, through increased insulation and control of body temperature (both a positive and negative effect depending on external temperature), or through a chemical signal— such as leptin or other hormones. This notion is explicitly contained within the equations we have developed.

Feed intake

The simplest mechanism we can invoke for regulation of feed intake is made of two elements: maintenance of body temperature, and need to obtain amino acids and energy yielding nutrients for development of cells, tissues, organs and the organism.

Ruminants, and mammals in general, are homeotherms. They regulate their body temperature within precise limits by altering respiration, posture, activity and feed intake relative to environmental heat load. For example, Kellaway and Colditz (1976) contrasted the effects of temperature on intake and nitrogen balance of two breeds of cattle. Holstein– Brahman cross cattle were better able to regulate body temperature (in our conjecture intrinsically low heat production is associated with a smaller gut and liver in Brahman cross cattle) and were able to maintain feed intake (and nitrogen balance) at higher levels than Holstein cattle. By analogy, we argue that feed intake

and rate of heat production arising from protein deposition and turnover are balanced to maintain a constant internal heat load (body temperature). Increased heat load, either from internal or external sources, will change the flux of heat between the animal and environment, and lead to alteration in feed intake.

We propose both a potential and a constraint such that at low weights heat loss per unit weight is high, which may have the effect of increasing feed intake, while at high weights heat loss per unit weight is low and may act as a constraint on feed intake. This concept is consistent with the model of Ketellars and Tolkamp (1996). They proposed feed intake was a function of the difference between the metabolisable energy that entered the body and the oxygen consumption. However, our model differs in so far as we are attributing no causative mechanism such as long term deleterious effects of oxygen as suggested by the above authors.

The behaviour of protein deposition has been discussed above. We intend to utilise characteristics of this behaviour as an attractor / potential / drive to obtain amino acids from food to permit growth of cells (which we have simplified to the protein mass of the animal). Webster (1989) indicated that a target for lean growth (protein deposition) dominated the regulation of feed intake and that fat deposition per se had little effect.

There is one additional feature of intake we believe it important to capture. Although, we are accustomed as experimentalists to holding feed intake constant, or specifically manipulating it to meet our experimental ends, this is not the real world. Inspection of data where animals have *ad libitum* access to feeds shows large and apparently irregular variation in short term feed intake regulation, but paradoxically long term stability as illustrated in Figure 9. Poppi *et al.* (1994) indicated that this irregularity in feed intake was a response to a series of constraints that are either additive or multiplicative (Emmans and Kyriazakis, 1995).
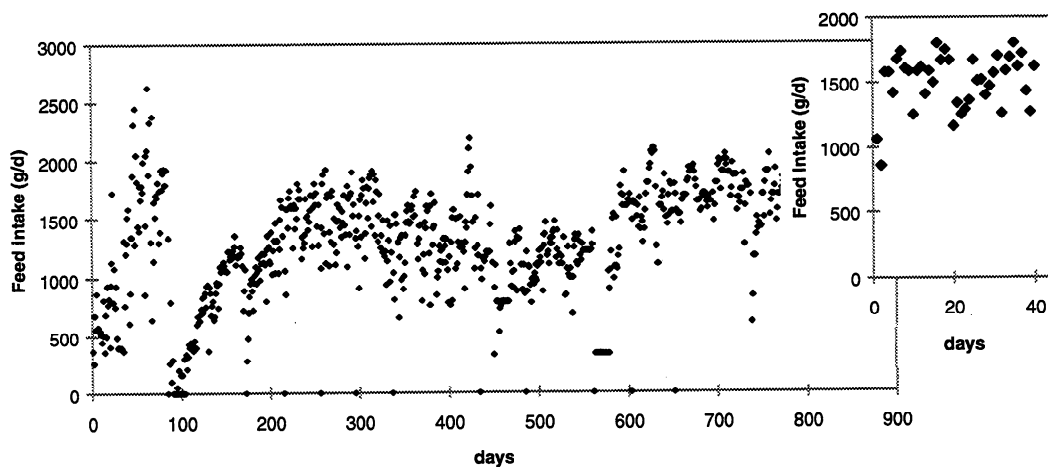
Figure 9 *Ad libitum* feed intake from birth to **840** days of age in a ram. Data shown are for milk replacer between birth and 90 d and a **pelletted** diet (**10** MJ ME, 150 g protein / kg DM) from 90 d. Note a long term pattern in intake emerging, but associated with substantial day to day variation. The range in daily feed intake is more clearly seen in the inset which shows intake from day 215 to 260.

Cycles of intake **with** regard to time occur **in ad libitum** feeding situations and some attempt has been made to describe the magnitude of these oscillations through sine functions (Stroup *et al.* 1987). In most cases we, as nutritionists, have tried to ignore, or worse, design such variation out of experiments by restricting intake. New mathematical techniques show that these events are not random but are signatures of underlying patterns that evolve from the interactions between the states and the variables within the animal. For example, limit cycles (Figure 10) arise in second order systems which when unravelled along the time axis look remarkably like our records of **ad libitum** feed intake over time (Figure 9). The mathematics of such systems exhibits both short term variation and long term stability because of the presence of a periodic attractor (or basin of attraction). Both stability and variability is the consequence of a dynamic balance between all components influencing daily intake.

Conclusion

By the above reasoning, the efficiency of energy and nutrient use of an animal and deposition of fat and protein can be simplified to a function of:

- relative size and growth of visceral protein and carcass protein pools;
- differences between energy utilisation within these pools; and
- amount and composition of feed intake.

These ideas are consistent with data generated from genetic (Perry *et al.* 1997; Herd *et al.* 1997) and nutritional experiments (Orskov *et al.* 1976; Ferrell *et al.* 1986;
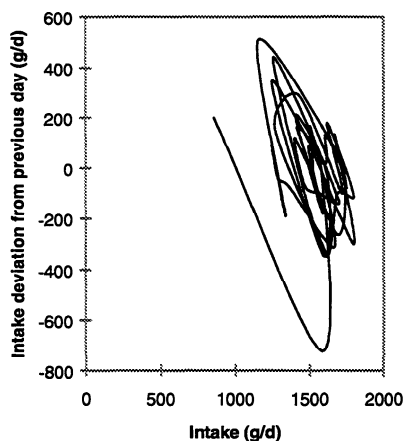
Fluharty and McClure, 1997). The simplicity derived from the process of putting these ideas together is to us a powerful argument for their utility.

Like all modelling tasks we face a problem with circularity, *i.e.* the system will only contain the assumptions that are put into it, regardless of being explicitly stated or (intentionally or unintentionally) implied. The challenge yet to be addressed is to determine if the new insights emerging from the simplifications we have proposed increase our understanding of the system, and lead to prediction (and verification) of new implications which did not previously exist. It is only then that we should feel that our approach is of long term value to the science of animal production.

Acknowledgements

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Figure 10   Plot of deviations in feed intake from previous day versus feed intake on each day for the data shown in the inset in Figure 10. When run in real time this diagram shows that the deviations circle about the mean, suggestive of a periodic attractor, yet the time series expressed as in Figure 9 suggests the variation is random.

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