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ENERGY PARTITIONING AND MODELING IN ANIMAL NUTRITION

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CONTENTS

ABSTRACT

We first present a brief discussion of early and current models (feeding systems) used to estimate animal energy and protein requirements and to predict performance based on feed composition and intake. We then touch on some limitations inherent in these systems. Next, we propose that dynamic (i.e. time-variant) models and mechanistic models (i.e. equations based on knowledge of physiological functions) are superior to earlier systems for both practical and research applications. Finally, we describe a number of applied and research models of animal growth and lactation to illustrate how biological concepts may be represented in equation form. Equations that represent current knowledge of underlying functions can be used to improve predictions of animal requirements and performance and to evaluate hypotheses about nutritional and physiological mechanisms that influence animal performance.

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INTRODUCTION

Several years ago we published a review entitled "Nutritional Energetics of Animals" (6). In that review, we presented the basic terminology developed by the National Research Council (NRC) to define animal energy requirements and feed-energy values. We also reviewed factors that cause variance in fasting heat production and efficiencies of productive functions. The final section of the review focused on problems associated with statistical analyses of data from studies of energy balance and on early stages in the development of dynamic, mechanistic models for use in research and in improving feeding systems used in animal agriculture. By feeding systems, we mean the equations and parameters used to estimate the values of feeds to support various animal functions and, conversely, to predict animal performance under varying dietary conditions. These feeding systems are therefore inextricably linked to the models on which they are based.

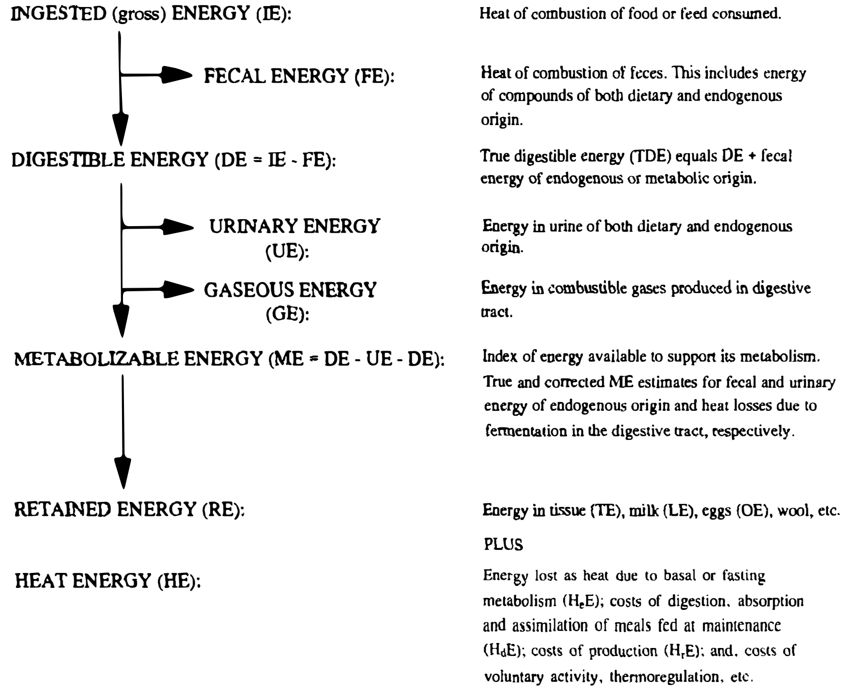
Some redundance with our 10-year-old review is unavoidable, but we have attempted to minimize repetition. After a very brief discussion of terminology, we turn to models of growth and lactation currently in use. Our main emphasis, however, is progress in the development of mechanistic, dynamic models that we hope will be adapted and adopted in the near future for the benefit of animal agriculture.

MODELS CURRENTLY IN USE IN ANIMAL NUTRITION

Historical Perspective and Basic Definitions

The application of models in animal nutrition dates back to the turn of the century and resulted from the development of methods to evaluate foods and feeds in terms of carbohydrate, fat, and protein content (35). For example, Atwater & Bryant (2) defined the physiological fuel value system (PFV; see below) wherein the energy values of foods were estimated by multiplying the carbohydrate, fat, and protein content of foods by the respective classical values of 4.0, 9.0, and 4.0 kcal/g (16.7, 37.6, and 16.7 kJ/g).

Armsby (1) defined metabolizable energy (ME) as "the gross energy in the feed minus the gross energy of the excreta" and as "energy capable of transformation in the body." Net energy (NE) values of feeds for maintenance were measured as the body energy loss prevented by an increment of feed, whereas NE values of feeds for productive processes were measured as the amounts of energy recovered in products such as gain, eggs, or milk per increment of feed provided above maintenance. These measurement methods enabled the development of models to predict animal energy and feed requirements based on their expected productivity or, conversely, to predict animal productivity based



INGESTED (gross) ENERGY (IE):	Heat of combustion of food or feed consumed.
FECAL ENERGY (FE):	Heat of combustion of feces. This includes energy of compounds of both dietary and endogenous origin.
DIGESTIBLE ENERGY (DE = IE - FE):	True digestible energy (TDE) equals DE + fecal energy of endogenous or metabolic origin.
URINARY ENERGY (UE):	Energy in urine of both dietary and endogenous origin.
GASEOUS ENERGY (GE):	Energy in combustible gases produced in digestive tract.
METABOLIZABLE ENERGY (ME = DE - UE - DE):	Index of energy available to support its metabolism. True and corrected ME estimates for fecal and urinary energy of endogenous origin and heat losses due to fermentation in the digestive tract, respectively.
RETAINED ENERGY (RE):	Energy in tissue (TE), milk (LE), eggs (OE), wool, etc.
	PLUS
HEAT ENERGY (HE):	Energy lost as heat due to basal or fasting metabolism (H_eE); costs of digestion, absorption and assimilation of meals fed at maintenance (H_dE); costs of production (H_rE); and, costs of voluntary activity, thermoregulation, etc.

Figure 1 Classification of energetic relationships.

on feed intake. The current NRC terminology for energetic relationships depicted in Figure 1 is therefore based on concepts developed at the turn of the century.

Several feeding systems are based generally on estimates of feed values and animal requirements in terms of ME that were developed early in this century. Atwater's (2) PFV system is still used by dieticians for both humans and laboratory animals. Data using the total digestible nutrients (TDN) system are still included in NRC publications on the nutrient requirements of several livestock species. These and other historical systems are factorial, empirical, and static. These terms are described more completely below; briefly, factorial means that nutrient supply and demand are considered additively; empirical signifies that they are estimated from whole-animal data without regard for underlying mechanisms, and static indicates that they are estimated for a single point in time.

Traditional feeding systems are factorial in that estimated energy requirements are calculated as the sum of energy required for maintenance, activity, pregnancy, lactation, growth, etc. For example, in the TDN system, the TDN requirement of a lactating dairy cow is calculated as follows:

$$TDN_{required} = TDN_{maintenance} + TDN_{growth} + TDN_{lactation} + \ldots$$

A factorial system is based on several presumptions. For example, it is assumed that values determined for feeds used to satisfy an animal's energy needs are additive for all functions and that interactions among feeds and functions do not occur. Usually, these presumptions do not hold true. For example, in the TDN system, values assigned to forage and concentrate feeds are neither equal nor additive for alternative functions (6, 9). TDN requirements for several functions are derived from tabular values based on factors such as body weight and rate and type of production. The tabular values, in turn, are based on experimental input:output data obtained with intact animals. These problems are also inherent to all the early feeding systems, including the PFV system (3).

According to current terminology, systems in which input:output data from animal experiments are used to predict animal performance are considered empirical. The term empirical implies that knowledge of underlying functions was not considered in formulating the system and, most importantly, that the system can be applied only to the animals, feeds, and conditions for which experimental data are available. In other words, the system does not apply generally. For example, TDN and PFV values for feeds and foods are estimated for animals fed at maintenance (i.e. animal energy balance equals zero). Under this condition, carbohydrate and protein have equal values as energy sources. In rapidly growing and lactating animals, however, this does not hold true because dietary protein incorporated into body and milk proteins does not result in energy losses in urea or in heat loss due to urea synthesis. As a result, the value assigned to protein used for growth and lactation should be 5.2 kcal (21.8 kJ)/g rather than 4.0 kcal (16.7 kJ)/g as in the PFV system. This miscalculation can lead to errors of up to 25% in estimates of the energy value of dietary protein, depending on what portion of dietary protein is used as an energy source or for a productive function. These portions clearly are variable in that they depend on growth rate, age, composition of gain, etc.

As used above, the term static simply indicates that all early and most current systems apply to a specific animal (body weight, rate of production, etc.) at a specific point in time. As a result, effects of previous nutrition on current performance (such as compensatory growth occurring after a period of undernutrition) or of current underfeeding on subsequent performance (a very prominent effect during lactation) are not accounted for (9). These same problems are inherent to all early feeding systems, including the starch equivalent system, which was the first feeding system based on NE concepts (3, 9).

Energy and protein feeding systems exemplified in publications of the Committee on Animal Nutrition of the National Academy of Sciences–National Research Council (NAS-NRC-CAN) describe the nutrient requirements of more than 20 species of domestic animals (38–42) and have evolved considerably over the past 40 years. Although the systems have remained static, factorial, and largely empirical in nature, mechanistic concepts have been incorporated into the statistical models used in analyses of input:output data and applied in the revised systems. In this context, the term mechanistic implies that some knowledge of underlying metabolic and physiological function has been incorporated into equation forms used in statistical analyses (usually multiple linear regressions) of animal data. A straightforward example of this increasingly mechanistic approach is the NE system adopted for beef cattle (39). In developing this system, Lofgreen & Garrett (34) recognized that the relative efficiencies with which feeds are utilized to support maintenance (i.e. prevent the loss of body energy) differ considerably from the relative efficiencies with which they are used to support growth. Thus, two values (NE_m and NE_g, denoting NE for maintenance and gain, respectively) are assigned to each feed, enabling estimation of the performance (i.e. growth from NE_g) of the animal after accounting for its maintenance requirements (i.e. NE_m). Although slow to evolve, this simple concept greatly improved the accuracy of the NRC system for feeding beef cattle.

We noted above that a unit of TDN from forage has a lower real value than a unit from a concentrate feed and that the relative values of forage and concentrate vary for different animal functions. This variation results in part from the fact that relative energy losses in methane from forage are greater than those from concentrates. This systematic error is corrected in current systems by definition of ME as feed energy minus energy losses in excreta and combustible gases (Figure 1). Other problems arising from nonadditive TDN values can be attributed to differences in heat loss during fermentation, to differential changes in digestibility associated with intake, and to differences in the products of fermentation and their efficiencies of utilization by the animal. These latter differences vary with ME content of the diet. Thus, most current ME-based feeding systems incorporate a correction factor based on ME contents of feeds. In most ME-based models, the ME requirement of an animal is calculated as the sum of ME required for maintenance, growth, lactation, and other activities. ME requirements for maintenance (ME_m, in MJ/d) are usually calculated from body weight (W, in kilograms) as

$$ME_m = a \times W^{0.75}/k_m,$$

where the maintenance coefficient, a, might range from 0.25 to 0.5 for animals on a low plane of nutrition to 0.5 for lactating animals and where k_m (i.e. the efficiency of ME utilization for maintenance) might range from 0.65 to 0.80, depending on the ME content of the feed. Similarly, the ME requirement for gain (ME_g, in MJ/d) would be calculated as

$$ME_g = RE/k_g,$$

where RE is energy retained in gain (MJ/d) and k_g (i.e. efficiency of ME utilization for gain) might range from 0.33 to 0.65, depending on the relative content of fat and protein in the expected gain and ME content of the diet. Alternatively, energy gain in fat and protein may be calculated separately, using estimates of their respective efficiencies that would vary with the ME content of the diet. The latter approach might be judged superior on academic grounds, but empirical estimates of the partial efficiencies of fat and protein gain are not very stable from experiment to experiment in animals of the same age or in animals of different ages. In conventional energy balance experiments, this instability may be due to our failure to satisfy the underlying assumption that parameters are independent. Independence of parameters is essential for estimating partial efficiencies of protein and fat gain using multiple linear regression (12, 48). This problem, together with the problem of variation in apparent maintenance requirements noted above, suggests that further improvement of current feeding systems and the models on which they are based will be limited by the classical input:output empirical data used to estimate the required parameters.

The NRC (42) feeding system for lactating dairy cows is presented below as an example of a current feeding system based on NE. Moe et al (37) demonstrated that in lactating cows, NE values of feeds for lactation (NE_l) and maintenance (NE_m) are essentially equal. Thus, animal requirements and feed values can be expressed in terms of NE_l. The following equations are used to estimate NE_l requirements (MJ/d) for the different functions of maintenance (NE_lM), pregnancy (NE_lP), weight gain (NE_lLW) and loss (NE_lWL), and lactation (NE_lL)

$$NE_lM = 0.335 \times W^{0.75}.$$

This equation is the sum of a maintenance requirement of 0.305 MJ $NE_l/kg^{0.75}$ plus activity at 0.1 × maintenance for cows in stalls or drylot.

$$NE_lP = 0.100 \times W^{0.75} \text{ (after 210 days of pregnancy)}$$

$$NE_lLW = 20.6 \times \text{weight gain in kilograms}$$

or

$$NE_lWL = 21.4 \times \text{weight loss in kilograms}$$

$$NE_lL = (1.47 + 0.4025 \times \%\text{ milk fat} \times \text{kg milk}).$$

Thus, the NE_l requirement of a 700-kg cow in her 220th day of lactation gaining 1 kg of weight/day and producing 25 kg of milk containing 3.7% fat would be (45.6 + 13.7 + 21.4 + 74.0) or 154.7 MJ/day.

The calculation of net protein requirements (g/day) of lactating dairy cows in the NRC (42) system is similarly static and factorial in nature:

$$\text{Net protein} = U + S + F + G + C + L + D,$$

where U is urinary protein equivalents (i.e. nitrogen × 6.25; $2.75W^{0.75}$); S is surface protein loss as hair, scurf, etc. ($0.2W^{0.6}$); F is the protein equivalent of fecal nitrogen loss (0.09 × indigestible dry matter); G is the protein content of body weight gain ($211.0 - 26.2 \times NE_g$); C is protein deposited in products of conception ($1.136W^{0.7}$); L is protein in milk {[1.9 + 0.4 × % milk fat]/100 × kg milk}; and D is protein associated with weight loss (256 × body weight loss). Requirements for absorbed protein (g/day) are calculated as follows:

$$\text{Absorbed protein} = U/0.67 + S/0.67 + F + G/0.5 + C/0.5 + L/0.7 + D.$$

The numerical coefficients represent estimates of the efficiencies of net protein use for these metabolic processes. A number of additional mechanistic concepts regarding protein digestion and microbial growth in the rumen were introduced into computation of protein availability to cows but are not discussed in this review.

MECHANISTIC, DYNAMIC MODELS OF PATTERNS OF ENERGY USE IN ANIMALS

As discussed in the previous section, the application of classical approaches (i.e. where only input:output data are used to parameterize models) to improving our feeding systems presents several problems and/or limitations. These include difficulties in accommodating variance in apparent maintenance requirements and in defining costs of productive functions due to differences in product composition or the efficiencies of protein and fat accretion (see 6). Additional problems that must be addressed include the effects of previous planes of nutrition on current and future performance and optimization of protein availability to producing animals. Resolution of these problems will require increased use of our knowledge of underlying biological functions in our models. This approach (mechanistic modeling; 55) requires that equations used to simulate, in this case, animal performance be based on concepts derived from studies conducted at the tissue, cellular, and organelle levels. Moreover, the parameters used to implement the equations should, if possible, be derived from data obtained at these lower levels. Significant progress toward this end has been made in recent years, and it appears that mechanistic elements are currently in use or will soon be introduced into various feeding system models to increase accuracy of prediction and general applicability. In this section we discuss progress in the development of some appropriate mechanistic elements.

The development of dynamic mechanistic models of animal functions is highly systematic. Because numerous publications (4, 22) discuss this process in detail, we give only a brief summary here. The first and most important step in the modeling process is setting the objective. In keeping with the thrust of this chapter, an appropriate objective might be to develop a model that can trace through time the effects of alternate nutritional strategies on animal performance and energy and protein requirements. The objective statement dictates what state variables (entities defined by differential equations, e.g. dx/dt) should be included in the model, what equation forms should be used, and most importantly, specifies criteria that must be satisfied in evaluations of the model for adequacy and subsequent publication. To meet the above objective, specific nutrients—glucose, fatty acids, amino acids, etc—must be included as state variables since their patterns of use as energy sources and for productive functions affect efficiency and productivity. In addition, factors such as relative organ weights (6) that influence maintenance energy requirements over time must be explicitly represented. The term "trace through time" in the objective statement requires that the model be based on differential equations of the form

$$dx/dt = f(a, b, c, \ldots).$$

Criteria that are required by the objective statement and employed during the model evaluation phase would include appropriate responses to changes in diets, undernutrition followed by refeeding, and other dietary and physiological manipulations.

The second step in the modeling process is formulating a block diagram that depicts the state variables for which differential equations will be required and the interactions among these entities. Most biologists are familiar with block diagrams, as these are commonly used to present conceptual views of complex biological systems in a concise fashion. However, most block diagrams are conceptual and qualitative in nature. Those constrained by the requirement that transactions and interactions be quantified in subsequent stages of model development are often simplifications of our conceptual view of reality.

The third step in model development is formulating equations for each transaction and interaction depicted in the block diagram. The most common equation forms used to represent rates of nutrient utilization are mass-action equations (rate = $k \times A$) or variations of the Michaelis-Menten equation [rate = $V_{max}/(1.0 + k_s/[S])$], where k_s is the affinity constant for the substrate S and [S] is the concentration of S.

The fourth and most laborious step in the modeling process is the formulation of numerical inputs required to implement the model. Parameterization of the model is based on data in the literature or, often, requires the performance of experiments to estimate required parameters not available in the literature. A useful practice in the estimation of parameters is the definition of a reference condition that is at steady state and wherein average nutrient transactions and interactions are defined for an animal in a specific physiological state fed a single diet. This useful approach serves a number of purposes. First, all dynamic data on animals in other physiological states or fed alternative diets are reserved for subsequent evaluations of the adequacy of the concepts that underlie the model. Second, the (in)ability of a dynamic model to hold the reference condition at steady state over time is a very useful tool for debugging the model, e.g. for identifying coding, typing, and arithmetical errors inadvertently introduced during model formulation.

The final step in model development is evaluation of the model in terms specified in the objective statement. If the (applied) objective is to develop a model to predict animal performance better than a preexisting system, the modeler(s) must prove that their (challenger) model yields better predictions than the current (defender) model. If the (research) modeling objective is to identify aspects of animal function for which current concepts and data are inadequate to explain or simulate reality, the evaluation phase should reveal and pinpoint inadequacies in those concepts and data as well as help identify critical experiments to improve understanding of these underlying functions.

Growth Models

In this section we focus on dynamic, mechanistic models of growth as opposed to the static and relatively empirical models such as the Gompertz equation (33). The main advantage of using more realistic representations of animal function is that they lead to improved applicability of these models in the real world. Nevertheless, these models can be subdivided into two groups: models that were developed for predictive purposes, and research models. The former were designed for application in the real world, i.e. to predict responses to diet and evaluate alternative management strategies. The latter were developed to aid in the investigation of physiological mechanisms. Naturally, the objectives and criteria for evaluation of these types of models are very different. Rather than attempt to cover this topic exhaustively, this discussion has two objectives: first, to demonstrate the enhanced applicability of predictive models resulting from the incorporation of mechanistic elements; and second, to give some examples of the use of dynamic, mechanistic models in the research process.

Application models of growth have been developed for several livestock species, including poultry (20), pigs (13, 47, 56), and beef cattle (45, 46). Although these models generally lack the metabolic detail of the research models discussed below, they include some consideration of accretion of individual body components (i.e. equations are based on concepts about mechanisms that underlie the growth process), which justifies their classification as mechanistic models. In addition, they represent growth dynamically over time. Several of these models incorporate concepts of the roles of hyperplasia and hypertrophy in organ and body growth validated by Baldwin & Black (5). The concepts include:

1. The primary genetic determinant of organ size is the final amount of DNA. It follows that differences in organ size between species or between strains within a species are largely due to differences in the amount of DNA observed in that organ in normal fully grown adults.
2. Each unit of DNA specifies, on a genetically defined basis for each tissue and each species, information required for the ultimate formation of a specific amount of cell material. Whether information specified by a unit of DNA leads to the formation of cell material depends on the animal's nutritional and physiological status.
3. The specific activities, expressed as units per gram of tissue, of enzymes or groups of enzymes responsible for tissue growth and general metabolism vary as an exponential function of organ size. In addition, the kinetic properties of enzymes are reasonably constant across species.

The model described by Emmans (20) assumes that each animal has a potential rate of growth (i.e. protein accretion) that is determined by its genotype and stage of maturity. The animal then attempts to eat enough of its diet to meet the demands for maintenance and this potential growth rate. Heat loss (and production) are described as functions of animal size, insulating value, and the environment, whereas lipid deposition comprises a minimum amount of body fat plus a sink for excess nutrients (energy). In formulating this model, the authors attempted to quantify effects of feed intake and environment. Unfortunately, the original publication gave no details of the behavior of this model or any indication of rigorous model evaluation. Nevertheless, it has found practical application in the poultry industry of the United Kingdom (GC Emmans, personal communication).

Whittemore & Fawcett (56) described a model of pig growth that represented protein accretion based on rates of synthesis and degradation, with fat deposition based on a variable ratio of lipid-to-protein gain. This model is included here because it too has been incorporated into management-aid software and has been used in the swine industry. As in the previous example, however, the original paper gave no clear statement of modeling objectives or any indication of the model's performance.

A more rigorously defined model of pig growth was described by Black et al (13). This model was extremely ambitious, attempting to predict feed intake (from potential energy requirements, environmental factors, and diet characteristics), growth rate (from absorbed energy and amino acids), and body composition. Specific effects of amino acids are represented, as are their interactions with energy supply. Description of environmental effects, particularly the interactions between climatic factors and energy metabolism, is detailed and based on sound physiological principles. Protein accretion is represented in less mechanistic detail than in the model described by Whittemore & Fawcett (56), with each pig having potential rates of protein and energy deposition based on its genotype, age, and sex. Achievement of these rates is dependent on nutrient intake and the environment. This model's predictions are in excellent agreement with field data after proper calibration to local conditions and is marketed in Australia as the AUSPIG® program. In addition, it is the core of the current Australian swine feeding system (52).

The US Department of Agriculture (USDA) has made a similar effort to produce practical software for the swine industry. As part of that effort, Pomar et al (47) developed a dynamic, mechanistic model of pig growth. In contrast to the models described above, this model incorporated the concepts of DNA and protein accretion validated by Baldwin & Black (5) in a manner similar to that described by Oltjen et al (46; see below). Owing to a lack of data on accretion of DNA by growing pigs, these authors were forced to make a number of serious assumptions and extrapolations, which meant that in the end, the driving force for protein deposition continued to be represented as an "intrinsic potential of protein accretion," presumably determined by sex and genotype. This variable is described in terms of body DNA (or protein precursor) but is functionally defined in terms of maximum body protein at maturity. Body composition is defined factorially, with dietary energy and protein used first for maintenance, then for protein growth, and finally for fat accretion. This model, which has no provision for environmental effects, predicts with reasonable accuracy the effects of sex, genotype, and diet on growth performance of pigs.

Oltjen et al (46) built on the concepts validated by Baldwin & Black (5), albeit in simplified form. They represented body protein gain as the difference between synthesis and degradation, with synthesis dependent on the amount of DNA present at any particular time. Owing to a lack of adequate data in cattle, the authors were forced to use rat data to validate equation forms (44), which they then applied to growing beef cattle using some heroic assumptions. Model equations are given below to illustrate the application of fundamental concepts in a practical context:

$$\mathrm{dDNA/dt,\ g/day} = \mathrm{K1} \times (\mathrm{DNAMX{-}DNA}) \times \mathrm{NUT1}$$
$$\mathrm{dPROT/dt,\ kg/day} = \mathrm{SYNTHESIS} - \mathrm{DEGRADATION}$$
$$\mathrm{SYNTHESIS} = \mathrm{K2}\ \mathrm{x}\ \mathrm{DNA}^{0.73} \times \mathrm{NUT2}$$
$$\mathrm{DEGRADATION} = \mathrm{K3} \times \mathrm{PROT}^{0.73},$$

where K1 (0.00429), K2 (0.0461), and K3 (0.143) are rate constants; NUT1 and NUT2 are nutritional constants set to 1 for normal ad libitum intake; and DNAMX is normal DNA content at maturity, calculated to be 385 g based on relationships derived by Baldwin & Black (5) in the absence of direct data at the time of model development. For animals of different mature size (A'), K1 is adjusted by the size-scaling factor proposed by Taylor (54). In addition, K2 is increased 4% for cattle with hormonal adjuvants based on observed additional rates of protein gain. Effects of energy intake on growth were added using the NUT1 and NUT2 terms, calculated from ME intake (MEI, MJ/d) as follows:

$$\text{MEINORM} = (1.83 - 1.094\ \text{EBW}/A') \times \text{EBW}^{0.75},$$

where MEINORM (MJ/day) is the pattern of MEI intake that supports normal growth of a reference steer (45) and EBW is empty body weight (in kilograms). Then,

$$\text{P} = \text{MEI}/\text{MEINORM}.$$

Rates of DNA accretion and protein (PROT) synthesis are respectively adjusted by NUT1 and NUT2:

$$\text{NUT1} = -0.7 + 1.7\ \text{P}$$
$$\text{NUT2} = 0.83 + 0.2\ \text{P}/(0.15 + \text{P}).$$

Finally, daily empty body fat gain (DFAT) is calculated as the NE_g available after daily feed intake (FI, kg/day) is used for maintenance (MAINT) and protein gain (DPROT, kg/day):

$$\text{MAINT, MJ/day} = a_m \times \text{EBW}^{0.75} \times (A'/750) - 0.02$$
$$\text{DFAT, kg/day} = [(\text{FI-MAINT}/\text{NE}_m)\ \text{NE}_g - 23.18\ \text{DPROT}]/39.27,$$

where a_m is 0.359 and where 23.18 and 39.27 are the energy contents (MJ/kg) of protein and fat gain, respectively (24). Therefore, this model may be considered to be equivalent to the NRC (39) energy utilization model, with mechanistic elements added to represent body protein gain (and body composition). Empty body weight is calculated as the sum of fat and fat-free body mass, where fat-free body mass is PROT/0.2201 (24). Because the model requires initial estimates of whole-body DNA, protein, and fat, empirical relationships between these components and animal weight, mature size, and condition score are used to determine beginning values for model implementation. The model accounts for variations attributable to initial body composition and mature size but does not always yield acceptable estimates of fat gain. This result is not unexpected, because fat accretion is computed after energy requirements for maintenance and protein gain have been satisfied. Thus, any errors in estimates of maintenance or protein gain result in biased fat-gain predictions. Furthermore, feed energy available for fat accretion is not used at the same net efficiency as it is for protein deposition, as is assumed for the NRC (39) system (and for the Oltjen model).

In summary, several dynamic, mechanistic models of animal growth have been developed for predictive or application purposes. These have generally incorporated some level of biological realism into existing empirical frameworks, with the intended (and usually attained) result of improving applicability across a wider range of genotypes, physiological states, and environmental and dietary conditions. In the next section we examine several dynamic, mechanistic growth models developed for research purposes. In contrast to the previous examples, these models were generally derived from first principles rather than by adding on to an existing empirical framework. This difference in approach is a consequence of the different objectives of research (as opposed to application) modeling. In research modeling, investigators are often involved in evaluating specific hypotheses relating to the system, which would be compromised by the inclusion of undocumented empirical relationships.

Mechanistic, dynamic models of growth have been used in research on cattle (17, 19, 21), sheep (14, 15, 27, 49), and pigs (13). The swine model of Black et al (13) was discussed above as an application model. Although its ultimate goal was application, model development required (and inspired) a great deal of research into the physiology of growth in pigs and the responses of different genotypes and sexes to diet and environmental factors. As mentioned above, the results of that research and the associated modeling analyses are summarized in the Australian pig feeding system publication (52).

France et al (21) proposed a dynamic model of cattle growth based on carbon and nitrogen metabolism. State variables are body protein, lipid, ash, blood acetyl-coenzyme A equivalents, blood glucose equivalents, and blood amino acids. Acetyl-CoA and glucose equivalents (i.e. two- and six-carbon metabolites, respectively) are used as a simplification to facilitate estimation of the stoichiometric conversion of volatile fatty acids absorbed from the rumen to the appropriate metabolic pools. Synthesis and degradation are represented for each body pool based on animal factors (e.g. sex, genotype, physiological state) and absorbed nutrient levels. Relatively good agreement was observed between model outputs and experimental data, although data on the profiles of absorbed nutrients and on body composition, obtained in the same animals, are limited. France et al (21) suggested linking the model with a simple model of rumen digestion (23) to complete the growth prediction system.

In a more complex model, DiMarco et al (19) extended the growth equations used by Oltjen et al (46) to two pools of protein (body and viscera), two associated DNA pools, and a body fat pool. Growth is represented as the difference between synthesis and breakdown of each protein and fat pool. Parameters for DNA accretion in each protein pool were estimated using data for a reference steer, based on measured DNA values (18). Protein synthesis and degradation for body and viscera were estimated similarly for the reference steer, but protein synthesis depends on blood amino acid concentration and protein degradation depends on catabolic hormone level, which varies inversely with plasma glucose concentration. Lipogenesis is represented by a Michaelis-Menten–type equation that depends on anabolic hormone (which varies directly with plasma glucose), plasma glucose, plasma acetate, fatty acids, and body fat content. Lipolysis is similarly represented and depends on catabolic hormones, plasma fatty acids, and body fat content. Empty body weight is calculated as the sum of the protein and fat pools plus the water and ash associated with the protein pool (PROT weight/0.243).

Next, DiMarco & Baldwin (17) integrated their growth model with digestion and metabolism elements. The integrated model represents the digestion of diet nutrients, and the products of digestion are used as inputs to a metabolism component. Separation of the protein pools by DiMarco et al (19) accounts, in part, for the variable maintenance requirements associated with changes in visceral mass. Moreover, the metabolism element helped correct errors in prediction of fat gain since the efficiency of each nutrient's use was explicitly represented. In previous models, nutrient prioritization was necessary to ensure that vital functions were preserved. For example, in the factorial systems, the requirements for maintenance must be met before any feed energy is allocated to production. The dynamic structure of this integrated model enables representation of direct competition for utilization of circulating metabolites by different tissues and simultaneous processes. Nutrients are therefore partitioned based on the relative maximum capacities (V_{max}) and affinities (k_s) for metabolites of various oxidative and growth functions. Most of the metabolic logic in this and other similar models was first developed by Gill et al (27) in a model of lamb metabolism.

Gill et al (27) developed that model to examine the effects of varying proportions of nutrients on efficiency of energy utilization. The model was formulated using mechanistic equations representing intermediary metabolism of absorbed nutrients, as described above for the DiMarco model. On the other hand, empirical relationships similar to those employed by Graham et al (28) were used to define deposition of body protein and fat. This model has been used successfully to examine the mechanisms responsible for differences in energetic efficiencies of use of acetate (14), lipids, and amino acids (15).

Sainz & Wolff (49, 50) developed another model of growing lamb metabolism for the purpose of evaluating alternative hypotheses about mechanisms responsible for the effects of growth-promoting compounds on growth and body composition. This model contains explicit representations of body fat and protein turnover, as these are the most likely candidates for alteration by anabolic agents. In order to accommodate changes in different tissues, with variable requirements for energy, amino acids, etc, the model is comprised of four protein pools (carcass, viscera, remainder, and wool) and three associated DNA pools. Metabolic elements are similar to those represented by Gill et al

(25–27), with entry and metabolism of amino acids, glucose, acetate, propionate, butyrate, and fatty acids represented explicitly. The model simulates lamb growth from 20 to 40 kg empty body weight under a variety of nutritional conditions and accommodates interactions among nutrients, giving reasonable predictions of growth patterns, energy utilization, and body composition. It was originally used to estimate the magnitude of change in protein and fat metabolism that might account for the effects of anabolic steroids, beta-adrenergic agonists, and growth hormone. Those simulations (50) showed that beta-agonists probably act by altering both processes, whereas the effects of growth hormone could be explained by changes in lipolysis alone, with the effects of the steroid being intermediate. Moreover, body composition was much more sensitive to changes in protein metabolism than to fat turnover. These results support the concept that adipose tissue is primarily a storage depot for excess energy. As summarized by Berg & Butterfield (11), energy surplus to the requirements for maintenance and growth of bone and muscle is deposited as fat. This concept is widely used in the less detailed models of growth, as described above. That this metabolically based model yields conclusions similar to those of earlier workers based on extensive empirical observations is encouraging.

In summary, dynamic, mechanistic models of animal growth have been extremely useful in the research process, providing a rigorous and quantitative method for integrating available information, for formulating and evaluating hypotheses, and for identifying research priorities. Some of the research problems examined using this approach include the roles of cellular hyperplasia and hypertrophy in growth, the impact of dietary and absorbed nutrients on efficiency, interactions between the animal and its environment, and metabolic adaptations to altered physiological states. In each case, the use of modeling has improved the researcher's ability to tackle a complex issue and distill it down to its most essential elements.

Lactation Models

Dynamic, mechanistic models of digestion and metabolism in lactating cows have been developed by Smith (51), Koong & Lucas (31), Koong et al (30, 32), Baldwin et al (7, 8, 10), and Danfaer (16). Of these, the model of Koong et al (30, 32) incorporates the greatest number of empirical elements and the least number of representations of specific biochemical and physiological mechanisms, whereas Danfaer's model (16) incorporates the greatest number of mechanistic equations and metabolic and physiological detail. All of these authors clearly stated that their models were research models and imperfect with regard to rigorous predictions of input:output relationships because available concepts and data were inadequate. On the other hand, evaluations of several of these models demonstrated that dynamic, mechanistic models have a number of properties that improve their utility relative to the static, factorial, and empirical models currently in use. These models enhance our ability to anticipate effects of previous and current planes of nutrition on current and future performance, respectively, and have improved our understanding of ruminant digestion and metabolism. We do not discuss the models of Koong et al (30) and Danfaer (16) herein. Rather, we focus on a current version of a model of the lactating cow that evolved from the Smith (51) model, and from the subsequent Baldwin et al (7, 8, 10) model.

The model of the lactating cow was developed to simulate and analyze overall energy transactions and within-day and longer-term day-to-day patterns of nutrient use throughout a lactation or growth cycle. It was also intended to aid in the design and interpretation of energy balance experiments. Complete documentation is presented in Ref. 4.

The body weight of the reference cow used to parameterize the model was 550 kg. Empty body weight (EBW) of the initial reference cow was 500 kg; lean body mass (wtB) was 350 kg and includes skin, brain, kidney, muscle, skeleton, and minor tissues. Adipose tissue (wtF) was 75 kg and comprised of triacylglycerol (Ts = 60 kg) and cytoplasmic elements (wtcytF = 15 kg). Visceral weight (wtV) was 75 kg and included blood, gut, liver, heart, and udder. Provisions have been added to adjust estimates of initial pool sizes, tissue sizes, metabolic capacities, etc when initial empty body weights other than 500 kg are specified as an input to specific stimulations using this model. Nutrient inputs were calculated for a 50:50 forage-to-concentrate ration and are continuous in the reference state. Milk production was set at 30 kg/day and energy balance at zero. Milk was 3.5, 4.8, and 3.3% of fat, lactose, and protein, respectively.

Documentation of the model for the lactating cow and its behavior in detail in this review is inappropriate, as this has already been done (4). Rather, we discuss selected aspects of the model to illustrate the approach used in model development and evaluation. Twenty-seven state variables are depicted in the model, 13 of which are associated with the digestive element and will not be discussed. Instead, we focus on equations that trace metabolic capacity of the udder through time, milk synthesis, and the turnover of carcass protein. The text for this discussion is drawn mostly from comments and equations (Fortran based) in a printout of the model, with minor adjustments to accommodate proper English. The equations and parameters for computing metabolic capacity of the udder were taken from Neal & Thornley (43; Table 1).

The primary precursors of milk fat (Tm) in cows are blood lipids (Fa) and acetate (Ac). The equation for the conversion of blood lipids to milk fat (FaTm) is

$$\mathrm{FaTm} = (\mathrm{VFaTm} \times \mathrm{UENZ} \times \mathrm{KMinh})/(1.0 + \mathrm{KFaTm}/\mathrm{cFa} + \mathrm{K1FaTm}/\mathrm{cGl}).$$

Table 1 Terms and equations of the mammary gland submodel

Term	Definition
LHOR	Lactation hormone complex (in kilograms)
KLHOR	Degradation rate constant for LHOR
BST	Term added to stimulate effects of bovine somatropin treatment
VUsyn	Enzyme synthetic capacity per cell
Ucells	(Arbitrary) number of secretory cells defines genetic potential of udder to produce milk
UENZ	Scalar representing general synthetic capacity per secretory cell
KUsyn	Michaelis-Menten–type constant for hormone response
KUdeg	Degradation rate constant for UENZ
KUdegM	Degradation rate constant defining effect of udder milk content (UMilk) on UENZ
Mave	Average milk in gland over past 21 days (TaveM-1/21)
KMdeg	Half response point for degradation due to udder milk
THETA5	Defines slope of response
KMinh	Factor defining inhibition of milk synthesis by milk in the udder

Key equations[a]

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DLHOR = -KLHOR × LHOR                   $ "LACTATION HORMONE"
LHOR = INTEG (DLHOR, ILHOR)
DUENZ = Usyn-Udeg                       $ "UDDER ENZYMES"
Usyn = VUsyn × Ucells × LHOR × BST/(KUsyn + LHOR × BST)
Udeg = UENZ × {KUdeg + KUdegM × [(UMave/KMdeg)**THETA5/(1.0+ UMave/
  KMdeg)**THETA5]}
DUMave = TaveM*(UMILK - UMave)          $ "RETAINED MILK EFFECTS"
UMave = INTEG(DUMave,IUMave)
KMinh = (MLKmax - UMILK)/(MLKmax - UMILK + KMILK)
UENZ = INTEG(DUENZ,IUENZ)
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[a] Equations beginning with D are differential equations. The command INTEG calls for integration of the equation (DAAA =) starting at the initial amount (IAAA =). Dollar signs separate equations from associated comments.

This equation is of the Michaelis-Menten type, where VFaTm × UENZ defines the maximum velocity ($V_{\max}$) of the reaction. The concentration of blood lipids (cFa) and glucose (cGl) can be rate limiting, as glucose is required for fatty acid esterification. The term KMinh essentially reflects the inhibitory effect of milk in the udder on blood flow to the mammary gland.

The equation for milk fat synthesis from acetate (AcTm) is

$$\mathrm{AcTm} = (\mathrm{VAcTm} \times \mathrm{UENZ} \times \mathrm{KMinh})/(1.0 + \mathrm{KAcTm/cAc} + \mathrm{K1AcTm/cGl}).$$

The product of VAcTm × UENZ defines the $V_{\max}$ at time t, and acetate (cAc) and glucose concentrations can be rate limiting. In this case, glucose is a required source of $NADPH_2$ for fatty acid synthesis and of α-glycerol-phosphate for fatty acid esterification.

The equation for milk protein (Pm) synthesis from amino acids (Aa) in blood (AaPm) is

$$AaPm = (VAaPm \times UENZ \times KMinh)/(1.0 + KAaPm/cAa).$$

Although this equation implies that the availability of total rather than specific amino acids (cAa) determines rates of milk protein synthesis, this is not true (29). Additional data required for the formulation of a more realistic representation are now available, and the model will soon be revised accordingly.

The equation for milk lactose (Lm) synthesis from glucose (Gl) in the udder (GlLm) is analogous to those presented above:

$$GlLm = (VGlLm \times UENZ \times KMinh)/(1.0 + KGlLm/cGl + KAaLm/cAa).$$

The availability of amino acids as effectors of lactose synthesis reflects the fact that α-lactalbumin, a milk protein, is an essential component of the lactose synthetase complex and must be synthesized continuously to support lactose synthesis.

Amino acids dervied from the digestive process and from protein degraded in animal tissues are available for milk (Pm), carcass (Pb), and visceral (Pv) protein synthesis and for degradation and gluconeogenesis (AaGl) in the liver. Rates of amino acid (Aa) use for these competing functions vary dynamically throughout the lactation cycle. The equations for carcass protein degradation (PbAa) and synthesis are

$$PbAa = KPbAa \times Pb$$

and

$$AaPb = (VAaPb \times BDNA)/[1.0 + KAaPbB/(AHOR \times cAa)],$$

respectively, where KPbAa is the first-order rate constant for degradation. The V_{max} (VAaPb × BDNA) for carcass protein synthesis therefore depends on the amount of carcass DNA (BDNA, primarily in muscle), as discussed above for models of growth.

The model for the lactating cow has been subjected to extensive testing over the past 10 years (4, 7, 8, 10). A number of experiments have provided data to more accurately parameterize critical elements of the model. More detailed models of adipose tissue, liver, and mammary gland metabolism have also been developed to advance our quantitative understanding of metabolism in these tissues and to help generate improved representations of the functions of these tissues in the cow model. At present, several aspects of this model need improvement. For example, explicit representations of the metabolism of several critical amino acids are lacking. However, model predictions of responses to alternative feeding strategies and diets throughout the lactation cycle, of ME values of feeds, of methane emissions by cattle, and of blood concentrations and interactions among metabolites and many other aspects of animal function range from very good to excellent. Unfortunately, the model is not very user friendly in the sense that a person must understand the model and have reasonable programming skills in order to use it readily. Several groups have undertaken the development of user-friendly interfaces that should help in this regard.

FUTURE PERSPECTIVES

We have stated many of our views of the future of modeling energy partitioning in animal nutrition in previous sections and will not reiterate them here. Our basic belief is that the static, factorial, and empirical models that comprise current feeding systems and whose origins can be traced to the turn of the century should soon be replaced by dynamic, mechanistic models. These latter types of models have greater utility, broader applicability, and greater explanatory power, both for application and research purposes.

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