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UNIVERSITY OF ALBERTA

SIMULATION OF PROTEIN AND ENERGY PARTITIONING IN THE REPRODUCING SOW

by

BETH WALKER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

Animal Physiology

Department of Animal Science

EDMONTON, ALBERTA

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ABSTRACT

Protein and energy partitioning in the dry, pregnant and lactating sow was predicted in a dynamic model. The model gave first priority for available nutrients to conceptus and product growth or milk secretion, which were met with maximal theoretical efficiency. Daily rate of protein accretion in maternal tissue was the driving force for growth, and was determined by maximal genetic capacity, available protein and energy, and live weight. Protein support costs were derived simultaneously with rate of protein accretion, and energy support costs were dependent on body protein mass and daily protein accretion (in maternal or uterine tissue and milk). Lipid accretion rates were derived from energy available after meeting energy required for the above processes.

Maternal body tissue changes depended on physiological state, and protein and energy intake. Dietary composition significantly influenced the proportion of protein to lipid accretion in dry and pregnant animals, and protein and lipid mobilisation in lactation. Uterine composition was not greatly influenced by nutritional regime, though hydration and protein anabolism were localised in utero. Milk secretion and composition were influenced largely by the ratio of protein to energy in the diet, which also became an important determinant of nutrient availability at high dietary intakes. With the catabolic state of lactation, increasing dietary protein and energy intakes were utilised with decreasing efficiency, such that tissue mobilisation became inevitable.

The reproductive link between weaning in one parity and return to estrous and conception for the next parity was modelled on the basis of compositional changes in maternal tissue over lactation. Average rate of protein mobilisation over lactation was exponentially related to weaning to conception interval in gilts, with the minimum interval being 9 days.

Thermal balance was evaluated on the basis of sow heat production and heat loss to the environment. Sow heat production was calculated as the sum of the heat produced from support costs, lipid and protein accretion in uterine or maternal tissue or secretion in milk, and processing costs of available nutrients. Heat loss to the environment was calculated from sensible and insensible heat exchanges for conditions below the lower critical and above the upper critical temperatures. The difference between heat production and loss was utilised to determine modifications to predicted feed intake, or nutrient utilisation on a fixed dietary scale. Feed intake when offered *ad libitum* was predicted on the basis of the drive to achieve maximal rates of each process in the model, depending on physiological state, and assuming a constant ratio of 2:1 lipid to protein accretion.

Model predictions for tissue changes and thermal balance throughout the reproductive cycle compared well with experimental data. The model therefore provided a tool for evaluation of feeding strategies and research hypotheses.

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KEY TO SYMBOLS IN TEXT

A	surface area of pig
Af	surface of pig in contact with floor
A_b	body ash content
A_{fe}	ash content of fetuses
A_{fm}	ash content of fluids & membranes
Ar_m	ash retention, maternal
A_{ut}	ash in empty uterus
A_u	ash in gravid uterus
a_p	efficiency of protein use for Pr_m
a_u	efficiency of protein use for Pr_u
DEi	digestible energy intake
DCPi	digestible protein intake
DM_{milk}	dry matter production as milk
Ea	available energy
Ei	energy intake
E_{milk}	energy secreted in milk
Es_T	energy support costs
EHp	extra thermoregulatory heat production
Ef	fecal energy
FI_{max}	maximum physical limit to feed intake
Gg	total gestation weight gain
H_{fe}	water in fluid and membranes
Hr_m	water retention, maternal
H_{fe}	water content of fetuses
H_{mm}	water in mammary
Hp	total sow heat production
Hp_u	heat production from gravid uterus
Hp_a	heat production from food processing
H_b	body water content
Hp_l	heat production from lactation
Hp_t	heat production from tissue accretion
H_u	water in total gravid uterus
H_{ut}	water in of empty uterus
k_f	efficiency of energy use for Lr_m
k_p	efficiency of energy use for Pr_m
k_u	efficiency of energy use for energy accretion in utero
L_{fm}	lipid in fluid and membranes
L_{fe}	lipid content in fetuses
L_{ut}	lipid in empty uterus
L_{mm}	lipid in mammary
L_u	lipid in total gravid uterus
L_b	body lipid content
LCT	lower critical temperature
UCT	upper critical temperature
L_{milk}	lipid and lactose in milk
Lmob	lipid mobilisation
Lr	rate of lipid accretion
Lr_m	lipid accretion, maternal
Lr_u	lipid accretion in utero
LS	litter size
LWT	live weight
LWG	live weight gain
MEi	metabolisable energy intake
MY	daily milk yield
MI	milk intake per piglet
Ni	nitrogen intake
Na	nitrogen available
Pr_u	protein accretion in utero
Pr_{max}	maximal protein accretion
Pr	rate of protein accretion
Pr_m	protein accretion, maternal
P_{milk}	protein secretion in milk
Pmob	protein mobilisation
Pf	fecal protein
P_b	body protein content
Ps_T	protein support costs
Pa	available protein
Pig_{gain}	daily gain of piglet
Pi	protein intake
P_{mm}	protein in mammary
P_u	protein in total gravid uterus
P_{fe}	protein in the fetuses
P_{fm}	protein in fluid and membranes
P_{ut}	protein in empty uterus
NB:	$P = N \times 6.25$
Q	total heat loss
Qe	evaporative heat loss
Ql	evaporative loss from respiration
Qs	evaporative loss from skin
Qn	thermoneutral heat production
Ra	thermal resistance of air
Rf	thermal resistance of floor
Rt	thermal resistance of pig tissue
Tb	body temperature of pig
Te	temperature of environment
t_d	day when animal is dry
t_g	day of gestation or t_l lactation
Ue	urinary energy
Up	urinary protein
W_{fe}	weight of fetuses
W_{fm}	weight of fluid and membranes
Wi	weight at day 1 of lactation
WMI	weaning to mating interval
W_{mm}	weight of mammary
W_u	weight of total gravid uterus
W_{ut}	weight of empty uterus
%E	percent sows in estrous by 8 days

I. INTRODUCTION

Sow model - problem definition

A large body of information exists in the scientific literature on the response of pregnant or lactating sows to variations in feed intake, feed composition, environment and management practices. Published observations on many topics of sow performance and biology appear conflicting because of the failure to consider some important factors and to view the system as a whole, rather than focus on isolated parts. Currently, the most effective basis for derivation of feeding guidelines to maintain sow condition and ensure sow productivity is still in question (Whittemore et al., 1988). Is there then enough information available to understand the nutrient partitioning of the sow and therefore formulate management strategies?

A large proportion of variable costs of maintaining the swine herd are associated with maintenance of the breeding sow. Throughput and efficiency are important determinants of profit and are directly tied to the reproductive performance of the sow. An example will serve to illustrate the importance of good sow management; in surveyed commercial units in the province of Alberta (Schuld and Goonewardene, 1988) the range in number of pigs weaned per sow per year was 13.3 to 21.0, which translates to a difference in profitability (return above costs) on an average farm (97.5 sows) of -$14,000 to +$45,000. Sow productivity is determined by management decisions, which are difficult to document precisely, genetic potential, and by nutrition.

The relationship between nutrition and reproduction has been the focus of a large amount of research recently since comprehension of this link is vital to the recommendation of sow feeding strategies (Figure I.3). The interest in linking reproductive performance with sow nutrient balance has occurred partly as a consequence of the large increase in reproductive failure observed in sows of lean genotypes and gilts bred at early stages in their growth (de Hovell et al., 1977). This problem has previously been described as the 'thin sow syndrome'. Early research on the problem focused on sow weight changes and the attainment of target weights at specific points in the reproductive cycle (Whittemore, 1987), but it is known that sows may be gaining weight while losing fat (Whittemore et al., 1988). Subsequent research has pinpointed variations in fatness (Whittemore et al., 1980), body protein mobilisation (King, 1987), and relative changes in body composition (Mullan and Williams, 1989) as being important in determining return to estrous. Research at the hormonal level has focused on changes in luteinising hormone profiles prior to weaning (Shaw and Foxcroft, 1985; Mullan and Close, 1989), but the link between the hormonal and tissue changes is yet to be established. It is evident that a more mechanistic approach is required to represent the mechanisms perceived to control these events within the reproducing sow. This will necessitate comprehension of the partitioning of nutrients through reproduction in response to manipulations in dietary intake in order to coordinate nutrient balance with hormonal changes.

Current nutrient requirements of sows (ARC, 1981) tend to be evaluated on the basis of a factorial approach which includes assumptions on maintenance, composition of body gain and milk production and empirically derived partial efficiencies of energy use. Although the factorial approach is simple, reasonable and useful, it does not allow for prediction of response with change in nutrient supply and time. No account is taken of the effects of diet on shifts in nutrient partitioning between body tissue and products of reproduction (uterine growth, including conceptus, and milk) and more importantly, no account is taken of the existing knowledge of energy-protein interactions within the animal (Gill and Beever, 1988). Though the existing recommended nutrient requirements have limitations, they are a good starting point on which to build, and can also be considered as a type of model. Computer simulation modelling provides the tool to incorporate the more mechanistic approach to nutrient partitioning which is required as a prerequisite to understanding the nutrition-reproduction link.

The modelling approach

Simulation modelling is not a new discipline and has received wide application in a number of scientific fields. Despite this the process remains something of a mystery to the large majority of animal scientists and modelling is not yet fully accepted as a discipline in it's own right, nor as an integral component of most scientific research. The purpose of this chapter is to provide an introduction to the modelling process and the terminology used, and thereby illustrate the utility and value of modelling as a tool in research, and its application to problems specific to sow nutrition and physiology.

Philosophy

A model can most generally be defined as "a simplified abstraction of the real world" (Spedding, 1988), or as a representation of a structure or system. A system is defined as a group or combination of interrelated, interdependent or interacting elements forming a collective entity, with a defined boundary, and reacting as an integrated whole to external or internal stimuli. Systems analysis is the examination of methods and mechanisms involved in scientific and industrial operations (eg. biological processes, economic forces), usually with the aid of a computer, and the use of modelling techniques. As such, model representations tend to be mathematical descriptions of systems and their behavior. Examples of systems which have been modelled range from tissue level biochemical reactions within the animal body to environmental responses within global models of the earth's climate. A wide variety of scientific and commercial areas have been addressed in modelling systems including crop and animal production, economics, space technology and cosmology.

Why then, do we need to model systems? It has been suggested that "models are needed because real life is out of the grasp of human comprehension and description" (Whittemore, 1986). This is a rather conceited view considering that it is only the human mind that has the capacity to formulate concepts and hypothesize accordingly about the nature of complex systems (Baldwin and Koong, 1980). However, at times the mind's capacity to accurately trace the quantitative and dynamic implications of changes in components of a system is exceeded (Black et al., 1989). Computer simulation modelling can therefore serve as a valuable tool to aid in comprehension and transfer of information and in support of research. As such modelling is an essential part of scientific interpretation, and should be an integral component of experimental research.

The modelling process

Modelling follows a defined methodology which is not dissimilar from the process undergone in conventional experimental research. The process can be divided into four phases (some of which may be going on simultaneously), though these may not have distinct end points since the process is circular in nature (Figure I.1).

i) **Problem definition** is the initial and most important stage of model development since, if the objectives of the model are not clearly defined it can never be fully validated. It is necessary to define the objective in terms of the area to be studied (ie. the knowledge base), the level of operation (eg. tissue or whole body), and the purpose or utility of the end product (ie. practical application). Each model has a set of overall objectives, but also usually requires sub-hypotheses concerning the functioning of the system.

ii) **System definition and formulation** involves specification of details pertaining to the constituents of the system being studied, the interactions and important processes for consideration. This is usually achieved through development of a flow diagram incorporating the minimum number of processes proven to be of importance in the behavior of the system. There are a number of accepted means of representing flow diagrams but the nomenclature of France and Thornley (1984) is advantageous for animal models. For a dynamic model (occuring over time) components are divided into the following groups;

Driving variables - data inputs eg. energy and protein intake

State variables - define the state at any given time eg. body protein content

Rate variables - define the process within the system eg. rate of protein accretion

Auxilliary variables - extra definitions to state variables eg. ratio of protein to water gain

Together these constitute the processes in the model and dictate the required data acquisition and mathematical formulations required to derive parameters and constants, which though they do not vary with time, may be dependent on experimental conditions. These concepts are illustrated it the flow diagram of the reproducing sow (Figure I.2), the true nomenclature (symbols and equations) is developed with the translation of these processes and transactions into mathematical functions. For example, the formulation of the transformation of available nitrogen to nitrogen accreted in the tissues, involves a rate variable (potential rate of nitrogen accretion per day), state variable (body protein), driving variables (energy and nitrogen available) and auxilliary variable (live weight).

iii) **Formulation of the mathematical model** involves the translation of processes defined above into algebraic or differential equations and subsequently into computer syntax. The translation process generally involves formulation of hypotheses and assumptions when representing biological transactions mathematically. Because of the complexity of biological systems most parameters enter the model non-linearly and the statistical procedures commonly used in animal science eg. analysis of variance, regression and correlation, are not applicable (Baldwin and Koong, 1980). The choice of a mathematical function is at times somewhat arbitrary since it may be difficult to accomodate discontinuities in data sets and maintain a function with biological meaning to the parameters (France and Thornley, 1984). It must be remembered that mathematical fit does not necessarily give biological reason; this is particularly important in more empirical equations. Empirical equations are fitted to describe a relationship, in experimental data, between two or more variables. Conversely a theoretical, or more mechanistic equation, is derived from hypotheses concerning the underlying forces of the system and the parameters are often considered to have biological interpretation. The terms empirical and mechanistic are relative and almost all models have empirical aspects, though the more mechanistic approach is generally preferred.

iv) **Testing and evaluation** occurs throughout model building and as a continuum through further development of the final model, and is essential. It may take the form of a number of aspects, namely verification, validation and sensitivity analysis. Verification simply ascertains that the model behaves in a manner originally described by the system. Validation is the testing of the model under conditions and with data not used in its derivation. Sensitivity analysis is done by modifying parameters in the model by, for example ± 10% or one standard deviation, and determining which components of the system are most sensitive and therefore require accurate description. A negative result in testing and evaluation is perfectly acceptable and usually the expected result, since it identifies where theory meets reality (Baldwin and Koong, 1980).

The value of modelling

The modelling process can bring numerous benefits;

- A model should meet its defined objectives, and test the hypotheses posed therein.
- successful modelling dictates comprehension of the whole system and the interaction of its parts, and a detailed and systematic analysis often leads to increased knowledge about the system.
- creation of the model pinpoints areas where knowledge is lacking and allows evaluation of current concepts and data for quantitative and dynamic adequacy.
- modelling can provide insight into critical experiments required and thereby lead to less ad hoc research and more rational use of animals.
- depending on the objectives, models can provide prediction of response where experimentation may not be possible or economically feasible and provide a tool to aid in decision making, optimisation and formulation of recommended practices.

In addition, there will be benefits specific to the system modelled in its practical application eg. pig growth models (Moughan and Verstegen, 1988). Modelling allows integration of information generated by research, analysis of the adequacy of our knowledge base, and guidance of scientific development through further research, and thereby serves as a pivotal circular link.

Existing models

A large number of models exist in different areas of animal science such as breeding herd dynamics, economics, nutrition and physiology. Some existing domestic animal models are listed in Table I.1. The growing finishing pig models in the area of nutrient partitioning have been shown to be reasonably effective in predicting animal response to nutritional manipulation (Black et al., 1986; Moughan et al., 1987). There have been few attempts at modelling nutrient partitioning in the reproducing sow, though two very different attempts have been made recently. These are an empirical model of the pregnant sow (Williams et al., 1985) and a highly mechanistic research model of the lactating sow (Close and Pettigrew, 1990). No models presently exist to encompass the dynamics of nutrient response across the complete reproductive cycle of the sow and thereby provide the capacity to accurately evaluate feeding strategies for sows.

Despite the large number of existing models, they have not yet received wide application in commercial agriculture. There may be a number of reasons for this, including resistance to new ideas on the part of the industry, inadequate marketing or inappropriate models. The modeller has little control over the traditions and inflexibility of the industry but he or she is completely responsible for ensuring the quality and appropriateness of the model to the designated end user. Of all the mistakes that can be made in modelling this is probably the most common area and includes; failure to define an achievable goal, inadequate user participation, inappropriate level of detail, poor communication, and use of unverified models (Annino and Russel, 1979).

Modelling itself is not a goal, it is a means of achieving a goal. The objective must be clearly defined with the end-user in mind, and communicated in an equally appropriate manner. The remainder of this chapter will therefore be dedicated to establishing the need for, and objectives of, the reproducing sow model developed in this thesis.

Objectives

The objective of the sow simulation model was to integrate the hypothesised mechanisms of protein and energy partitioning in the sow, over the reproductive cycle, into an interactive system. This system would then provide the means of evaluating current concepts in sow nutrition and serve as a predictive tool for evaluation of management strategies in sow production. Emphasis was placed on effective communication of the present research knowledge base into a form for use by industry people; farmers, advisors, and nutritionists. A number of sub-hypotheses were introduced as primary driving forces to achieving the model objectives:

- Protein growth is the main drive behind nutrient partitioning and is genetically determined, thus accounting for the differences observed between breeds of pig.
- By virtue of the priority given to protein accretion, both energy and protein intake, and their interactions are important in determining nutrient partitioning.
- The drive for body protein growth will be responsible for the observed differences in response between gilts and sows.
- Modelling compositional changes in the sow body provides information on the underlying mechanisms of parity to parity interactions, and pregnancy-lactation interactions in sow response to level of feed intake.
- Priority of nutrient partitioning in the sow always goes to the products of reproduction first (uterine growth, conceptus and milk).
- Subsequent reproductive response is a function of the changes in

nutrient balance of the sow body, as predicted by the model.

The model does not encompass the complexities of predicting puberty attainment in the gilt, predicting ovulation rate and embryonic mortality, nor does it include extrapolation of tissue changes to carcass composition, and subsequent economic optimisations. Neither is the model designed for feed formulation, though it is hoped that it can be integrated with other packages that provide these facilities.

It is unlikely that only one optimal feeding program exists for sows, though much controversy exists as to the most efficient method of feeding for the complete reproductive cycle. By modelling the mechanisms of nutrient response in the sow, this question can be addressed.

The sow modelling problem is dealt with in the following chapters on the basis of the assumption that the first module to be derived, that of the growing female pig and dry sow, provides a common core for the development of subsequent modules. As such, the hypotheses postulated within the problem definition are dealt with first ie., the basic relationships concerning protein accretion, and are central to the protein and energy requirements of the dry animal. The assumption in subsequent modules is that these fundamental relationships are not altered by changes in physiological state.

In the following chapters, mathematical models are formulated to represent protein growth in the growing female pig under optimal (Chapter II) and restricted (Chapter III) nutrient availability; nutrient partitioning in the dry (Chapter IV), pregnant (Chapter V) and lactating (Chapter VI) sow. Modelling body composition of the sow over the reproductive cycle was then a necessary preliminary to prediction of the link between nutritional status and return to estrous (Chapter VII). Chapters II through VII are developed on the basis of given nutrient intakes, hence the final chapter deals with prediction of feed intake under ad libitum conditions. Thermal balance is included as a factor in nutrient balance, through its effect on nutrient intake (Chapter VIII).

An overview of the order of events and interaction of the model components is provided in Figure I.4. The model is validated throughout the formulation of the separate modules and ultimately as a complete system. Programming was done using a daily time integral and the complete computer program is given, in Turbo 'C' programming language, in Appendix 1., for the computer model named 'TURBOSOW'

Table I.1. Selected simulation models of farm animals

Species	Type of model	Authors
Cattle:		
Lactation	Digestion, energetics, mechanistic	Baldwin et al., 1987
Lactation	Ration formulation, nutrient partitioning	Hulme et al., 1986
Lact/Preg	Energy partitioning, empirical	Bruce et al., 1984
Lact/Preg	Energy partitioning, environment	Young 1989
Growing	Nutrient utilisation, mechanistic	France et al., 1984
Herd	Herd production systems, dynamics	Kahn & Spedding, 1983
Growing	Growth and composition, DNA, protein	Oltjen et al., 1986
Sheep:		
Growing	Ion transport, protein turnover	Gill et al., 1990
Growing	Nutrient utilisation, mechanistic	Gill et al., 1984
Growing	Energy and protein utilisation	Graham et al., 1976
Swine:		
Lactation	Nutrient utilisation, mechanistic	Pettigrew et al., 1989
Pregnancy	Energy partitioning, empirical	Williams et al., 1986
Growing	Energy and amino acid utilisation	Black et al., 1986
Growing	Energy and protein utilisation	Moughan et al., 1987
Growing	Thermal balance, empirical	Bruce and Clark, 1979
Growing	Energy and protein partitioning	Whittemore & Fawcett, 1976
Bioeconomic	Genetic, life cycle efficiency	Tess et al., 1983
Biochemical	Energy metabolism, mechanistic	Schultz, 1978

Figure I.1 The modelling process

Taken from Baldwin & Koong, 1980

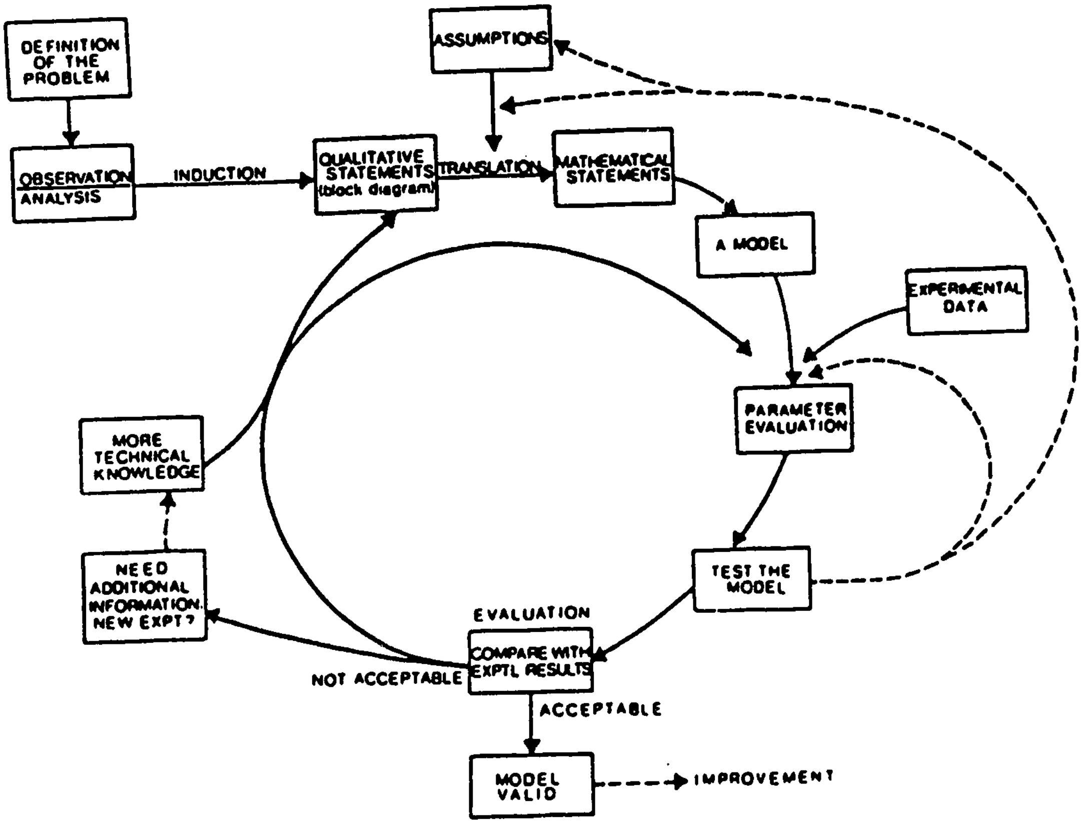


Figure I.2 Nutrient partitioning in the sow

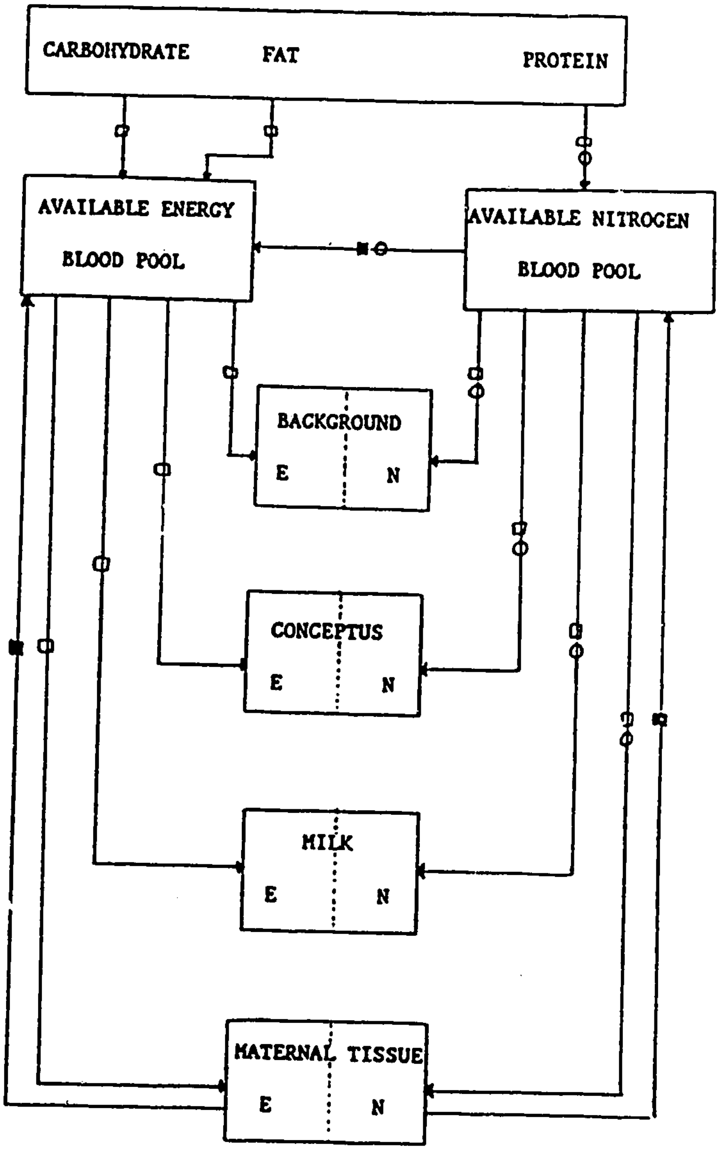


Figure I.3 The interaction of nutritional regime and reproductive performance

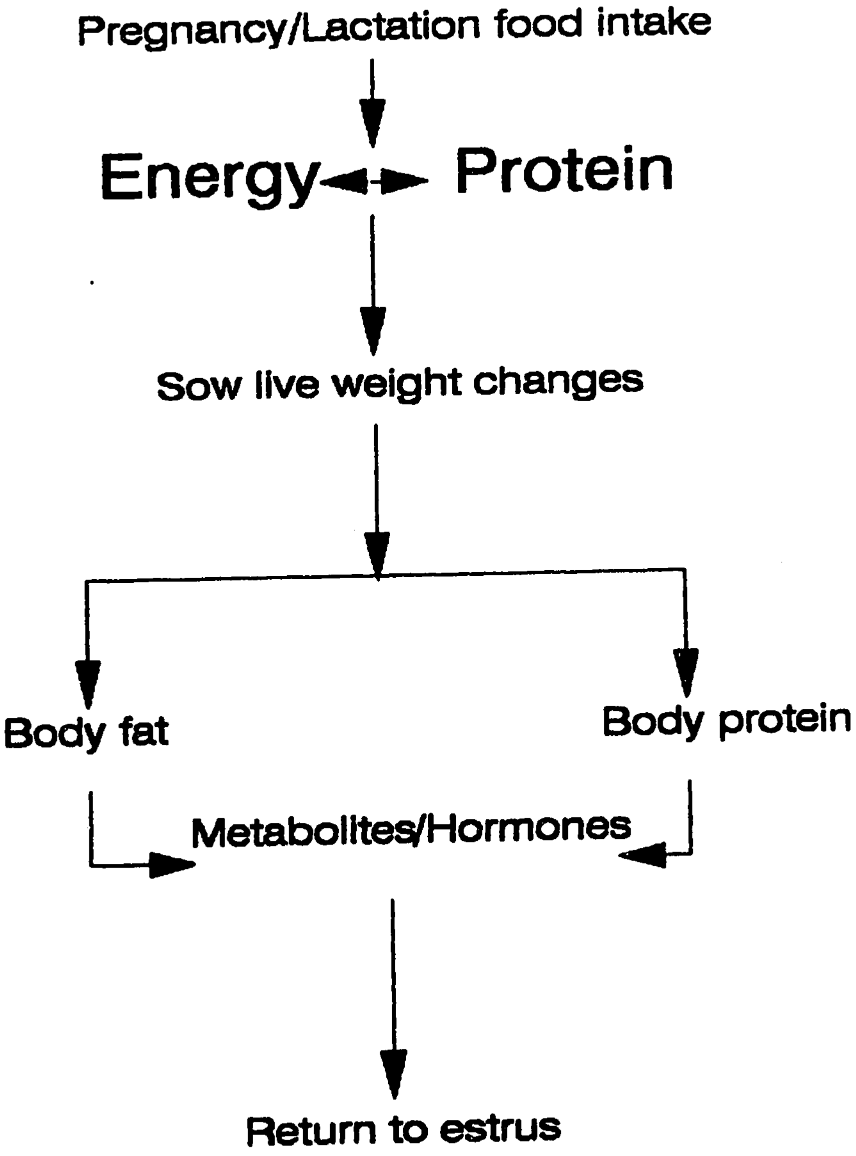
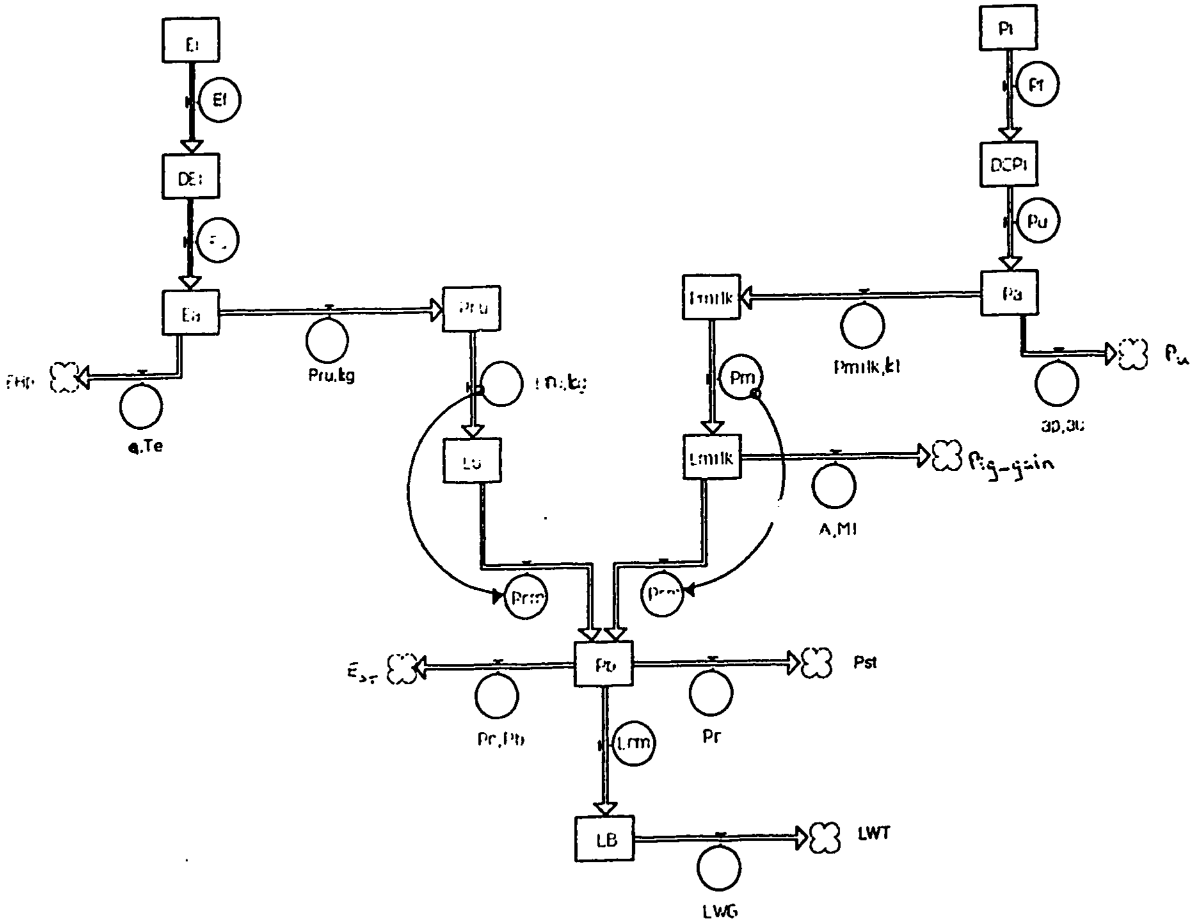


Figure I.4 Flow diagram of the reproducing sow model



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II. MATHEMATICAL REPRESENTATION OF PROTEIN ACCRETION IN THE FEMALE PIG MAXIMAL ACCRETION RATES FROM BIRTH TO MATURITY[1].

A. Introduction

To determine the requirement of an animal for dietary protein and energy and their body composition at any point in time, quantitative information is required between live weight and potential for protein and energy accretion (Campbell, 1988). Mathematical modelling with the use of more mechanistic relationships provides an ideal means of attacking this problem. Computerised mathematical models already exist for growing finishing pigs (Whittemore and Fawcett, 1974; Moughan and Smith 1984; Moughan et al., 1987; Black et al., 1986), and for digestion, metabolism, nutrient partitioning and production in a number of other domestic species (Baldwin et al., 1987a,b; France et al., 1987; Graham et al., 1976). More recently these attempts have been extended to include the gestating and lactating sow (Williams et al., 1985; Pettigrew et al., 1989). The compositional changes and resulting reproductive response of sows to nutrient input is not easily predicted (Mullan and Williams, 1989) and requires consideration of the driving forces associated with growth and development.

Most mammals and birds are thought to have a finite body size, determined primarily by the potential number of cells in each organ (Munro and Gray, 1969). In contrast, the majority of animals show

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unlimited growth; they continue growing, though usually at a constantly diminishing rate, until they die (Huxley, 1972). Even among mammals a change in proportions may continue throughout life (Huxley, 1972). Mathematical descriptions of relative growth of farm animals over time have traditionally been sigmoidal in nature, advancing over time relative to a hypothetical mature size and age (Brody, 1945; Taylor and Murray, 1987; Taylor et al., 1981). Mature size is hypothetical since in most instances it has not actually been measured, and most farm animals are generally slaughtered at a relatively young age. In addition any hypothetical mature size is influenced not only genetically (species, breed or strain) but varies between sexes within species (Walstra, 1980), and may be modified by environmental factors, including nutrition (Taylor et al., 1981). Estimates of mature size may be dependent on the definition of maturity used eg. weight equilibrium, fatness level, or mature body protein mass. Traditional mathematical expressions of growth have been criticised for not having an adequate description of the biological factors known to be involved in growth (Moughan and Verstegen, 1988). Since body protein is less influenced by nutrition than body fat, more accurate descriptions of growth have been defined in terms of potential protein deposition rates over time (Black et al., 1986; Black, 1983).

The potential rate of energy and protein accretion represent the maximum capacity of the animal to lay down body tissues when growing between birth and 'maturity', with free access to a high quality diet, and where growth and feed intake are not limited by gut capacity, disease, climatic or other environmental factors (Black, 1989).

Theoretically, under ideal conditions of diet and environment, the upper limit to protein accretion will be determined by genotype and endocrine status (Carr et al., 1977; Whittemore, 1983; Moughan et al., 1987). This concept is supported experimentally by the work of Campbell et al (1983; 1985; Campbell and Taverner, 1988) for pigs between 20 and 90 kg live weight. The relationship between potential protein accretion and live weight is generally considered to increase sharply in the young pig, with a broad maximum plateau, possibly remaining constant between 40 to 100 kg (Whittemore 1987; Moughan et al 1987), followed by a gradual decline to zero at the projected mature mass. There is wide variation in the estimates of two important parameters of mathematical models of protein accretion over time; the maximum rate of protein accretion and mature mass (defined as the point at which rate of protein accretion is not significantly different from zero). For pigs the maximum rate of protein accretion ranges between 90 and 175 g/d (14 to 28 gNr/d) depending on sex and genotype (Whittemore, 1983) and values for the mature mass of female pigs range between 208 and 340 kg live weight (Carr et al., 1977; Whittemore et al., 1988; Williams et al., 1985). Within a specific breed or strain of pig, large variation still remains in the estimates of these parameters. Discrepancies may arise partially as a consequence of errors associated with methodology used in the experimental data sets, but also as a result of the mathematical functions applied to the data (ie. the point at which the function intercepts with the horizontal axis). Specifically, extrapolation of equations, derived from growing finishing pig data, to a higher range of live weights (maturity) have given widely varying estimates of the mature mass of swine.

This study was undertaken to establish a mathematical function to represent the relationship between potential protein accretion and live weight in the female pig, as a prerequisite to modelling protein growth and the reproductive responses of sows to nutrient input.

B. Approach and Analyses

With the objective of determining a fundamental relationship for the prediction of potential rate of protein accretion, the study focused on two main areas; firstly the relationship between body protein, live weight and age, and secondly, on the relationship between potential protein accretion measured by nitrogen balance and body protein content or live weight.

Complete data sets from experiments on female pigs containing measurements of body protein content at specific weight and age were few, and are often confounded by prior nutrition. It was hoped that by including weight for age of an animal this would partially account for animals of a similar weight but different protein content as a consequence of different nutritional regimens. Nevertheless data were taken from studies in which the pigs were grown under *ad libitum* conditions because of the desire to utilise this function as one method of generating the potential protein accretion function. Since the concept of 'maturity' includes the presumption that body protein must reach a stable mass (at potential protein accretion rate equal to zero) linear plateau, hyperbolic and sigmoidal functions were fitted, in addition to linear, allometric and log transformations to the data of body protein mass (Whittemore et al., 1988; Walstra 1980; Shields et al., 1983). These included Gompertz, Logistic, Morgan-Mercer-Flodin (Parks, 1982; Ratkowsky, 1983) and Parks' diminishing returns function (Parks, 1970) (Table II.1). Differentiation of any of these functions with respect to weight gives an estimate of the rate of protein accretion. Judgement on the fit of a function was assessed on the basis of r^2 (of observed versus predicted), coefficient significance and residual sum of squares (RSS). Non linear analyses were carried out using SPSSX (SPSS Inc. Chicago), SAS (SAS Inst. Inc. Cary, N.C.) and BMDP (BMDP-77, Berkley, Calif.). It was not the purpose of this paper to evaluate differences between sources of data. In addition to two dimensional functions, the three dimensional function of body protein, weight and age was fitted. The potential rate of protein accretion can be calculated along a vector in the age, live weight plane, using the partial derivative of body protein with respect to both age and live weight.

A second method of deriving maximal protein accretion rates, rather than depending on derivation from maximal body protein content, was to derive them directly from experimental measurements. The data used for the development of the relationship between potential protein accretion and protein in the body or live weight, were taken from experiments in which nutrient input was considered to be adequate to achieve maximum protein accretion (Table II.2). Only experiments in which protein accretion was calculated from nitrogen balance studies (nitrogen retention, Nr) were included, due to the differences observed between balance data and protein accretion determined from carcass analysis (Metz et al., 1984). In this case "potential protein accretion" is used to refer to maximum protein accretion (Protein = Nitrogen X 6.25) achievable, and reflects more closely the daily changes rather than estimation from body protein mass measured at larger time intervals. The breeds included were combinations of Large White, Landrace and Dutch Landrace, and all were non gravid females. The approach assumed that protein accretion measured under conditions of adequate nutrients and non-limiting environmental conditions approaches the genetically determined upper limit to protein accretion. The data were analyzed using parabolic and quadratic functions, and transformations to fractional rate (measured nitrogen retention per unit of body protein or weight, per day) data for logarithmic and linear/curvilinear analysis. Where linear transformation was achieved, confidence and prediction bands were calculated to provide an indication of variation in mean values and individual predictions, respectively (Kleinbaum and Kupper, 1978).

Confidence intervals were given by:

$$CI = Y_x \pm t_{n-2, 1-\alpha/2} \cdot Sy_x$$

where the standard deviation of Y_x is given by:

$$Sy_x = S_{y/x} \cdot \sqrt{1/n + (X_o - X)^2 / (n-1)Sx^2}$$

and S_x^2 is the sample variance of the x's, and predicted Y at X_o is:

$$Y_x = \beta_1 X_o - \beta_o = Y + \beta_1 \ (X_o - X)^2$$

Prediction intervals were calculated as:

$$Y + \beta_1 \ (X_o - X) \pm t_{n-2, 1-\alpha/2} \cdot \ S_{y/x} \ \sqrt{1 + 1/n + (X_o - X)^2/(n-1) \ S_x^2}$$

C. Results

Relationship between body protein, weight and age.

Body protein mass increased almost linearly with body weight and within the range of the data used in the analyses did not plateau at a distinct live weight. Most functions evaluated tended to linearity as a consequence of the data, and where an asymptote could be achieved, a large range in asymptotic values was observed depending on the function chosen. None of the conventional growth functions provided a distinct 'mature' protein mass or live weight. All functions had high non-linear r^2 values, possibly as a result of the small number of data sets and low between set variation. Rate of protein accretion derived from differentiation of these functions with respect to weight, continued to increase with live weight.

The combined function for body protein (P_b;kg) against weight (LWT;kg) and age (A;days) is given in Equation II.1., and although asymptotic, a constant body protein content was not reached (Figure II.1). The regression coefficient of the combined equation was slightly better ($r^2 = 0.9901$) than that of any other function tried (Table II.1.), and each coefficient in the equation was significant at $P < 0.001$, suggesting a strong interaction between age and liveweight.

$$P_b = \beta_0 + \beta_1/\ln(A) + \beta_2.\ln(LWT) + \beta_3.\ln(LWT)/\ln(A) \quad \ldots\ldots \text{II.1.}$$

Where $\beta_0=-103.4$ $\beta_1=396.58$ $\beta_2=32.07$ $\beta_3=-118.37$

Since age and weight vary simultaneously, the rate of protein accretion must be derived by differentiation in both dimensions (dP_b/dt; g/d) and runs along a vector (t) in the A.LWT plane, making an angle θ with the age axis, equation II.2, (Figure II.1).

$$dP_b/dt = \delta Pb/\delta A.\ \cos\theta + \delta Pb/\delta LWT.\ \sin\theta \quad \ldots\ldots \text{II.2.}$$

At optimum growth, body protein is predicted along the peak of the response surface; any imbalance in weight for age therefore reduces the angle theta. Alternatively, an animal previously restricted in growth, fed an optimal diet could achieve growth of body protein along a vector with angle theta greater than that travelled by the peak of the response surface. Predictions of protein accretion rates by this method agreed well with experimental values but never reached zero and therefore a value for mature body mass or age at maturity could not be defined in terms of body protein. Equation II.2 is, nevertheless, not intended to be a predictive equation, since *theta* must be defined. Equation II.1, was considered to be advantageous to other functions which only allow for variation in P_b with LWT and not A. In addition differentiation of conventional growth functions is theoretically with respect to weight ($dP_b/dLWT$) and therefore not a true reflection of daily rates of accretion over time.

Relationship between rate of protein accretion, live weight and body protein.

In the analysis of daily rate of protein accretion it might be expected that as body protein content approached the theoretical mature mass, the rate of protein accretion (measured as Nr, g/d) would diminish proportionately to zero. When plotted against body protein content or liveweight, the relationship of measured daily rates of protein accretion (Nr data from table II.2.) was parabolic in appearance but within the range of the data set, did not cross the horizontal axis, and also tended to be skewed to the right. As a consequence the data were not fitted well by parabolic or skew parabolic functions, which tended to give large errors at both ends of the data range. When expressed as a proportion of body protein (Nr/P_b; g/g/d) or liveweight (Nr/LWT; g/kg/d), rate of protein (nitrogen x 6.25) accretion decreased exponentially and linearly, respectively. Fractional rate of protein accretion (Nr/LWT/d) showed a more extreme exponential decline relative to log (LWT). Values of body protein content for the animals used for nitrogen retention data in most instances were not available from the literature and were estimated using Equation 1. Regression of log.log fractional rate of nitrogen retention per gram nitrogen in the body per day ($Nr/N_b/d$) against body nitrogen gave evidence of a curvilinear relationship (r^2=0.8695). As a consequence of the form of the resulting equation, small errors in estimating fractional rates become multiplied when translated into estimates of absolute rate of nitrogen retention.

A logarithmic transformation of fractional rates of nitrogen retention per kg body mass per day (Nr/LWT/d) gave an excellent linear fit (r^2=0.9836) to the data between 20 and 165 kg LWT. Confidence bands were calculated for the predictive equation at the 95% level as were prediction bands (Figure II.2). When the fractional rate relative to liveweight was used to predict rates of nitrogen retention over a range of liveweights, the accuracy was acceptable (Table II.3). The function developed, Equation 3., was skew parabolic in nature but never crossed the x axis (Figure II.3) in agreement with the indirect prediction of protein accretion from body protein content (equation II.2). Equation II.3 is advantageous from a practical viewpoint since it is independent of both age and body protein, for which there is little data.

$$Nr = LWT.e^{(a+b.LWT)} \qquad \text{.... II.3.}$$

Where a = -0.327 (± 0.069) and b = -0.0136 (± 0.0003), n = 38

The function derived for potential rate of nitrogen retention and liveweight agreed well with the observation of a rapid increase in early life, plateau between 40 to 100 kg and a gradual decline in the older animal. As with the function for body protein, potential rate of protein accretion would never actually reach zero, but would progressively decrease, being less than 2 gNr/d (12.5 gPr/d) for liveweights greater than 350 kg. The predicted value for maximum rate of protein accretion was 122.5 gPr/d, 19.6 gNr/d and occurred between 65 and 85 kg LWT. The prediction bands are of course wider than the confidence bands since they are a function of the individual animal variation, rather than the variation of a sample mean.

D. Discussion

There appeared to be an almost linear relationship between body weight and body protein mass for pigs in the growing-finishing range, but this was modified with age (Figure II.1). In other studies, the relationship has been described as allometric, but the exponent for weight is close to, and often not significantly different from one (Whittemore et al., 1988). The apparent linearity in these analyses could have been a consequence of the lack of body protein data for older and heavier sows (>100 kg), but also may be an indication that protein growth does not actually cease at a specified 'mature' live weight. The non-linear function (equation II.1) was chosen over other growth functions because the inclusion of weight for age appeared to be important and may reflect differences in rate of maturation, evident between breeds. This may be manifested as differences in potential for protein accretion, represented by a change in the vector at angle θ in equation II.2. The equation has the advantage, over conventional growth functions relative to LWT, of not being forced through an asymptote although the β coefficients may have little biological meaning and be associated with considerable noise as a consequence of variance in the data. Most importantly, the vector of weight and age more closely approximates the advancement of time, than simple differentiation with respect to weight.

In contrast, in the equation of Whittemore et al. (1988), $dP_b/dLWT$ will never reach zero, but dP_b/dt ($dP_b/dLWT.dLWT/dt$) is forced through the x axis as a result of dLWT/dt being defined by a Gompertz equation with an asymptotic value ('mature mass') of 215 kg.

The derivation of rate of protein accretion on the basis of differentiation of the body protein curve may not reflect well the daily changes occuring in potential accretion rates, particularly since carcass data tends to be taken at wide time intervals. This results in increased flattening of the curve with increasing slaughter interval. In addition, rates of protein accretion estimated from carcass data tend to be lower than short term measurements of nitrogen balance, which in turn tends to overestimate actual accretion as a consequence of losses during urine collection (Metz et al., 1984).

It was considered more appropriate in light of the results of body protein analysis to attempt to estimate rate of protein accretion directly from measured nitrogen balance data, rather than indirectly from any of the functions for body protein. The function derived from analyses of fractional rates of protein accretion followed the pattern described by a number of other workers (Carr et al., 1977; Williams et al., 1985; Black et al., 1986) with one major exception; there was no distinct 'mature mass' and as a result the curve declined more gradually, indicating higher levels of protein accretion (Nr) in sows (Figure II.4). This conclusion was therefore achieved independently in both methods of analysis used to predict protein accretion rates. The derived value for maximum potential protein accretion (122gPr/d; 19.6d Nr/d) was in general agreement with values reported for females pigs in other studies (Siebrits et al., 1986; Whittemore et al., 1988; Moughan et al., 1987).

There is considerable variation for female pigs in experimental estimates of nitrogen balance even within similar breeds (Figure II.3).

Predicted values of the potential rate of nitrogen retention, for the 'average' pig, will be most accurate in the centre of the experimental region as seen from the parabolic nature of the confidence bands. The prediction bands show that a larger proportion of variation is associated with prediction of individual animal response, hence extrapolation beyond the range of the data used is potentially associated with large errors. Despite these errors, which are inherent in all the equations estimating nitrogen retention or protein accretion potentials, the higher levels of nitrogen retention predicted for sows (greater than 140 kg) in this study are supported by recent experimental data measuring nitrogen balance in gravid and non-gravid sows (Jones and Maxwell, 1982; Willis and Maxwell, 1984; de Lange et al., 1980; B. Knudson, 1989, Personal communication). In addition Williams et al., (1985) found that their equation under-predicted nitrogen retention in sows, but not gilts. There, are however, some data from both nitrogen balance studies and carcass analyses (R. King, 1989, Personal communication) indicating lower levels of nitrogen retention which would be closer to the predictions of Black et al., (1986) and Williams et al., (1985). Hence, more data is needed on protein accretion in sows.

High levels of nitrogen retention in older gravid pigs may partially be due to pregnancy anabolism (Close et al., 1985; Elsley et al., 1966; de B. Hovell et al., 1977) or in the non-gravid animal, which has undergone nutritional restriction in lactation, to "catch-up" gain in certain tissues (Salmon-Legagneur, in Williams et al., 1985), or replenishment of labile protein stores. If either of these cases exist, then equation II.3 would be more likely to allow for these scenarios than previously developed functions.

The diminishing fractional rate of accretion with increasing live weight (and body protein content) in the older sow could be explained by an increasing maintenance cost of body protein with increased protein mass. The better fit of expressing protein accretion relative to liveweight than to body protein could be due to errors in the prediction of body protein content, or may reflect the fact that potential protein accretion is not dependent solely on protein mass. Fractional rates of both protein synthesis and degradation progressively decline in the whole body of rats throughout both pre- and post-natal life, mainly as a result of a progressive decline in ribosomal capacity (Goldspink and Kelly, 1984).

Considering the potential problems inherent in measuring nitrogen retention and hence protein accretion it could be said that nitrogen retention approximated zero (ie. was not significantly different from zero) by about 350 kg liveweight (Nr<2g/d). This apparent 'mature' mass is slightly above that predicted by Williams et al. (1985), but considerably greater than most other estimates (Carr et al., 1977; Parks, 1970; Black et al., 1986; Whittemore et al., 1988). Sows fed *ad libitum* have been shown to reach weights in excess of 340 kg without reaching equilibrium weight (Walstra, 1980), in agreement with the statements made by Huxley (1972).

In conclusion, the equations developed for female pigs have the advantage of being independent of an absolute 'mature mass' of protein or live weight, a concept which has confounded previous attempts at modelling protein growth. In addition, the equations can be parameterised with additional data to reflect differences in breed or sexes. Under conditions of limiting nutrients, protein accretion will fall below the potential described in Equation II.3, depending on intake of energy and protein. A systematic approach to modelling the underlying mechanisms behind the response of protein growth in pigs to variations in energy and protein intake is a necessary corollary to this study.

Table II.1. Fit of mathematical models to data on body protein mass and live weight, as determined by regression (r^2) of observed vs predicted values and residual sum of squares (RSS).

MODEL	Function	r^2	† RSS
MORGAN-MERCER-FLODIN (MMF)	$\frac{1391\ \text{LWT}^{0.925}}{6804 + \text{LWT}^{0.925}}$	0.9897	22.69
MODIFIED MMF	$223\ \text{LWT}/(1453 + \text{LWT})$	0.9894	23.39
ALLOMETRIC	$0.214\ \text{LWT}^{0.913}$	0.9897	22.71
LINEAR	$0.864 + 0.132\ \text{LWT}$	0.9878	26.99
SEMI-LOG	$-15.42 + 6.839\ \ln(\text{LWT})$	0.7299	595.25
QUADRATIC	$0.261 + 0.147\ \text{LWT} - 0.00007\ \text{LWT}^2$	0.9894	23.38
GOMPERTZ	$41.879\ e^{(-e(1.055 - 0.0086\ \text{LWT}))}$	0.9799	-
PARKS	$0.222 + 138.08\ (1 - e^{-0.001\ \text{LWT}})$	0.9894	23.27
LOGISTIC	$35.957/(1 + e^{(2.27 - 0.0176\ \text{LWT})})$	0.9688	71.20
LOG	$e^{(-0.859 + 1.008\ \ln(\text{LWT}))}$	0.9937	0.044

†RSS = Residual Sum of Squares (BMDP-77, U. Calif., Berkley)

n = 31

Table II.2. Data used in evaluation of relationship between liveweight and potential rate of protein accretion (measured as nitrogen retention).

SOURCE	BREED‡	WEIGHT RANGE (kg)
1. Oslage and Fliegel, 1965	GM	45 to 165
2. Kotarbinska and Kielanowski, 1967	LW	60 to 90
3. Elsley et al., 1966	LW	130 to 150
4. Thorbek, 1967	DL	30 to 85
5. Thorbek, 1975	DL	23 to 80
6. Hodge, 1974	LW	4 to 15
7. Carr et al., 1977	LW x L	5 to 160
8. Campbell and Dunkin, 1983	LW	6.5
9. Campbell et al., 1983	LW x L x B	20 to 45
10. den Hartog and Verstegen, 1984	DL	36 to 66
11. Campbell et al., 1985	LW x L x B	45 to 90

‡LW - Large White, DL - Dutch Landrace, L - Landrace, B - Berkshire
GM - German Meat Type

Table II.3. Comparison of measured nitrogen retention data used in parameterisation of Equation II.3 with predicted nitrogen retention rate.

LIVEWEIGHT[1] (kg)	Measured Nr† (g/d)	Predicted Nr (g/d)	%Error §
23	11.6 (5)‡	12.13	-4.57
30	13.8 (4)	14.38	-4.24
35	16.7 (5)	15.68	7.05
40	16.0 (1)	16.74	-4.63
45	17.0 (4)	17.59	-3.50
51	18.9 (5)	18.38	2.70
55	17.5 (1)	18.77	-7.26
60	19.4 (7)	19.13	1.38
66	21.6 (10)	19.39	10.20
70	20.2 (4)	19.48	3.84
75	17.6 (1)	19.50	-10.8
80	20.3 (5)	19.43	4.26
85	20.1 (4)	19.29	4.02
90	18.2 (2)	19.08	-4.62
95	17.1 (1)	18.81	-10.0
100	19.0 (7)	18.50	2.59
105	16.6 (1)	18.15	-9.34
110	16.5 (1)	17.77	-7.70
125	18.6 (1)	16.46	11.43
135	14.5 (1)	15.52	-7.00
145	15.6 (1)	14.55	6.71
155	13.9 (1)	13.57	2.31
165	13.0 (1)	12.61	2.95

† Nr= Nitrogen retention ‡ Numbers in parentheses relate to data source (Table II.2)

§ % error = [(actual - predicted)/actual] * 100

1. Mean liveweight of pigs at which nitrogen retention was measured. Data shown are selected at intervals from data given in Table II.2

Figure II.1 Response surface of body protein mass with live weight and age (equation II.1) vector theta is dPb/dt

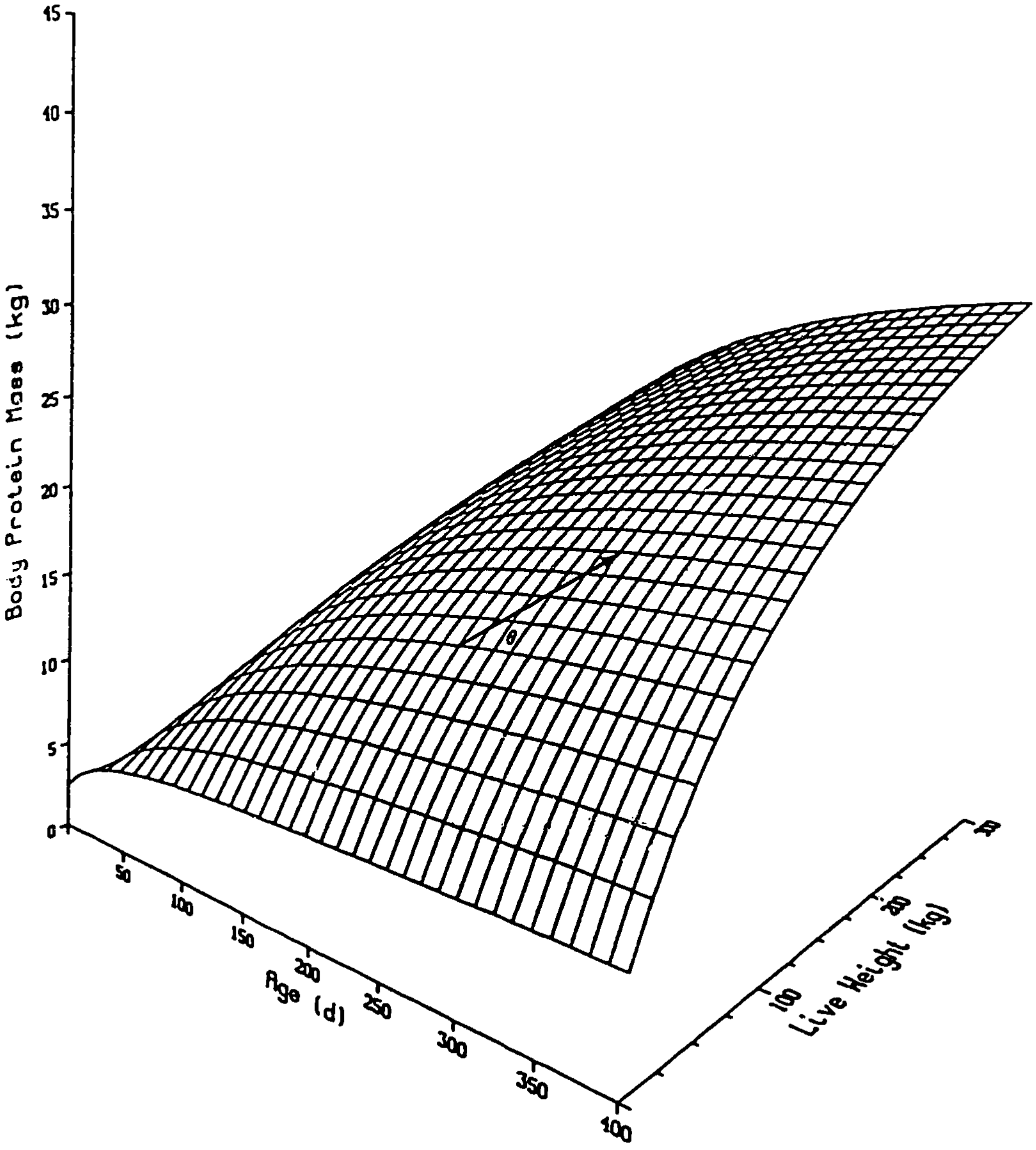


Figure II.2 Relationship between fractional rate of nitrogen retention and live weight. Observed points and 95% confidence bands.

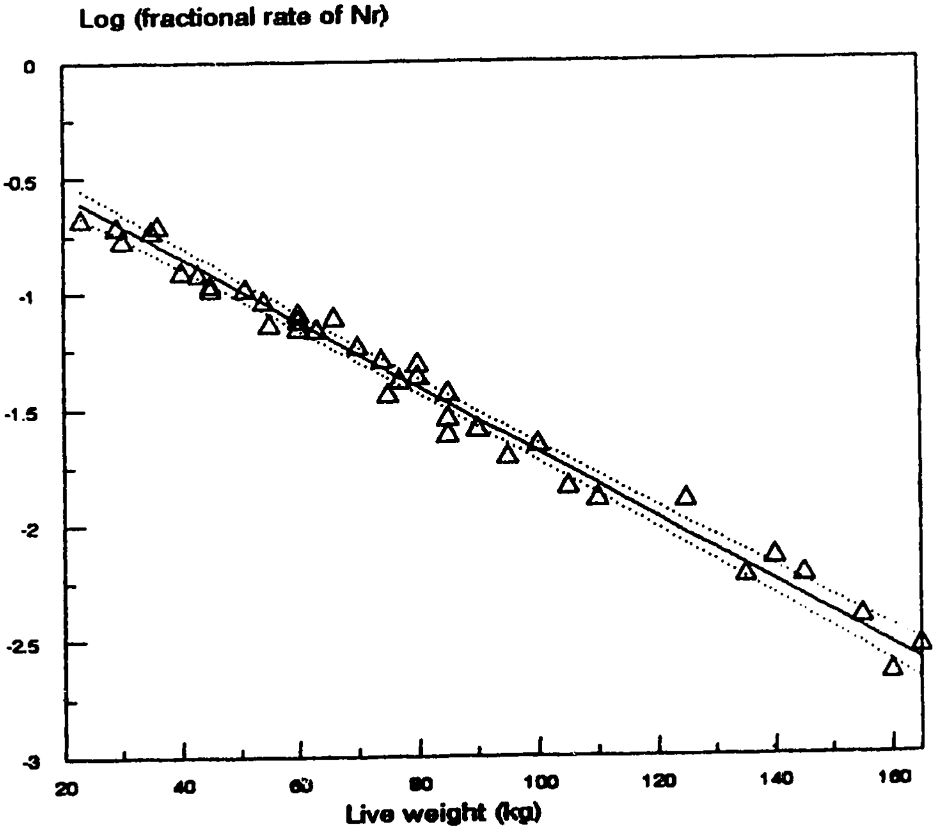


Figure II.3 Predicted response of nitrogen accretion to live weight.

Observed points and 95% confidence and prediction bands (outer range)

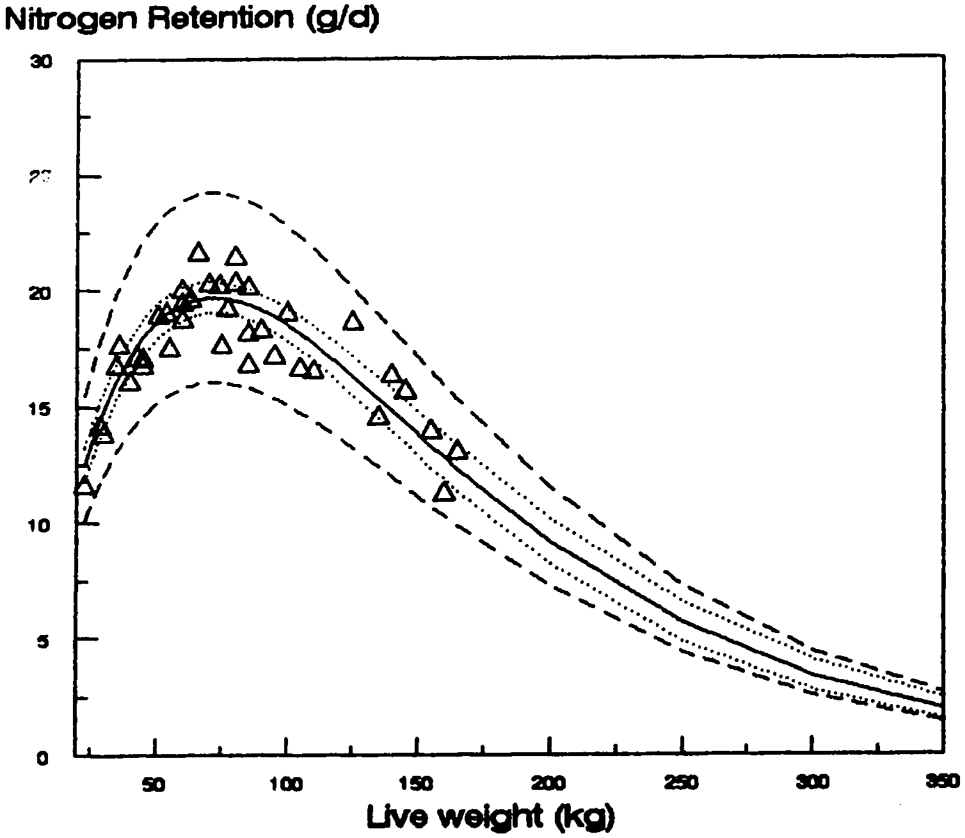
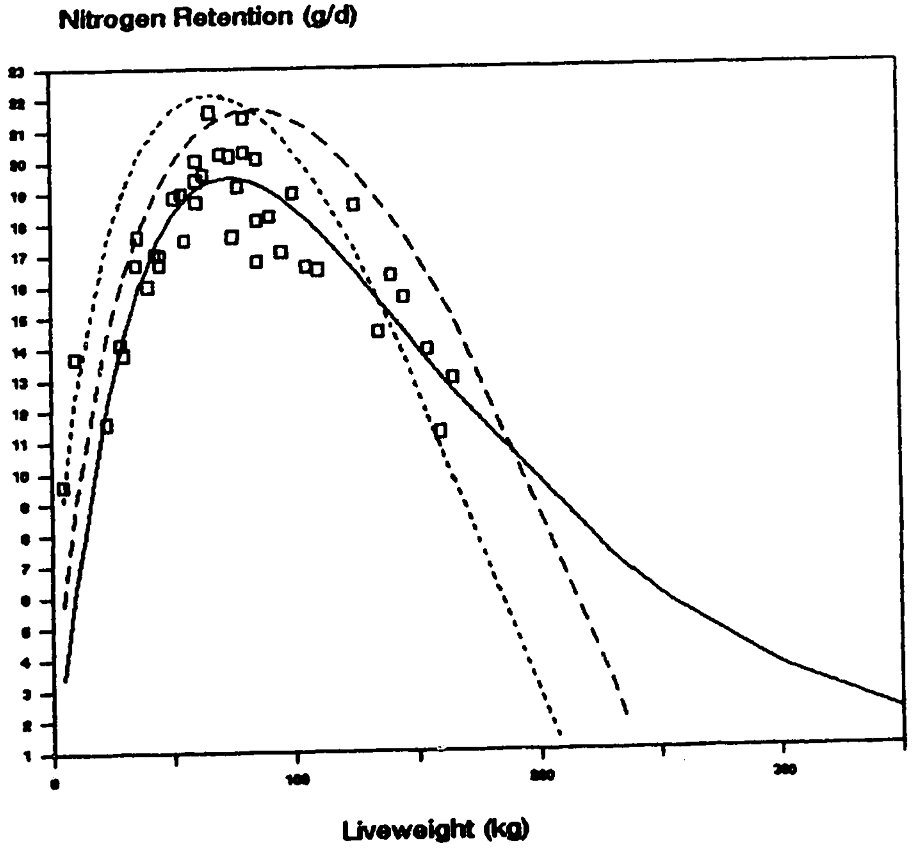


Figure II.4 Comparison of predictions of nitrogen retention equations.

Equation II.3 (—) versus Whittemore et al (....) and Black et al (—)



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III. MATHEMATICAL REPRESENTATION OF PROTEIN ACCRETION IN THE FEMALE PIG PROTEIN ACCRETION UNDER LIMITING NUTRIENT SUPPLY.

A. Introduction

Maximal protein accretion rates in swine are determined by intrinsic factors such as genotype, sex and strain (Siebrits et al., 1986), and vary with live weight which can be described by the relationship developed in Chapter II. These rates of accretion are assumed to be achievable under conditions of optimal nutrition and environment. Most commercial swine after 90 kg live weight are fed restricted levels of intake to achieve less than maximal growth rates, due to excess lipid deposition, and may therefore be accreting protein at less than the genetic maximum. In addition, animals fed ad libitum may not be receiving a diet of optimal quality, since maximum daily live weight gain is not necessarily concomitant with maximal lean tissue growth. It is therefore of prime importance in determining animal response to nutrient intake to consider the relationship of protein accretion to both nitrogen and energy intake, together.

A number of experiments have been completed recently aimed at elucidating the relationship between nutrient intake and protein accretion in pigs at different live weights, and these have been reviewed by Campbell (1988). In addition to the consistency of responses with other species (Black, 1989), there appears to be general agreement on the extent to which lean tissue growth is influenced by nutrient intake in the pig. A number of reports have focused on different breeds and sexes of the growing finishing pig (Campbell et al., 1983; 1984; 1985; Campbell and Taverner, 1988), while very little information is available on the gravid gilt, or pigs greater than 90 kg live weight. The response of protein accretion to increments of nitrogen and energy intake has most commonly been described as 'linear-plateau' (Whittemore and Fawcett, 1976). Evidence for this form comes largely from work on lambs (Black and Griffiths, 1975) and the work of Campbell et al., on growing pigs. Exceptions to the 'linear-plateau' form are boars of high growth potential (Campbell and Taverner, 1988) and young pigs fed highly digestible diets (Campbell and Dunkin, 1983), which appear to follow a linear response. The proponents of the 'linear plateau' form have postulated the existence of separate and independent phases of the protein accretion response, namely protein- and energy intake- dependent phases.

Under conditions of adequate nitrogen intake, protein accretion is independent of nitrogen intake and linearly related to energy intake. Similarly, when the diet is insufficient in nitrogen, protein accretion is independent of energy intake and linearly related to nitrogen intake, up to a plateau point, equivalent to the animals intrinsic capacity or maximal protein accretion rate. In turn, the maximal level of protein accretion is probably determined hormonally, since it may be manipulated by treatment with exogenous growth hormone (Campbell et al., 1989). Given the functional form of the response, it should be possible to define differences in response of animals at different live weights in terms of a number of parameters; the slope, plateau, intercepts and breakpoint (Dunkin and Black,1985).

Incremental protein accretion per unit energy or nitrogen intake (slope) and maximal rate of accretion (plateau) appear to vary with live weight (Black and Griffiths, 1975; Carr et al., 1977) and sex (Campbell and Taverner, 1988). For the purposes of this investigation, the use of females pigs of a similar genotype will eliminate some known sources of variation (Siebrits et al., 1986), and the focus will be on the direct response to change in nutrient intake and live weight. This chapter evaluates different mathematical approaches to represent the response of protein accretion in female pigs to a variety of combinations of dietary energy and nitrogen intakes at various live weights.

B. Analyses and Approach

The requirements of the mathematical models was that they incorporate the dynamics of both the apparent energy and protein intake phases as well as the interaction of energy and protein in determining the rate of protein accretion. Also, it was desirable to include any changes in these components with live weight (LWT;kg). The individual component responses were analysed first to determine which functional shape they conformed to and evaluate relationships between slope, intercepts, breakpoints and live weight. This analysis included data on male and castrate pigs (Campbell et al., 1983; 1984; 1985a,b; Campbell and Taverner, 1988) as well as female pigs. Linear, curvilinear and linear-plateau forms were fitted to data relating nitrogen intake (Ni;g/d) to nitrogen retention (Nr;g/d), or protein intake (Pi;g/d) and protein accretion (Pr;g/d) depending on experimental method used to derive the data set. In most instances, Nr and Ni were used in equation development, Pr being estimated by Nr*6.25. Equations were also fitted to data on protein accretion and energy intake (Ei), for female pigs only (Table III.1). Some of the analyses performed cannot be described as mathematically pure since in a number of experimental data sets both Ni and Ei appear to vary simultaneously.

Data were also analysed on the basis of Ni to Ei ratio because of the apparent interaction of the two, and the wide variation in this ratio across data sets and live weights. This led to the combination of data sets, and the inclusion of some gravid sow data (Rippel et al., 1965; Miller et al., 1969), adjusted to maternal Nr, on the basis of the equations derived in Chapter V, for evaluation of mathematical models encompassing all variables and significant interactions. Equations considered included multiple regressions, exponential functions, Morgan Mercer Flodin (MMF) and Michaelis Menton kinetics. Goodness of fit was determined initially by residual sum of squares (RSS), regression coefficients (r^2) and significance of coefficients, using SAS (SAS Inst. Inc. Cary, N.C.). It should be noted that r^2 from linear and non-linear functional fits are not necessarily comparable.

The mathematical models were tested for sensitivity to Ni, Ei and LWT to determine if they behaved sensibly, biologically, and in accordance with previously described theories. The models were also examined for biological relevance of the coefficients and parameters of efficiency derived from them.

C. Results

Individual data set plots, for each LWT group, followed a curvilinear function form (Figure III.1) rather than a linear-plateau, though an asymptotic value was reached. These asymptotic values were in general agreement with the relationship between maximal rate of nitrogen accretion (Nr_{max}) and LWT developed in chapter II. The data from all LWT groups fell within the bounds of a common function given by equation III.1, relating Nr to Ni (Figure III.2). Equation III.1 gave a positive 'x' intercept (Ni for Nr=0; nitrogen maintenance) and negative 'y' intercept (Nr at Ni=0; endogenous nitrogen loss). The individual LWT plots consisted of data at Ni values close to Ni required to reach the plateau phase of the curve (Nr_{max}). As a consequence of this and large inherent variation, extrapolation (linear or MMF) of some individual plots back to the 'y' axis gave positive values of endogenous nitrogen loss. The common function for Nr against Ni would suffice for most LWT groups, provided the pigs were receiving near optimal Ni, but did not account for variations in endogenous losses and 'maintenance' nitrogen intakes with LWT. It was not possible to determine the relationship between LWT and the 'x' and 'y' intercept values from the separate or combined individual data sets for Nr response to Ni.

$$Nr = \beta_0 + \beta_1 \, e^{(1-\beta 2 \, Ni)} \qquad \text{.... III.1.}$$

β_0=24.365 (±2.84) β_1=-9.87 (±0.88) β_2=0.0248 (±0.0056)

It was not clear, from individual plots, whether live weight influenced the slope of the so called 'linear phase' of the curve, particularly since slope ($\delta Nr/\delta Ni$) changed with Ni. Individual data set plots of Nr against Ei did not consistently follow a 'linear plateau' or curvilinear form, largely as a consequence of some data sets being confounded by changing Ni. The importance of considering Ni and Ei together in the response of Nr was illustrated by plotting Nr against the ratio of Ni to Ei (Figure III.3). Nr tended to increase in a curvilinear manner with increasing Ni:Ei ratio, though in some instances, particularly at ratios greater than 2:1 and in LWT groups below 70 kg, Nr decreased. These results indicated that the data on Ni and Ei are not independent and that the interaction of Ni and Ei in determining Nr needs to be considered. In order to predict Nr under different combinations of Ni, Ei and LWT, it was necessary to examine the interrelationships in a more interactive mathematical model, which might encompass all the essential parameters.

A multiple regression analysis of the combined data set indicated that Ni, Ei and LWT were important in determining Nr, as were the interactions between Ni and Ei, and Ni and LWT. The regression coefficient for the equation encompassing these parameters for dry female pig data (equation III.2) was 0.948, RSS=333, and all coefficients included were significant ($P<0.05$).

$$Nr = \beta_0 + \beta_1\, LWT + \beta_2\, Ei + \beta_3\, Ni + \beta_4\, LWT.Ni + \beta_5\, Ni.Ei \quad \ldots\ldots III.2$$

Where $\beta_0=-2.56(\pm2.11)$ $\beta_1=-0.0107(\pm0.053)$ $\beta_2=0.624(\pm0.376)$

$\beta_3=0.426(\pm0.074)$ $\beta_4=0.0011(\pm0.0009)$ $\beta_5=-0.012(0.0039)$

Parameterisation with growing finishing pig data alone gave a higher regression fit (r^2=0.976, RSS=131) and inclusion of corrected gravid sow data reduced the goodness of fit (r^2=0.934, RSS=509). The logarithmic transformation of LWT, or expression relative to metabolic weight ($W^{0.75}$) did not improve the prediction. A second expression was developed combining exponential expressions for LWT and Ni, with an interaction of Ni and Ei, (equation III.3). The expression generally gave higher predicted Nr at low LWT and high Ni than equation III.2, (r^2=0.947, RSS=85.4).

$$Nr = \beta_0 + \beta_1 \, LWT \; e^{(\beta_2 \, LWT)} + \beta_3 \, Ni. \; e^{(1-\beta_4 \, (2Ni-Ei))} \quad .... \quad III.3$$

Where β_0=-5.069(±1.249) β_1=1.314(±0.61) β_2=-0.143(±0.067)
β_3=0.251(±0.027) β_4=0.006(±0.0007)

The inclusion of dry sow data in the parameterisation of equation III.3 allowed for higher predicted Nr in older animals, but tended to overpredict Nr in lighter weight pigs (r^2=0.956, RSS=342). Equations III.2 and III.3 both compared well, in terms of direction and magnitude of response, with the actual data sets (Table III.2), observed verses predicted Nr gave r^2 of about 0.85. It is therefore possible to tailor each of equations III.2 and III.3 to specific LWT groups of pigs.

The variables (Ni, Ei and LWT) in both equations III.2 and III.3 were highly correlated, hence varying one parameter while maintaining the others constant allows for unrealistic scenarios and is not truly representative of the normal physiological conditions. As a consequence, only the combinations of values encountered under practical feeding situations gave sensible results and extreme combinations of Ni:Ei or very low intakes per LWT should not be considered.

Within the boundaries of practical dietary intake levels, both equations gave curvilinear response relationships for Nr with Ni or Ei, and showed variation in 'x' and 'y' intercepts in response to LWT. Ni and Ei at Nr=0, and Nr at Ni=0 and Ei=0 were greater for heavier LWT indicating greater so called 'nitrogen maintenance' requirement and endogenous losses in agreement with the findings of Black and Griffiths, (1975). The efficiency of use of Ni for Nr, ie. $\delta Nr/\delta Ni$, expressed per metabolic LWT decreased with LWT as reported by Carr et al., (1977). $\delta Nr/\delta Ei$ appeared to be similar, regardless of LWT.

An estimate of the partial efficiencies $\delta Nr/\delta Ni$ and $\delta Nr/\delta Ei$ and the Ni and Ei required for zero Nr can be obtained by rearrangement of equation III.2. The Ni requirement for zero Nr (equation III.4) was best estimated using a value of Ei equivalent to energy maintenance. Values calculated for Nr for Ni=0 and Ni at Nr=0 gave values close to, but greater than estimates of obligatory losses and protein maintenance calculated on the basis of LWT (Whittemore, 1987; Carr et al., 1977). In this instance, Ni at Nr=0 is considered to be the Ni required to meet vital processes and to support the processes of digestion, absorption and metabolism, and as such may be called nitrogen for total support processes (Ns_T; g/d). It is evident from Equation III.4 that Ns_T increases with LWT and Ei, but the equation does not account for increased Ns_T as a result of increased Ni.

$$Ns_T = (-\beta_0 - \beta_1\,LWT - \beta_2\,Ei) / (-\beta_3 - \beta_4\,LWT - \beta_5\,Ei) \qquad \ldots.\ III.4$$

Where the coefficients are those in Equation III.2 above.

Obligatory N loss (Nr at zero Ni or Ei) is simply related to LWT. The partial efficiencies of Ni and Ei for Nr (a_p and k_p, respectively) vary with intake of the respective nutrient (equations III.5 and III.6). The decreasing partial efficiencies at higher nutrient intakes are probably a result of increasing process costs and changing proportions of 'maintenance' to productive processes.

$$\delta Nr/\delta Ni = \beta_2 + \beta_5\,Ni \qquad \ldots.\ III.5$$

$$\delta Nr/\delta Ei = \beta_3 + \beta_4\,LWT + \beta_5\,Ei \qquad \ldots.\ III.6$$

The last functional form attempted on the combined data set was an adaptation of Michaelis Menton kinetics used in the models of France et al., (1987) and proposed by Black (1989) for use on a more empirical basis. The plateau or maximal Nr was fixed relative to LWT by the equation derived in Chapter II. Below maximal Nr was presumed to be determined by substrate availability, assuming the affinity constants, k_1 and k_2 were not influenced by LWT.

$$Nr = (LWT\ e^{(a + b\,LWT)}) / (1 + k_1/Ni + k_2/Ei) \qquad \ldots.\ III.7$$

where $a=-0.327(\pm 0.069)$ $\quad$ $b=-0.0136(\pm 0.0136)$

$k_1=28.42(\pm 15.33)$ $\quad$ $k_2=-8.81(\pm 6.61)$

This equation gave a poor fit ($r^2=0.893$, RSS=710) and the negative affinity constant for Ei indicated possible problems with the assumption that k_1 and k_2 are independent of LWT. While all of the equations derived herein suffer from the limitations of combining static and dynamic responses into one equation, this limitation was most noticeable with the Michaelis Menton equation, as a consequence of being unable to parameterise the numerator and denominator together.

D. Discussion

The shape of the response of Nr to Ni is not of great significance when considering animals fed at intakes allowing near maximal Nr rates where linear approximation leads to only small errors. Two important problems arise however, from application of a 'linear-plateau' response form to the relationship between Nr and Ni. The first is that linear extrapolation from data in the top region of the curve, back to the 'y' intercept, gives highly erroneous estimates of obligatory nitrogen loss. This is in agreement with the findings of Black and Griffiths (1975) who found obligatory nitrogen loss was underestimated when predicted on the basis of a linear fit to Nr values measured at higher Ni levels. The second problem inherent in the 'linear-plateau' approach arises from the assumption that there are two separate and independent phases of Nr response, to Ni and Ei, respectively (Campbell, 1988). This assumes that the Ni-dependent and Ei-dependent phases arise through separate mechanisms and therefore can be measured and analysed independently. 'Ni-limiting' and 'Ei-limiting' phases may be more appropriate, and less misleading terms to apply. It was evident from the analyses performed on the experimental data set used here, that the effects of Ni and Ei on Nr are inextricably linked, and therefore require a more integrated mathematical model to incorporate their interaction.

In light of these inconsistencies, there is no reason to assume, considering the complexity of biological systems, that the relationship of Nr to Ni and Ei should follow a 'linear-plateau' form. The same type of response can be observed for Nr in response to changes in individual dietary amino acid composition (Fuller and Chamberlain, 1985), and has best been described as a diminishing response type curve. The principles applied to that particular issue (ARC, 1981) in development of the ideal protein concept, may have application when considering the balance of Ni and Ei in determining Nr. Excess Ni alone or in relation to Ei was observed to cause a reduction in the rate of Nr, which may be explained by considering the link between the two nutrients. Although energy is obviously required for protein synthesis, any excess nitrogen for which there is insufficient energy to synthesise Ni into body protein has to be deaminated, a process which also requires energy (Whittemore and Fawcett, 1976). Hence an imbalance of Ni:Ei or excess Ni leads to an increase in heat production, reduction in the efficiency of use of energy, and reductions in both protein accretion and lipogenesis (Campbell, 1988).

In the curvilinear response, there is therefore no real "plateau" for Nr, though a maximum value (Nr_{max}) is reached at optimal Ni and Ei levels. Nr_{max} is clearly influenced by LWT (Black and Griffiths, 1975) in agreement with the pattern described in chapter II. LWT also appears to influence the efficiency with which Ni is used for Nr ($\delta Nr/\delta Ni$), and the Ni required to meet nitrogen support costs (Ns_T). At the present time, there is insufficient data in individual LWT ranges to formulate a relationship between the slope, intercepts and breakpoints, of individual plots, with LWT. Large inherent variation exists in measured values of Nr on the basis of nitrogen balance (Dunkin et al., 1986) though this is presently the most commonly used indicator of nitrogen utilisation.

The combined equation forms (Equations III.2 and III.3) go part way to including all three parameters (Ni, Ei and LWT) and their interactions into one mathematical model. Biologically unrealistic inputs into these equations gives meaningless results but within the range of practical dietary intakes, the equations are fairly responsive in the prediction of Nr. The combined equations gave a predicted curvilinear response of Nr to Ni alone, Ei alone or changing feed intake (Ni and Ei together), and appeared to overcome the limitations inherent in the two phase 'linear-plateau' model. The derivation of a mathematical function for Ns_T and obligatory nitrogen loss is preferable to estimation by extrapolation, though Equation III.4 does not yet account for all the processes known to contribute to Ns_T. Furthermore, values of obligatory nitrogen loss calculated from equation III.4 do not support the contention of Carr et al, (1977) that a common 'y' intercept exists for all LWT's. Nevertheless, values for LWT greater than 75 kg were relatively constant on a metabolic weight basis ($g/d/kg^{0.75}$) and agreed fairly well with literature values (Whittemore 1987; Moughan and Smith, 1984).

It is interesting to note that although the inclusion of corrected gravid sow data reduced the goodness of fit of equations III.2 and III.3, maternal Nr in gestating animals did not appear to deviate from the described response (Rippel et al., 1965; Miller et al., 1969), indicating that pregnancy may not influence the efficiency of use of Ni for Nr in maternal tissue. This concept warrants further investigation and, experimental data on the response of protein accretion in sows to manipulation of Ei and Ni is much needed.

The possibilities for using Michaelis Menton kinetics at an empirical level also holds promise, though modification is required to allow for variation in the affinity constants with LWT. Perhaps through individual fits of this functional form, the affinity of the Nr process for Ni and Ei (a_p and k_p, respectively) might show an increase with age (and increasing LWT) as a consequence of increasing 'maintenace costs', thus making Nr in the older animal less sensitive to nutrient input. This would be in general agreement with the observed changes in a_p and k_p reported in the literature.

In conclusion, in order to succesfully predict the response of pigs to variations in feed intake, more detailed and controlled experimental data are required, and a more interactive, dynamic mathematical approach must be taken. This chapter is an initial attempt at providing better comprehension and representation of the existing data in this area.

Table III.1. Data used for evaluation of the response of protein accretion to nitrogen and energy intakes and live weight.

Source	Weight range(kg)	Breed †	Sex ‡	Variable §
Campbell and Dunkin, 1983	1.8 - 6.5	LW	M,F	E,P
Campbell et al., 1983	20 - 45	LWxB	M,F	E,P
Campbell et al., 1985	48 - 90	LWxL	M,F	E,P
Hodge 1974	3.8 - 33	LW	M,F	E,P
den Hartog & Verstegen 1984	35 and 65	DL	F	E,P
Close et al., 1985	115 - 154	LW	F	E,P
Shields & Mahon, 1983	118 - 144	HxDxY	F	E,P
Rippel et al., 1965	140 - 150	Xb	F	P
Miller et al., 1969	158 and 191	XbxY	F	P

†LW-Large White, L-Landrace, B-Berkshire, DL-Dutch Landrace, H-Hampshire, D-Duroc, Y-Yorkshire, Xb-crossbred, U of Illinois

‡ M-Male, F-Female

§ E-Energy level, P-Protein level

Table III.2. Comparison of nitrogen accretion predicted by equations III.2 and III.3 with measured values.

	Intake			Predicted Nr	
Live weight kg †	Nitrogen g/d	Energy MJME/d	Actual Nr g/d	Eqn 2 g/d ‡	Eqn3 g/d §
4.2	8.5	3.4	3.8	2.3	2.8
4.2	13.2	5.3	5.3	5.0	5.4
4.2	16.8	6.7	6.4	6.8	7.2
4.2	21.1	8.4	7.9	8.9	9.1
32.5	33.6	14.2	10.2	12.5	14.2
32.5	44.0	19.9	13.9	16.0	17.1
32.5	57.8	24.4	18.4	18.5	19.2
32.5	68.2	28.8	20.5	19.3	20.2
32.5	79.3	34.2	20.2	18.7	20.8
69	49.5	22.5	10.1	15.5	13.2
69	59.2	26.9	13.5	17.1	14.7
69	71.0	32.3	15.5	17.8	15.7
11[illegible]	40.0	20.2	6.7	10.6	10.4
136	41.4	20.5	7.2	9.8	10.7
132	57.6	28.0	10.9	14.2	13.7
131	40.8	23.0	7.3	10.4	10.9
158	18.2	26.5	1.8	4.5	3.9
158	27.4	25.9	7.9	6.5	7.7
158	36.5	26.0	9.9	8.6	10.4
158	45.6	26.0	12.9	10.6	12.2
140	0	23.7	-6.5	0.6	-8.2
140	8.8	23.7	-1.2	2.7	-1.6
140	17.5	23.7	6.6	4.5	3.4
140	26.2	23.7	8.7	6.7	7.1
140	35.0	23.7	12.0	8.7	9.7
140	43.7	23.7	12.4	10.7	11.5

† Mid range of balance period.

‡ Parameterised without corrected gravid sow Nr data

§ Parameterised with corrected gravid sow Nr data

Figure III.1 Variation in observed nitrogen retention with nitrogen intake for pigs of different live weight

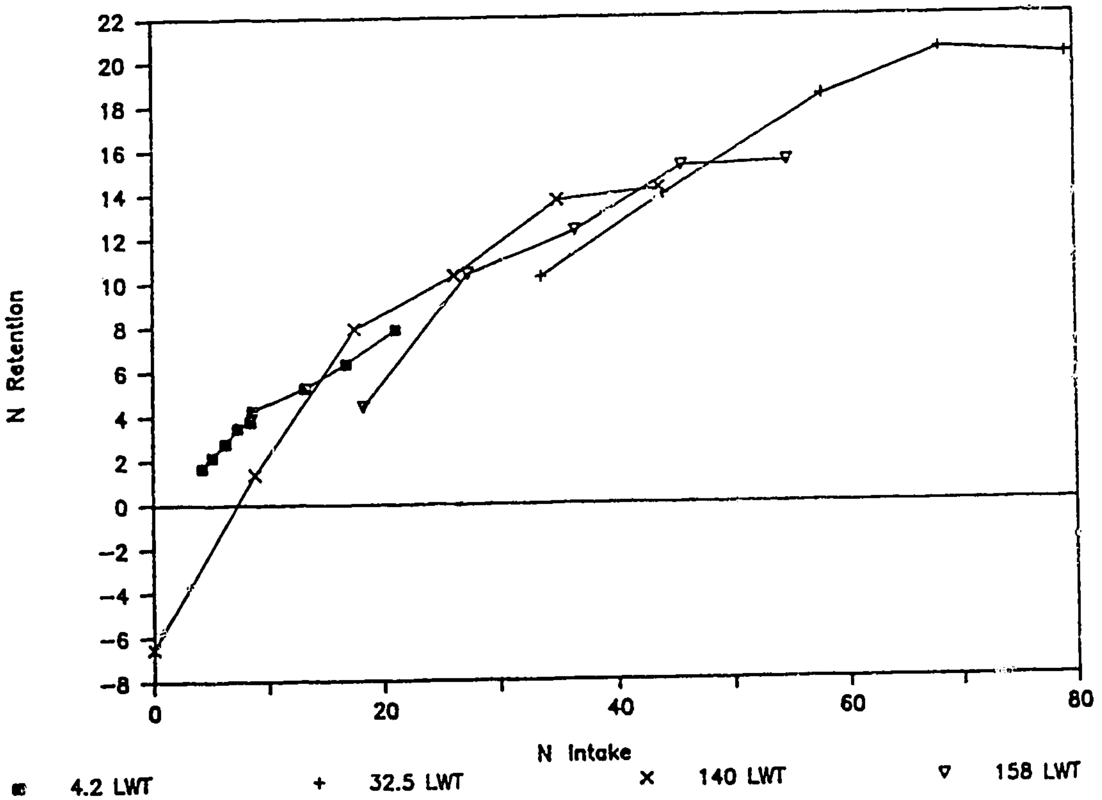


Figure III.2 Fit of overall function of nitrogen intake versus nitrogen retention for all live weights

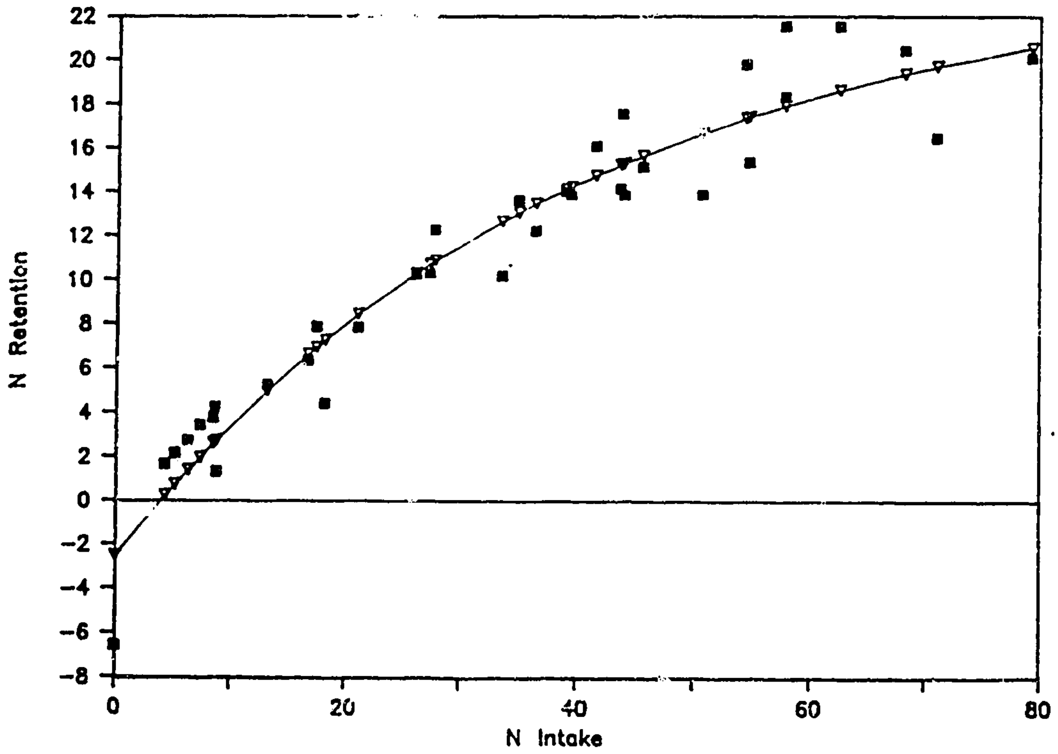
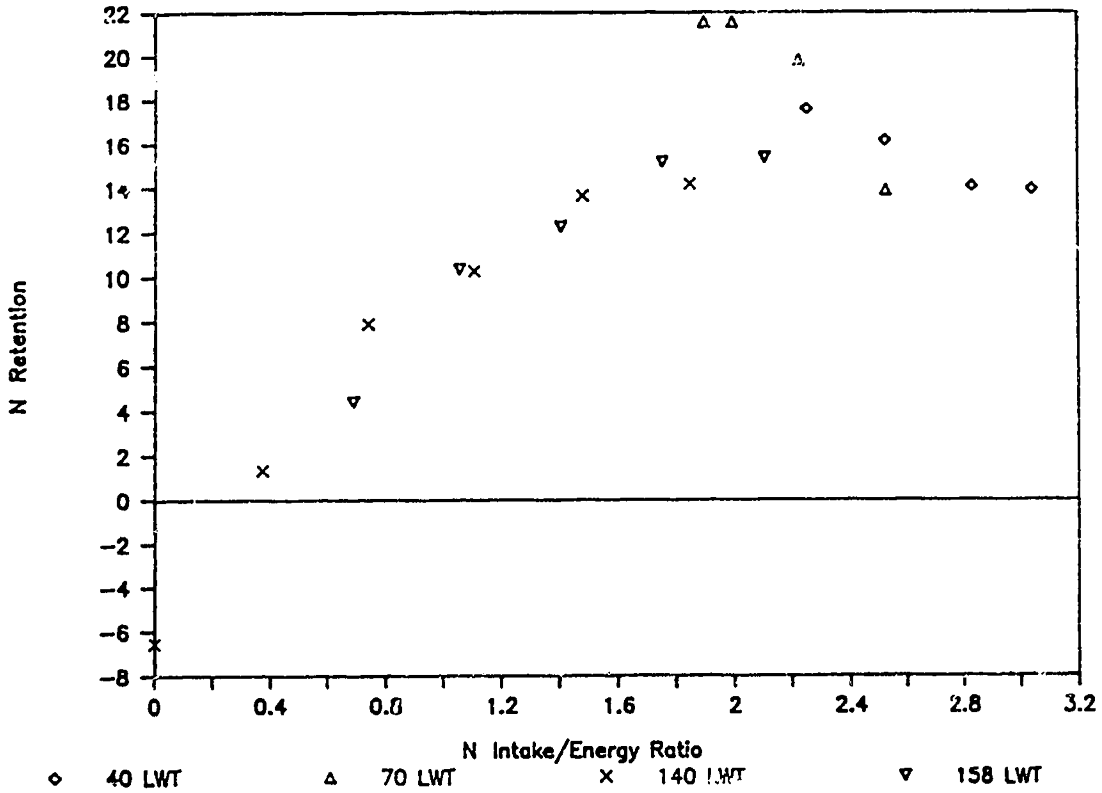


Figure III.3 Plot of observed nitrogen retention with ratio of nitrogen to energy intake for pigs of different live weight



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IV. MODELLING THE REPRODUCTIVE RESPONSE OF SOWS TO NUTRIENT INTAKE. PROTEIN ACCRETION, SUPPORT COSTS AND LIPID ACCRETION IN THE GROWING FEMALE PIG AND DRY SOW[1]

A. Introduction

Expressions of the nutrient requirements of farm animals have previously been based on two central assumptions; (i) the priorities for allocating ingested nutrients, after waste excretion has been accounted for, are to maintenance followed by tissue accretion, and (ii) energy intake is the variable determining productivity. This approach assumes that maintenance requirements for energy and protein are definitive (in terms of live weight, LWT; kg) and independent of productivity. Maintenance has been defined as "that level of feeding where the animals requirement for a nutrient, or for energy, for the normal continuance of vital processes within the body, is just met so that the net gain or loss of nutrient from the tissue of the animal as a whole is zero" (MAFF, 1975). Most expressions of maintenance requirements for energy and protein relate directly to LWT or metabolic weight, ($W^{0.75}$), (Carr et al., 1977; Maughan and Smith, 1984; Black et al., 1986), while a few are given relative to protein mass (Whittemore 1983; 1987; ARC, 1981; Tess et al., 1984b).

Much discussion has surrounded the derivation of so-called 'maintenance', particularly the metabolisable energy required to meet this state (MEm) in growing and producing animals. Concommitant efforts

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[1] A version of this paper has been submitted for publication: Walker, B., and Young, B.A. 1990. Livestock Production Science.

to estimate the relative efficiencies of use of energy for protein (k_p) and fat (k_f) deposition have produced a large number of estimates of these efficiencies in the literature; though there is general agreement on k_f, estimates of k_p are quite variable. Much of the confusion surrounding these biological concepts stems from mathematical interpretation of the correlated parameters (MEm, k_p and k_f) of the linear regression equation relating energy intake and energy retention, [illegible] e no absolute meaning (Webster, 1989). Problems inherent in [illegible] lationship are the possibility of non-linear responses (variable partial efficiency of gain) and high correlation of variables involved (Kielanowski, 1965). It has been well established that 'maintenance' comprises a large number of biochemical processes (Baldwin et al., 1986), some of which are known to vary with production level (Summers et al., 1986), hence it is unrealistic to suggest that 'maintenance' is constant with increasing feed intake, and production level.

There is an obvious parallelism between established energy based feeding systems (ARC, 1981) and the utilisation of protein, hence similar concepts exist for protein utilisation for 'maintenance' and production (Whittemore and Fawcett, 1974). The purpose of this chapter was to bring together the parallel processes of protein and energy utilisation for non-productive and productive processes, without the assumptions of 'fixed maintenance' inherent in previous models, into a predictive model of the growing female pig and dry sow.

B. Approach and Analyses

The processes considered in the partitioning and priorities of energy and protein in the pig are depicted in Figure IV.1. The concepts and hypotheses contained herein represent a different approach to that taken in energetics in the past, with regard to recognised limitations of existing systems. It is not intended at this stage, to refute or discount previous attempts concerning these issues in growing pigs (Whittemore and Fawcett, 1976; ARC, 1981; Black et al., 1986), but simply to examine an alternative approach and hypotheses, with the intention of extrapolation to the different physiological conditions of the reproducing sow.

Protein: Prediction of achievable rate of protein accretion (Pr;g/d) is determined by two things; the animal's inherent genetic capacity (Campbell, 1988), and the relationship of Pr to nitrogen and energy intakes (Ni;g/d and Ei;MJ/d, respectively) with live weight (LWT;kg) (Black, 1989; Black and Griffiths, 1975). Under conditions of optimum nutrient intake, assuming ideal environmental conditions, maximum Pr (Pr_{max}) can be achieved (Whittemore, 1983), and is determined by LWT, sex and strain (Siebrits et al., 1986). Pr_{max} was determined from data on female pigs of Large White, Landrace and Dutch Landrace breed combinations (Walker et al., 1990) over the live weight range 25 to 165 kg. Fractional rates of accretion (Pr/LWT;g/d/kg) were linearly related to live weight when expressed logarithmically, giving a skew-parabolic form to the relationship between Pr_{max} (Nr_{max} x 6.25) and LWT (equation IV.1). In contrast to the functions derived by Whittemore et al. (1988), and Black et al. (1986), for growing pigs, Pr_{max} does not reach zero at a discrete "mature" LWT, instead the function tends to zero after about

350kg LWT, thereby allowing protein accretion in heavier sows. The necessity for this property becomes evident in the pregnant sow, and details on its derivation are provided in Walker et al., (1990).

$$Nr_{max} = LWT\ e^{(-0.324-0.0136\ LWT)} \qquad \ldots\ IV.1.$$

At dietary intakes of protein or energy below that required for Pr_{max}, the relationship between Pr and nitrogen and energy intake (Ni;g/d and Ei;MJ/d, respectively) has been described as linear-plateau (Campbell et al., 1983; Campbell and Taverner, 1989). Previously the response to Ni and Ei has been considered to be composed of two separate and independent phases (Black and Griffiths, 1975), each of which vary with LWT. This approach was considered inappropriate for the present analysis since it does not take sufficient account of the important interaction of available nitrogen (Na) and energy (Ea) in determining Pr, or the possibility of curvilinear behaviour. Pr below Pr_{max} was therefore calculated using an equation accounting for all three variables (Na, Ea and LWT) and their interactions (Equation IV.2). Protein accretion in response to nitrogen and energy intake is considered the prime driving force in the growing female pig and dry sow, though it can only be achieved once the requirements for support processes (Ps_T;g/d) have been met.

$$Nr = -2.56 - 0.0107\ LWT + 0.624\ Ea + 0.426\ Na + 0.0011\ LWT.Na - 0.012\ Na.Ea \qquad \ldots\ IV.2.$$

In contrast to other models (Whittemore and Fawcett, 1976; Maughan et al., 1987), protein accretion in the present scheme is determined simultaneously with the derivation of protein requirements for 'maintenance'. By virtue of the derivation of Pr response from nitrogen balance data, Ps_T can be estimated (Ns_T x 6.25) at any particular rate of protein accretion, by rearrangement of Equation IV.2, and is assumed to be the Ni required for zero Nr (Equation IV.3). Ps_T therefore includes protein utilised in so called 'maintenance' (resynthesis and endogenous losses) and, in the growing pig, extra protein costs associated with the increased productive state above 'maintenance', without the requirement to calculate each separately. In this instance, available protein (Pa;g/d), was considered to be digestible protein, and the inefficiency of Pr (the slope of the response; dPr/dPi) accounts for the sum of the processes of digestibility, absorption, availability and metabolism (Low, 1982). The equation therefore allows the efficiency of protein use for Pr to vary with level of intake and live weight, in agreement with Whittemore and Fawcett (1974).

It is evident from Equation IV.3 that Ns_T varies with LWT and Ea, but the expression is limited since it does not account for extra Ns_T resulting from increased Na and concommitant protein turnover. Estimates of the efficiency of use of protein and energy for protein accretion (a_p and k_p, respectively), can alternatively be derived from the respective partial derivatives of Equation IV.2 ($\delta Nr/\delta Na$ and $\delta Nr/\delta Ea$). The equation presented here also has the advantage of allowing negative rates of accretion where Ea and/or Na are limiting. It does not, however, provide an estimate of total protein synthesis.

$$Ns_T = (2.56 + 0.0107\ LWT - 0.624\ Ea) / (0.426 + 0.0011\ LWT - 0.012\ Ea) \quad .... \text{IV.3.}$$

Separate efficiencies of protein use for support processes and protein accretion were not required since both are inherent in the derived equation (IV.2). In addition it is generally not possible, nor meaningful, to split support costs between 'maintenance' and the extra costs associated with productivity, since increased protein accretion leads to increases in ancillary energy expenditures, independent of costs for concomitant protein resynthesis (Summers et al., 1986).

Energy: In accordance with the terminology used in partitioning available protein, here onwards, what has previously been called 'maintenance' will now be referred to as energy support costs. Total energy support costs (Es_T;MJ/d) are taken to be the sum of energy used for vital processes and extra energy costs associated with the productive state. The increased energy expenditure of growing pigs relative to 'maintenance' may arguably be considered as reduced efficiency of tissue accretion (Whittemore and Fawcett, 1976) or, as in the present scheme, part of the machinery costs necessary to support the animal in a productive state, and therefore be considered as an increase in support costs. These extra energy costs are not only associated with increased total protein synthesis, but also increased energy and protein utilisation in the visceral organs, ion pumping and substrate cycling (Summers et al., 1986). Whether 'maintenance' or efficiency of protein accretion varies will be a consequence of the assumptions used in their calculation, since 'maintenance', and the efficiencies of energy use for protein and lipid accretion are not independent. Similarly the reported decline in efficiency of protein accretion with LWT (Whittemore and Fawcett, 1976) may be attributed to the costs (protein requirements) of maintaining a larger protein mass, rather than a change in the basic biochemical processes directly associated with protein retention ie. a larger proportion of total protein synthesis is required to meet endogenous losses and resynthesis.

Available energy (Ea;MJ/d) is that energy available for support and productive processes in the animal, after fecal and urinary losses and assimilation costs have been accounted for. It is assumed that, of the digestible energy intake (DEi), 96 % is metabolisable (MEi;MJ/d) in the pig. Having determined the rate of protein accretion (for given Ea and Na), the energy content of protein gain and the energy cost of net protein accretion were accounted for before energy for support processes and fat deposition could be established. The energy contents per gram of protein and fat are well established and may be reasonably taken to be 23.6 and 39.8 kJ/g, respectively (ARC, 1981). The biochemical estimate of the energy cost of protein synthesis has been calculated to be 7.3 kJ/g protein synthesised, but net accretion costs estimated from slaughter and balance trials (Kielanowski, 1965; Close, 1978; Tess et al., 1984a; Whittemore, 1987) are much greater and more variable; 76 to 37 kJ/g (k_p of 0.31 to 0.63). A constant value for energy cost of protein accretion, at the lowest end of the range of swine values and similar to values reported in rats (Pullar and Webster, 1977) has been assumed (53.5 kJ/g protein, k_p=0.44), regardless of LWT and feeding level of the animal. Since net accretion measured in these experiments includes the result of increased turnover, assuming the lowest value will result in the extra costs of increased productivity or turnover being attributed to energy support costs. This contrasts with the approach of Whittemore and Fawcett (1976) where maintenance energy is corrected for the cost of protein synthesis, and the cost of protein accretion is variable. Literature estimates of the efficiency of energy use for lipid accretion and the energy cost associated with it encompass a fairly narrow range, hence a value of 54.6 kJ/g (k_f=0.73) was utilised.

Data: In order to establish the energetics of support costs (Es_T) data containing measured protein and lipid accretion rates were gathered for various live weights of female pigs, on varying levels of known protein and energy intake (Table IV.1.). The efficiencies indicated above were used to calculate energy costs and content of protein and lipid accreted. The remaining energy support costs, were then analysed in relation to LWT, nutrient intake (available), relative intake (Pi/LWT;g/kg/d and Ei/LWT;g/kg/d), body protein content (P_b;kg), and rate of protein accretion. Support costs were also split between 'background' costs (assumed constant) and production costs, using the expression $aLWT^{0.75}$. Goodness of fit was determined on the basis of linear and non-linear r^2, residual sum of squares (RSS) and significance of coefficients, using SAS (SAS Inc., Cary, NC). Non-linear r^2 values are generally high when applied across numbers of data sets from different sources, due to the wide spread of data hence RSS will be a better indicator of fit, along with application of equations to new data. All standard errors reported are the asymptotic standard errors for non-linear regression (SAS Inc).

Once energy costs of support processes were established, the rate of lipid accretion (Lr;g/d) was calculated as a residual, following calculation of Pr and Es_T from the derived equations. Live weight gain (LWG) was estimated from calculated Pr and Lr on the basis of Whittemore and Fawcett's (1974) equation (LWG = 1.082 (4.0 Pr + 1.1 Lr)), and compared to measured gains or gain estimated from given Pr and Lr.

B. Results

The commonly used simple linear regressions revealed weak correlations between lipid accretion or energy retention with energy intake ($r^2=0.735$), and good correlation between protein intake and protein excretion ($r^2=0.964$). Total calculated energy support costs (Es_T) increased with LWT, but variation existed between animals within LWT groups; support costs increased with increasing intakes of protein and energy, younger animals having a greater relative response to increased feed intake than heavier pigs (Figure IV.2). It is obvious from this observation that if 'maintenance' were calculated on the basis of LWT alone, estimates of k_p and k_f would vary with feed intake. The average Es_T for all animals was 0.465 MJME/kg $LWT^{0.75}$ which is similar to previous estimates of 'maintenance' in swine (Verstegen et al., 1987). The average of the values for animals given the lowest feed intake in each LWT group was 0.384 MJ/kg $LWT^{0.75}$, approximately 17% lower than above. When expressed on the basis of relative intake (Pi/LWT and Ei/LWT) Es_T decreased exponentially, and support costs per metabolic weight increased sigmoidally with relative intake. The logarithmic function of this relationship showed separate responses for different LWT groups. Es_T per kg LWT decreased exponentially with LWT, however, Es_T per kg body protein was relatively constant for pigs between 20 and 154 kg LWT.

Es_T was highly correlated (r^2=0.945) with body protein content (P_b; kg), (equation IV.4, Figure IV.3), though the 'y' coefficient was not significant; both coefficients were significant in the allometric relationship (equation IV.5, r^2=0.989). Equation IV.5 is similar to that developed by Whittemore (1983) but, as indicated by Black et al (1986) does not account for the effects of growth rate, ie. increased support costs of the increased productive state in rapidly growing animals.

$$Es_T = 1.6098\ (\pm 1.15) + 0.6551\ (\pm 0.037)\ P_b \qquad \ldots.\ \text{IV.4.}$$

$$Es_T = 1.4616\ (\pm 0.313)\ P_b^{0.7663\ (\pm 0.076)} \qquad \ldots.\ \text{IV.5.}$$

Additional variation in Es_T could be accounted for by equations relating combinations of the effects of P_b, Pr, and relative protein intake (Pi/LWT; g/d/kg). Equation IV.6 was considered to be the most appropriate functional form for all female pigs since the RSS was lowest, both coefficients for P_b were significant and the equation showed good predictive capacity of actual verses calculated Es_T (r^2=0.944). In young pigs estimation of Es_T was improved slightly when predicted (r^2=0.991) on the basis of a non-linear regression of the allometric P_b function with the inclusion of Pr/LWT (g/d/kg) and Pi/LWT (g/d/kg).

$$Es_T = 1.136\ (\pm 0.451)\ P_b^{0.849\ (\pm 0.0.134)} + 0.0702\ (\pm 0.093)\ Pr/LWT^{0.75}$$

$$(r^2=0.989,\ RSS=24.9) \qquad \ldots\ IV.6.$$

Lipid accretion, calculated after estimating Es_T (equation IV.6) and Pr (equation IV.2) on the basis of the assumptions stated herein, was compared with measured lipid deposition rates (Table IV.2). Pr was curvilinear with increasing Pi but Lr continued to increase linearly with increasing Ei. Predicted versus observed rates of lipid deposition were close ($r^2=0.972$) and followed the same types of response to feed intake. Lipid to protein ratios in live weight gain varied between 0.6 and 3.9, which is in accordance with the observed range (0.3 to 3.7) calculated from the data in table IV.1. With increasing feed intake, particularly Pi, Pr increased relative to Lr. Predicted Pr for dry sows was slightly greater than the measured rates of Pr, possibly as a consequence of the derived equation (IV.2) being parameterised on the basis of data including values from older sows which achieved higher Nr than the sows of Close et al., (1985). Rates of live weight gain (g/d) calculated from estimates of Pr and Lr were close to those calculated by the same expression from given Pr and Lr, and were also close to measured values, where these were available (Table IV.2). With increasing feed intake at higher LWT, live weight gain became curvilinear. Variation in the ratio of protein to water assumed for lean tissue with age and LWT may account for some of the discrepancies between observed and calculated LWG.

Application of the model to data not used in the parameterisation of model equations showed good agreement between measured and predicted rates of protein accretion (Table IV.3). Rates of protein accretion derived from balance trials tended to be higher than those derived by slaughter trials and predicted by the model. Conversely, rates of accretion derived from carcass composition do not fully reflect the changes in accretion rates experienced over wide ranges in live weight.

D. Discussion

Assuming that the unit energy costs of protein and lipid accretion are constant (fixed at the lowest literature estimates), and independent of production level, designates the extra cost of increased production to support costs and therefore leads to variation in estimated energy support costs with LWT, and level of energy and nitrogen intake. That the accretion of any one unit of protein or lipid should not cost any more, or less, than any other unit would appear to be reasonable in light of the fact that each increment should involve the same biosynthetic processes. Total synthesis and breakdown of protein, as well as endogenous losses, vary with a number of factors, including level of intake, environment, and disease, and estimates of these parameters in pigs do not reconcile well with observations from slaughter or balance trials. It would therefore be difficult to estimate the variation in the individual components of accretion, the energy costs of each and additional ancillary energy costs. There is however, some evidence to suggest that the unit cost of breakdown and formation of peptide linkages may be variable, hence the energetic efficiency of bond synthesis may not be fixed (Summers et al., 1986).

Conversely, if so called 'maintenance' or support costs were constant, regardless of level of production, this would result in variation in the estimates of k_p and k_f. Estimation of k_p would appear to be more sensitive to variation in the calculation of maintenance (Tess et al., 1984a) which could account for the range of values of k_p reported in the literature. This observation may be a result of the large increase in support costs associated with increased protein accretion relative to lipid, and hence if these are not included in the estimate of 'maintenance', k_p would diminish.

In addition, it is possible to calculate theoretical costs of protein or lipid accretion on the basis of the biochemical pathways involved (Baldwin, 1980). Practical estimates of the energetic costs of protein and lipid accretion are generally higher in growing animals than the theoretically calculated estimates, probably as a consequence of being confounded by the increased Es_T necessary to support an animal in a productive state.

Detailed discussion concerning which empirical approach is most appropriate is futile at this stage, in light of our inability to accurately distinguish between changes occuring in the various net energetic processes being considered. Measurement and modelling at a more mechanistic or biochemical process level may overcome some of these problems. However, consideration of some circumstantial evidence lends support to the present interpretations. Measurements of changes in individual components of 'maintenance' with increased feeding level, eg. substrate cycling, ion pumping and service functions (Summers et al., 1986; Baldwin et al., 1980; Gill et al., 1990) would indicate that a large proportion of these extra costs, in the producing animal, may be considered under the auspices of extra support costs associated with production. The fact that small pigs showed a greater response in Es_T to changes in feed intake is largely a consequence of the fact that intake per kg LWT was much greater, hence processing costs make up a much larger component of total support costs. In the larger animal relative feed intake is lower and relative productivity (Pr/kg LWT) is reduced, hence turnover of body protein mass accounts for a large proportion of Es_T. This is in agreement with the suggestions of a number of other authors who have related maintenance or fasting heat production to components of body composition (Webster, 1981; Whittemore, 1983; Tess et al., 1984b). In addition, protein turnover and associated costs, particularly in the visceral organs, have been shown to account for a substantial proportion of basal heat production (Baldwin et al., 1986; Gill et al., 1990).

Including both body protein content and rate of protein accretion in the prediction of support costs (Equation IV.6) takes consideration of both the previous and present nutritional status of the animal, as an indirect effect of P_b and Pr, respectively. Black et al., (1986) chose to use the concept of a lag in 'maintenance' following an abrupt change in feed intake, since it has been suggested that 'maintenance' does not change immediately with changes in feed intake (Turner and Taylor, 1983). The equation used here (Equation IV.6) accounts for change in support costs associated with change in protein accretion as a result of changes in Ea and Pa, but it is not yet evident which components of the Es_T take time to adjust to a new level of intake. In addition, the energy costs of 'maintenance' and protein synthesis are obviously not independent (Pullar and Webster, 1974; Kielanowski, 1975), and would therefore be difficult to separate.

The efficiency of energy use for support processes is already inherent in the Equation (IV.6), which is an advantage over the classical 'k_m' which is generally defined between fasting, and 'maintenance' (ARC, 1981) and neither fasting or maintenance are normal conditions under practical feeding situations. Prediction of lipid deposition on the basis of last priority for available energy did not give erroneous predictions or unreasonable ratios of lipid to protein accretions, indicating that it may not be necessary to fix this ratio within certain limits, as suggested by Whittemore and Fawcett (1976). However, the present method used for calculating lipid accretion would not allow for prediction of ad libitum feed intake, since the desired level of lipid deposition would need to be known in advance. This becomes important when considering the lactating sow (Walker and Young, 1990c).

The concepts unique to the approach of the model described here are; the use of protein accretion as a primary driving force, the prediction of Pr on the basis of an interactive equation involving Ea, Pa and LWT, and the combination of production costs with background costs into total support costs. The validity of these concepts under conditions of gestation and lactation are tested separately in chapters V and VI in order to address issues specific to these physiological conditions eg. estimation of support costs and protein accretion at low available nutrient intakes.

In conclusion, the development of equations for the growing female pig and dry sow, parameterised with data encompassing a wide range of live weights and feed intakes, and the development of equations focusing on protein accretion as a driving force in body composition changes provided good predictions of animal response. The equations developed here provided an alternative approach to the problems of 'maintenance' and energetic efficiencies, and the derivation of protein accretion, for use in the prediction of response to nutrient input in the reproducing sow.

Table IV.1. Data used in the calculation of energy cost of support processes.

Source	Live weight range (kg)	† Data given
Campbell & Dunkin, 1983	1.8 - 6.5	LWG,Pr,Lr,P_b,L_b
Campbell et al., 1983	20 - 45	LWG,Pr,Lr,L_b
Campbell et al., 1985	48 - 90	LWG,Pr,Lr,P_b,L_b
Close et al., 1985	115 - 154	Erp,Erl,Nr,HP
Shields & Mahon, 1983	118 - 144	P_b,L_b

† Notation: Daily live weight gain (LWG); retained nitrogen (Nr), retained protein (Pr) and retained lipid (Lr); body protein (P_b) and lipid (L_b) mass; energy retained in protein (Erp) and lipid (Erl); and heat production (HP).

Table IV.2. Measured and predicted nitrogen and lipid accretion rates and daily live weight gains in female pigs from birth to 154 kg live weight.

Mid range	Intake		Nitrogen accretion		Lipid accretion		Live weight gain	
Liveweight (kg)	Nitrogen (g/d)	Energy (MJ/d)	Measured (g/d)	Predicted (g/d)	Measured (g/d)	Predicted (g/d)	Measured‡ (g/d)	Predicted (g/d)
4.2	8.5	3.4	3.8	2.1	7.2	13.9	105	80
4.2	13.2	5.3	5.3	4.8	21.8	28.5	182	185
4.2	16.8	6.7	6.4	6.7	35.3	40.3	240	262
4.2	21.1	8.5	7.8	8.8	53.2	54.8	296	350
32.5	33.6	14.5	10.2	11.8	73.0	58.3	409	436
32.5	44.0	20.3	13.9	15.4	136.0	107.7	540	562
32.5	57.8	24.9	18.4	17.9	192.0	159.8	699	673
32.5	68.2	29.4	20.5	18.8	228.0	225.2	780	779
32.5	79.3	34.2	20.1	18.4	286.0	286.5	832	806
69	49.5	23.0	10.4	14.5	125.0	123.3	357	578
69	59.2	27.5	13.5	16.2	208.0	192.3	541	672
69	71.0	33.0	16.5	17.0	279.0	282.9	656	783
69	80.7	37.5	16.3	16.5	322.0	365.5	740	859
69	84.4	39.2	15.8	16.0	371.0	400.7	784	865
115	40.0	20.2	6.7	10.6	98.7	57.2	† 305	348
129	40.6	20.7	6.1	10.0	78.3	48.2	† 266	323
136	41.4	20.5	7.2	9.8	43.4	32.2	† 259	300
132	57.6	28.0	10.9	14.2	169.0	158.9	† 506	556
154	57.7	28.5	10.0	13.3	126.0	147.7	† 434	519
131	40.8	23.0	7.3	10.4	89.5	80.7	456	386

† LWG calculated on the basis of P:Water ratio in given data, using equation of Whittemore and Fawcett (1974)

‡ LWG calculated from calculated Pr and Lr using Whittemore and Fawcett (1974)

Table IV.3. Measured and predicted rates of protein and lipid accretion for data not used in parameterisation of model.

Live weight Range (kg) Measured	Live weight Range (kg) Predicted	Daily intake Energy (MJDE)	Daily intake Protein (gCP)	Protein accretion Measured (g/d)	Protein accretion Predicted (g/d)	Lipid accretion Measured (g/d)	Lipid accretion Predicted (g/d)
†Zhang et al., (1986):							
5-22	5-22	10.8	141	63.7	51.5	51.8	66.4
5-22	5-22	10.3	177	70.6	57.7	39.9	53.0
5-22	5-22	10.1	134	70.0	49.2	53.7	57.9
5-22	5-22	10.3	178	71.2	57.8	40.4	52.3
Metz et al., (1984):							
25-105	25-105	incremental		99†(127‡)	85.8	166.0	173.2
	35	13.2	175		56.9		81.4
	65	27.0	359		89.6		155.6
	105	36.0	477		97.0		275.8
‡Metz et al., (1980):							
43	35-43	17.1	339	130.6	95.5	-	91.2
42	35-42	13.7	277	118.1	79.5	-	56.4
69	60-69	28.3	451	130.6	107.1	-	197.9
65	60-65	22.6	361	110.6	93.9	-	116.9
99	60-100	31.1	537	126.8	119.8	-	193.3
88	60-100	24.8	431	112.5	105.0	-	107.0

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† Measured by carcass evaluation

‡ Measured by balance trials at various periods through growth

Table IV.4. Legend to Figure IV.1. and symbols used in text of papers in this series.

Ei	energy intake
Ni	nitrogen intake
Ea	available energy
Es_T	energy support costs
Fe	fecal energy
Ue	urinary energy
Lr	rate of lipid accretion
Lr_u	lipid accretion in utero
Lr_m	lipid accretion, maternal
L_{milk}	lipid and lactosein milk (L_{sl})
E_{milk}	energy secreted in milk
L_b	body lipid content
A_b	body ash content
Ar_m	ash retention, maternal
W_{fe}	weight of fetuses
H_{fe}	water content of fetuses
W_{fm}	weight of fluid and membranes
H_{fe}	water in fluid and membranes
W_{ut}	weight of empty uterus
H_{ut}	water in of empty uterus
W_u	weight of total gravid uterus
H_u	water in total gravid uterus
MY	daily milk yield
LS	litter size
LWT	live weight
Wi	weight at day 1 of lactation
t_d	day when animal is dry
k_p	efficiency of energy use for Pr_m
k_f	efficiency of energy use for Lr_m
k_u	efficiency of energy use for energy accretion in utero
Pig_{gain}	daily gain of piglet
Pi	protein intake
Na	nitrogen available
Pa	available protein
Ps_T	protein support costs
Pf	fecal protein
Up	urinary protein
Pr	rate of protein accretion
Pr_u	protein accretion in utero
Pr_m	protein accretion, maternal
P_{milk}	protein secretion in milk(P_{sl})
DM_{milk}	dry matter production as milk
P_b	body protein content
H_b	body water content
Hr_m	water retention, maternal
P_{fe}	protein in the fetuses
L_{fe}	lipid content in fetuses
P_{fm}	protein in fluid and membranes
L_{fm}	lipid in fluid and membranes
P_{ut}	protein in empty uterus
L_{ut}	lipid in empty uterus
P_u	protein in total gravid uterus
L_u	lipid in total gravid uterus
MI	milk intake per piglet
Pr_{max}	maximal protein accretion
LWG	live weight gain
Gg	total gestation weight gain
t_g	day of gestation or t_l lactation
a_p	efficiency of protein use for Pr_m
a_u	efficiency of protein use for Pr_u

NB: $P = N \times 6.25$

Figure IV.1 The mechanisms of nutrient partitioning in the pig

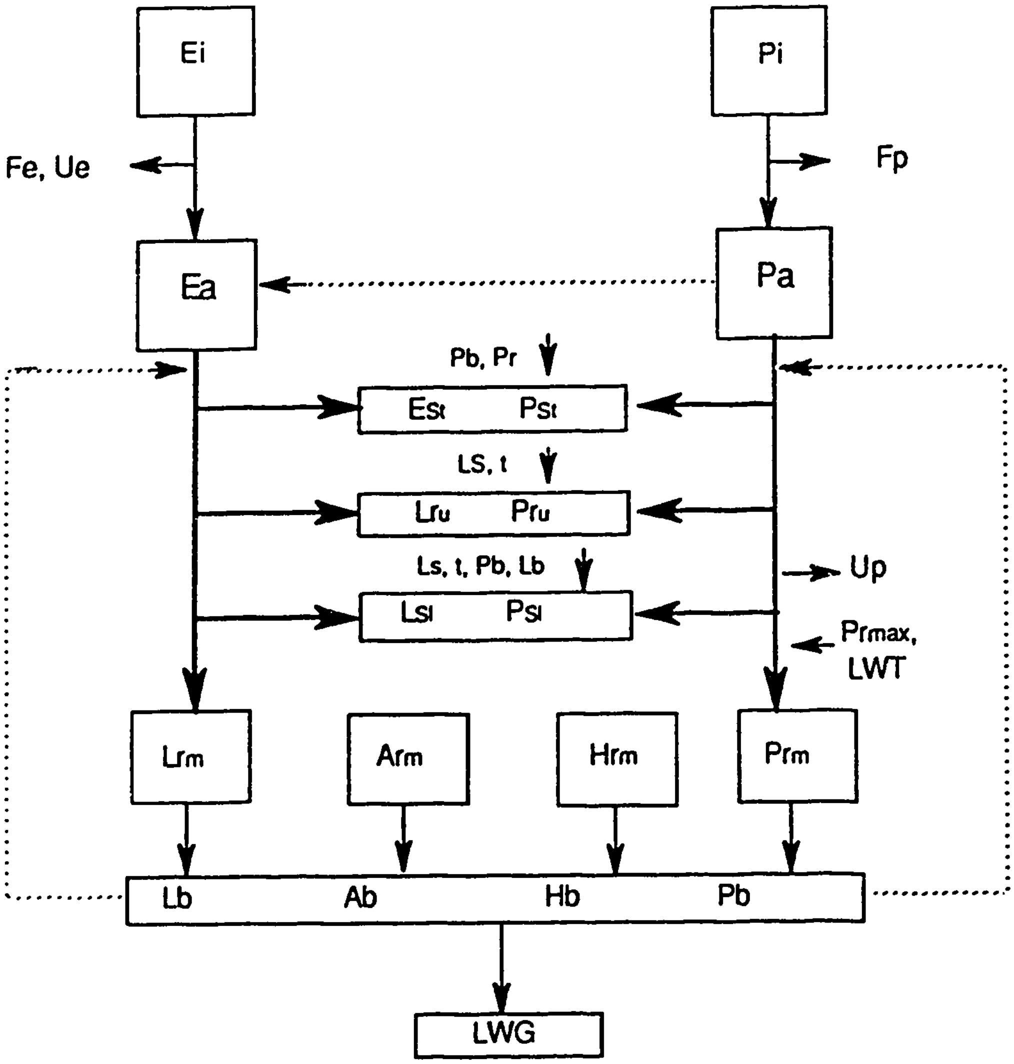


Figure IV.2 Relationship between calculated energy support costs and live weight

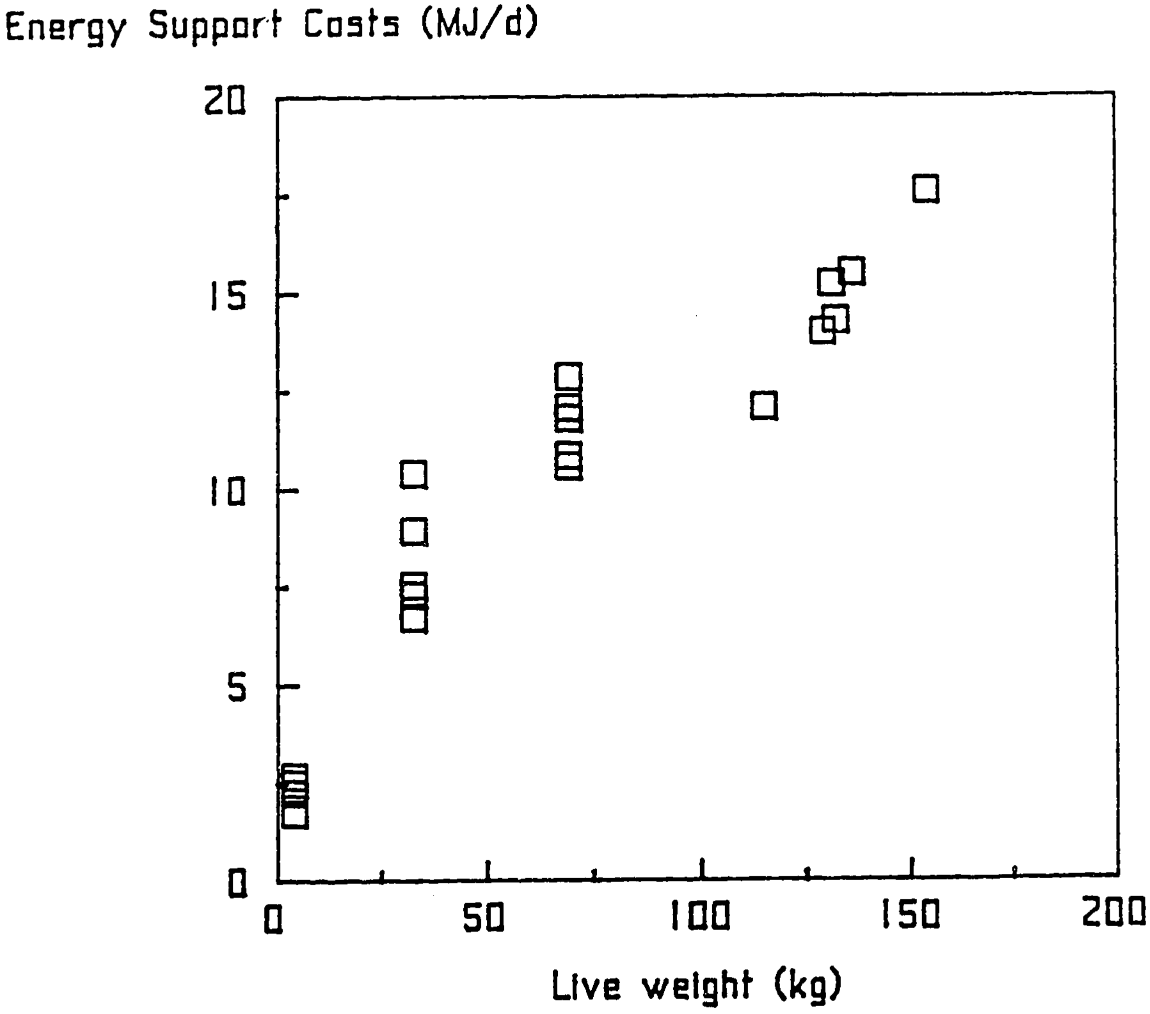
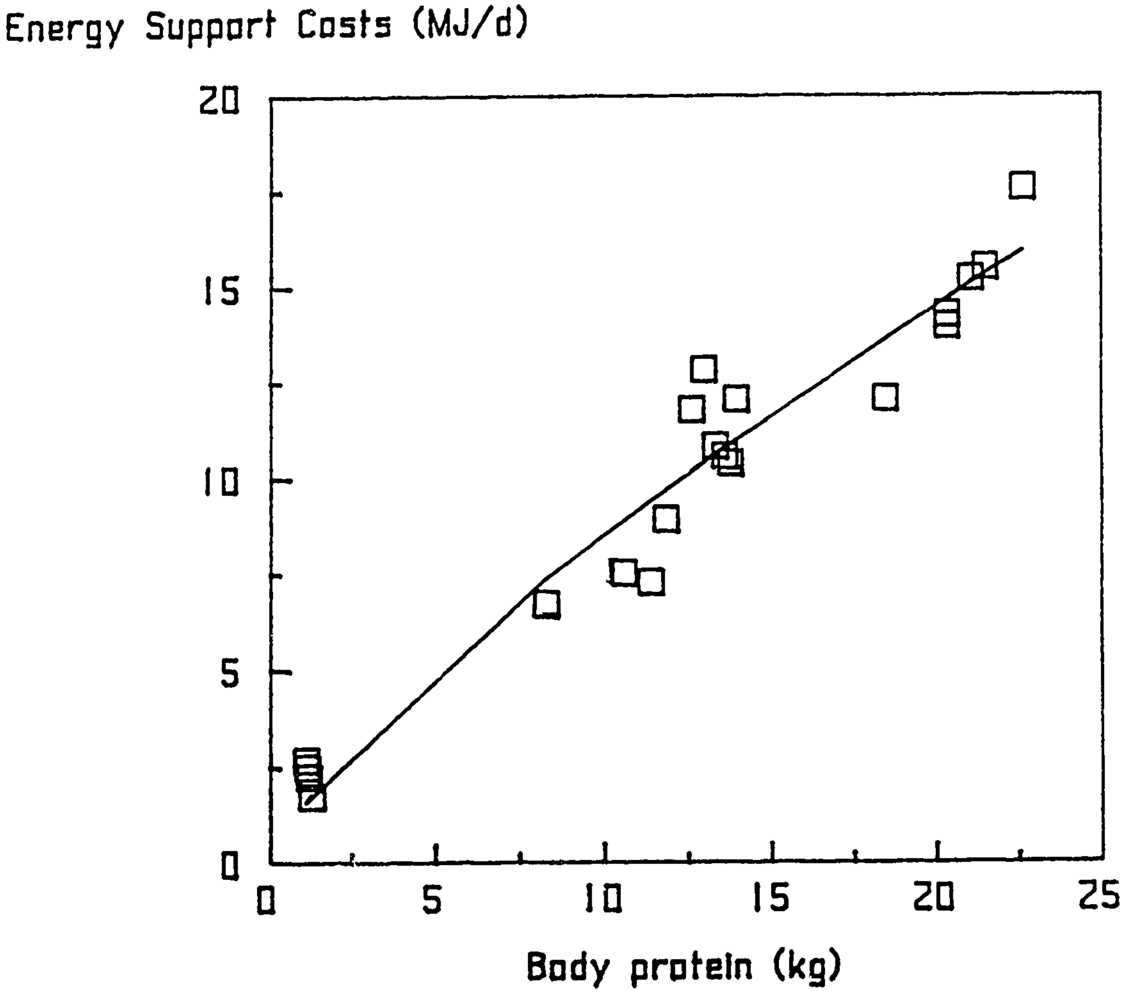


Figure IV.3 Relationship between actual energy support costs (□) and predicted energy support costs (___) with body protein



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V. MODELLING THE REPRODUCTIVE RESPONSE OF SOWS TO NUTRIENT INTAKE. UTERINE DEVELOPMENT AND BODY COMPOSITION DURING PREGNANCY[1]

A. Introduction

The nutrient demands of pregnancy are relatively small through the first two trimesters, and even in late gestation the demands of the fetus are small relative to the total nutritional costs of supporting the sow. Nevertheless, much controversy has arisen, from energy balance studies, concerning the concepts of pregnancy anabolism, increased estimates of 'maintenance' costs and reduced efficiency of reproductive tissue accretion. It is important to establish maternal tissue changes during gestation, in conjunction with the subsequent lactation period, since the status of maternal body reserves influences the ability of the sow to rebreed (Mullen, et al., 1989; Whittemore et al., 1988). From early pregnancy the fetus and accompanying uterine developments take priority over maternal tissue accretion, and in late pregnancy they can have a large influence on maternal tissues. This is particularly evident for sows on low nutrient intakes, where body lipid mobilisation may occur to support fetal development (Walach-Janiak, et al., 1986).

Current recommendations concerning sow nutrition advise that maternal lipid reserves be at least maintained during pregnancy (Verstegen et al., 1987) in anticipation of the mobilisation occuring during lactation, and to maximise piglet birth weight (ARC, 1981).

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[1] A version of this chapter has been submitted for publication: Walker, B., and Young, B.A. 1990. Livestock Production Science.

Support for these recommendations comes from the low negative correlation between maternal backfat thickness and the interval from weaning to return to estrous (Whittemore et al., 1988).

Maternal nutrition does not appear to influence uterine development unless intake is severely restricted (Close et al., 1984; Verstegen et al., 1987). Total uterine growth (fetuses, fluids, membranes and the uterus) can be reasonably predicted on the basis of exponential growth (Black et al., 1986). However, the reported efficiency of energy use for total uterine growth varies widely, ranging from 0.21 (de Lange et al., 1980) to 0.8 (ARC, 1981). Possible reasons for this variance include the use of assumed 'maintenance' requirements and nutrient utilisation efficiencies, and reliance on measures of live weight change rather than body composition changes. In a number of species, pregnancy is known to be associated with body hydration (Degen and Young, 1980; Shields et al., 1984) and hence protein and lipid accretion may be overestimated when based on live weight alone, or body water measurements. Furthermore, conditions of pregnancy anabolism may confound estimates of energy utilisation (Salmon-Legagneur and Rerat, 1962; Elsley et al., 1966; Lodge, 1972).

The purpose of this chapter was to formulate equations to represent the components of uterine development in the sow, and in conjunction with equations developed in the the previous chapter (Walker and Young, 1990a), to examine the compositional changes occuring in maternal tissue through pregnancy. Model formulation would then allow for evaluation of anabolism, hydration, maintenance and nutrient utilisation efficiencies associated with pregnancy.

B. Approach and Analyses

Data representing weight and compositional changes over the progression of gestation were collated for fetuses, fluid and membranes, and uterine development (Table V.1). The data included variations in maternal energy and protein intake (Ei;MJ/d and Pi;g/d) and sow weight (LWT;kg). These were used as parameters in the analyses, where significant, and equations were developed for protein, water, fat content and wet weight of each component of uterine growth. Equations were fitted using SAS (SAS Inc., Cary. NC), and evaluated on the basis of non linear regression coefficients (r^2), residual sum of squares (RSS) and significance of parameter coefficients.

Development of the gravid uterus: Total uterine weight, protein, water and lipid contents were taken to be the sum of all the components on any particular day of gestation, and daily rates of accretion were the differential forms.

Development of mammary tissue: Few data were available for weight and composition of mammary tissue during development in late gestation and through lactation (Moustgaard, 1962; Shields and Mahan, 1983; Noblet et al., 1985). This imposed limitations on the derivation of any complex functions, and additional variation would likely be introduced in separating the mammary tissue from the sow body.

Maternal tissue changes: Once suitable equations had been established for development of the components of the total gravid uterus, varying efficiencies of energy use for total uterine protein and lipid accretion, and protein for protein accretion, were evaluated. Metabolisable energy and digestible protein intake were used to support uterine protein and lipid accretion primarily. Available protein (Pa;g) and energy (Ea;MJ) (the nutrients available following allocations to the uterus) were then used to determine maternal protein accretion (Pr;g/d), protein and energy support costs (Ps_T;g and Es_T;MJ) and maternal lipid accretion (Lr;g/d), in that order as described in Figure IV.1., of the previous chapter (Walker and Young, 1990a). In the calculation of energy support costs of the pregnant sow, Pr was taken to be the sum of Pr in maternal tissue and Pr in utero. It was then possible to examine maternal composition changes over gestation, and the possibilities of variations in maternal Pr efficiency, support costs and water to protein ratios (H:P) with pregnancy.

C. Results

<u>Fetal growth:</u> The equation developed to represent fetal weight with day of gestation (t_g) included both litter size (LS) and nutrition (Ei and Pi) as limiting factors to maximal fetal weight on any particular day (W_{fe};g). This resulted in a sigmoidal shape (Equation V.1, Table V.2; r^2=0.995, RSS=60,274) when these limits were applied as compared to the unlimited exponential form commonly observed for weight change over gestation in the fetus (litter) and gravid uterus (uterus plus fetuses, fluid and membranes) in a number of species (Giesler and Jones, 1979; Pomeroy, 1960; Moustgaard, 1962). The equation predicts lower fetal weights for gilts as a direct consequence of their smaller litter size, similarly for thin sows in poor condition.

Fetal protein weight (P_{fe};g) was best described by a double exponential (Gompertz) relative to fetal weight (Equation V.2, Table

V.2; r^2=0.986, RSS=183,728). Though variation still remained for P_{fe} at specific W_{fe}, it was not consistently related to maternal feed intake, as has been described in the rat (Afsher and Grimble, 1983). Weight of water in the fetus (H_{fe};g) increased linearly with fetal weight (Equation V.3, Table V.2; r^2=0.999) and ranged between 90 and 80% of W_{fe}. The ash content of the fetuses (A_{fe};g) was assumed to increase linearly as a constant fraction of W_{fe} (Equation V.4, Table V.2; r^2=0.949) and fetal lipid mass (L_{fe};g) was calculated by difference, giving a range of 1.6 to 5.12% of W_{fe} over gestation. These estimates of lipid content are a little higher than found in sheep (Rattray et al., 1974) but may be considered to include up to about 2% of W_{fe} as glycogen.

Predicted changes in weights of fetal components over gestation are illustrated in Figure V.1. The daily rates of accretion of protein, lipid or water can be derived by differentiation of the above equations with respect to time.

Fluid and membrane development: Fluid and membrane weights (W_{fm};g) during gestation were modelled together in relation to fetal growth (Equation V.5, Table V.2; r^2=0.912, RSS=14.52) since both develop in response to fetal developments (Warwick, 1928), and will therefore also depend on litter size. The content of protein in fluids and membranes (P_{fm};g) increased exponentially over gestation (Equation V.6, Table V.2; r^2=0.978, RSS=0.0002) and no consistent nutritional effect could be identified. Water content of the fluids and membranes followed a 3rd degree polynomial relative to time but was closely related to protein content, in an exponential manner (Equation V.7, Table V.2; r^2=0.989).

Fluids and membranes account for a large proportion of the hydration in utero early in pregnancy since together they contain about 95 to 96% water. Lipid content in fluids and membranes (L_{fm};g) increased in a positive exponential manner relative to time (Equation V.8, Table V.2; r^2=0.995) and ash content was assumed to be 0.99% of W_{fm}.

Uterine development: Empty uterine weight (W_{ut};g) appeared to follow two distinct phases of development with two separate exponential or curvilinear fits (Equation V.9, Table V.2; r^2=0.977, RSS=3615,371). The inclusion of W_{fe}, LS, Ei and Pi in the equation did not enhance the accuracy of prediction. Protein content in the uterus (P_{ut};g) increased linearly with W_{ut} (Equation V.10, Table V.2; r^2= 0.954) and therefore exponentially over time. Water content of the uterus (H_{ut};g) increased exponentially over time and linearly relative to W_{ut} (Equation V.11, Table V.2; r^2=0.999). Ash content was estimated to be 1.5% of W_{ut} (Lodge et al., 1979), and lipid content of the uterus was calculated by difference.

Weights of the total gravid uterus (W_u;g) and its composition (P_u, H_u, and L_u) were estimated from the sum of its components (fetuses, fluids and membranes and uterus). The components by weight of the gravid uterus are illustrated in Figure V.2. Similarly the rates of protein (Pr_u;g/d), lipid (Lr_u;g/d) and water (Hr_u;g/d) accretion in the total gravid uterus were estimated from the differential functions for each component (Table V.3). A marked decline in rate of protein accretion in the total gravid uterus in the last two weeks of gestation, was partially due to restrictions on fetal growth, and utilisation of fluids and membranes by the developing fetuses.

The efficiency of energy accretion in utero (k_u), calculated from different estimates of k_p and k_f (Noblet and Close, 1985; Noblet and Etienne, 1987) varied from 0.47 to 0.73, though at any assumed value of k_p and k_f, the estimated k_u was relatively constant (5-8% variation), regardless of sow LWT, Pi, Ei, or stage of gestation. The highest efficiency was chosen on the basis that the inefficiency of use of nutrients would most likely be borne by the sow. The efficiency of uterine protein accretion (a_u) was varied on the basis of literature values for young pigs (Whittemore, 1987). Within a range of a_u between 0.7 and 0.95 the value chosen had minimal effect on the protein requirement for uterine deposition. Since the efficiency of use of protein for Pr in growing pigs appears to decrease with weight (Whittemore and Fawcett, 1974), the higher value of 0.9 was taken as the preferred value for uterine efficiency.

Mammary development: Mammary tissue growth was modelled relative to day of lactation (t_l), hence at day 110 of gestation, t_l becomes -5, allowing a continuum between the stages of reproduction. The weight of mammary tissue (W_{mm};g) increased exponentially (Equation V.12,Table V.2; r^2=0.971, RSS=2.147) from the last two weeks of gestation to about day 7 of lactation, beyond which it was considered to be constant, until weaning. Mammary protein content (P_{mm};g), water content (H_{mm};g) and lipid content (L_{mm};g) were exponentially and allometrically related to mammary weight (Equations V.13,14 and 15, respectively; r^2=0.991, 0.996, and 0.994). Data were not available to model the regression of the mammary gland following weaning.

Maternal tissue changes: Maternal rates of protein and lipid accretion

(Pr_m;g/d and Lr_m;g/d, respectively), as calculated from protein and energy available following Pr_u and Lr_u followed the same response to the advancement of pregnancy at different feed intakes as reported in the literature (Table V.4). This result lends support to the use of the same response function for Pr relative to Pa, Ea and LWT in pregnant sows, as that derived in dry sows (Walker and Young, 1990a). Total Pr (Pr_m + Pr_u) was always greater than Pr calculated for a dry sow of similar LWT, on the same Pi and Ei, though Pr_m was always less in the pregnant sow than in the dry sow. This is a reflection of the fact that Pr_u is met from Pa with a high efficiency in the model, as a consequence of the processing costs of available protein being borne largely by the sow. With the advancement of pregnancy the proportion of Pr_u to Pr_m increased, and Pr_m and Lr_m decreased (Figure V.3). Low feed intake levels markedly reduced Pr_m and Lr_m, and Lr_m was negative in the last week of gestation, but the effect on uterine accretion rates was minimal. The ratio of Pr:Lr in maternal gain was related to Pi and Ei and ranged between 0.32 and 1.02. On low feed intakes, the ratio of maternal Pr:Lr increased with the progression of pregnancy, whereas the ratio decreased on higher feed intakes. The estimated energy value of maternal gain was relatively constant; 31.2 to 35.7 kJ/g.

The ratio of Pr:Lr in the gravid uterus varied with stage of gestation and nutrient intake. The ratio of Pr:Hr in the uterus increased with the advancement of pregnancy and with increased Pi. Assuming a constant Pr:Hr (0.29) in maternal tissue gave estimated live weight gains closely approximating measured values (Table V.4). Total body P:H ratios may actually decrease to 0.25 in late gestation as a consequence of the high proportion of water contained in uterine and mammary tissues (Kotarbinska, 1983). Calculated Es_T for pregnant sows were not markedly different (increased by 0.2 to 0.7%) from values estimated for dry sows, the difference being simply a function of the greater total Pr.

Utilisation of model equations on data from total nitrogen balance trials (Miller et al., 1969; Pike, 1970) revealed some discrepancy between observed and predicted total Pr, though there are also differences between data sets. Actual measurements tended to be higher than predicted, though for a wide range of intakes and feeding regimens, the direction of the predicted response closely approximated observed response (Table V.5). Model predictions of rates of accretion in maternal and uterine tissues determined by carcass dissection (Table V.6) were much closer than in the balance trials.

D. Discussion

A number of interesting results evolved when the developing gravid uterus was analysed by separate components (fetus, fluids and membranes, and empty uterus). Unlimited fetal growth would appear to follow the previously reported exponential form (Moustgaard, 1962), but the limitations of nutrition and/or space tend to give a more sigmoidal nature to the function as suggested by Rattray et al., (1974). Data from fetal lambs (Rattray et al., 1974) and swine in utero (Mellor and Murray, 1982) show a decline in growth with reduction in available space or competition for available nutrients in the latter part of gestation. Measurements of fetal oxygen consumption (Bell et al., 1985) and protein turnover (Goldspink and Kelly, 1984) also provide evidence of reduced fetal growth intensity in late gestation. However, nutrition per se does not appear to influence the composition of uterine growth (Verstegen et al., 1987), only the weight of individual uterine components (Noblet et al., 1985; Pike and Boaz, 1972; Kemm and Ras, 1976).

The multiple regressions developed by Noblet et al., (1985) and Kemm and Ras (1976) to include nutrient intake, sow weight and litter size did not work well for other data in the present data set. The effects of nutrition on reproduction (litter parameters) have been postulated to be more noticeable through reduced ovulation rates at low feed intakes, resulting in reduced numbers of fertilised ova, rather than subsequent in utero mortality (Pike and Boaz, 1972).

The empty uterus seems to undergo two distinct phases of development during gestation, which may reflect initial hyperplasic growth in preparation for fetal development, followed by later tissue hypertrophy in response to fetal growth. Rapid involution of the uterus, observed as excretion of nitrogen immediately following parturition (de Hovell and MacPherson, 1977) may be indicative of a labile source of amino nitrogen to the sow in early lactation. Uterine weight (empty uterus) may be influenced slightly by nutrition, though there is insufficient evidence to know if nutrition per se influences uterine composition (Lodge et al., 1979; Noblet et al., 1985). Relating fluid and membrane development to fetal growth appeared logical in the latter part of pregnancy, but the converse may be true in early pregnancy when nutritional or thermal effects may cause placental stunting and therefore reduced fetal growth (Bell et al., 1989).

The k_u estimates from the present equations were within the range reported in the literature (Noblet and Etienne, 1987; Reynolds et al., 1985), and closely approximated the range suggested by Close and Noblet (1985) using regression techniques. The derived value of k_u (0.57), using k_p and k_f values suggested by ARC (1981) was considerably lower than the value for k_u (0.8) used by the ARC system, though much greater than the estimate of deLange et al., (1980). It seems reasonable to assume that the efficiencies of energy use for protein and lipid accretion in utero are similar to the tissues of young growing pigs, hence k_u is expected to be low as a consequence of the high protein accretion in utero. Similarly the efficiency of use of protein accretion in uterine tissue should be similar to that in young pigs since the nutrient intake and protein support costs of both are small.

The agreement between predicted Pr_m and measured values supports the assumptions used in the model; that there is no difference in the efficiency of Pr_m in pregnant versus non-pregnant sows, but that Pr_u is achieved with high efficiency. This would tend to support the validity of the relationship between Pr, Pa, Ea and LWT developed for the dry sow in the previous chapter (Walker and Young, 1990a), where Pa and Ea are nutrients available for maternal production. Hence, although pregnant sows had more total protein accretion than dry sows as suggested by Elsley et al., (1966), protein anabolism as such is localised in the gravid uterus and does not occur in maternal tissue, (de Wilde, 1980a,b; de Hovell et al., 1977a,b; Shields and Mahan, 1983; Close et al., 1985). Predicted Pr_m declined with the advancement of pregnancy in agreement with ARC (1981), though some variation was observed in measured values derived from combined slaughter and balance trials. It is not clear whether the discrepancy between predicted total Pr and Pr from nitrogen balance trials is a result of an over estimation in nitrogen balance trials or under-prediction in the model, though the agreement with slaughter results would indicate the former.

The situation with Hr appears to be similar to Pr in that hydration appeared to occur in utero and possibly in the mammary tissue, but not in maternal tissue, (Shields et al., 1984; Close et al., 1985). The predicted ratio of Pr:Hr in utero varied from 0.04 to 0.22 whereas in maternal tissue P:H was on average 0.29. The actual ratio (from Noblet and Etienne, 1987) decreased slightly over gestation, though carcass data indicate the opposite trend (Kotarbinska, 1983, Young et al., 1990), illustrating the importance of separating maternal, uterine and mammary tissues.

Predicted Es_T for pregnant sows was only slightly higher than that predicted for dry sows, as a consequence of the increased total Pr in the former. This does not provide validation for the use of the Es_T equation, derived from dry animals, in the pregnant sow, though it is included in the model as a means of dealing with the controversy concerning 'maintenance' in pregnancy. Such a small difference would be unlikely to be picked up by experimental techniques for measuring 'maintenance' . This and the use of assumptions concerning the efficiency of use of energy for protein accretion in experimental calculations might account for the contradictory results concerning 'maintenance' and energetic efficiency of pregnant and non-pregnant sows (Verstegen et al., 1971; deWilde et al., 1980; Close et al., 1985;

Noblet and Etienne, 1987). The assumptions described in the model have provided a more mechanistic approach to nutrient partitioning in pregnancy than the more rigid factorial methods (ARC, 1981).

In conclusion, modelling uterine development on the basis of individual components, and first priority on 'available nutrients' allowed for the prediction of maternal tissue accretion through pregnancy, and the evaluation of some disputed physiological concepts and commonly used assumptions. The full utility of the gestation model will be realised when it is combined with the lactation module, chapter VI (Walker and Young, 1990c) to provide a continuous, dynamic representation of reproducing sows.

Table V.1. Data sources used in the calculation of weights and composition of components of uterine development.

Source	Sow live weight	Day of gestation	Data used‡
Pomeroy, 1960	NA	51 - 113	W_u,%P_u,%H_u
Moustgaard, 1962	NA	41 - 108	W_{fe},W_{fm},W_{ut}
Ullrey et al., 1965	NA	30 - 114	W_{fe},W_u
Elsley et al., 1966	134	110	W_u,W_{ut}
Pike and Boaz, 1972	155-198	70	W_u,W_{fe},W_{fm},W_{ut}
de Hovell et al., 1977	100	114	W_{fe},W_{ut},P_{fe}
Lodge et al., 1979	118-145	0 - 112	W_u,W_{fe},W_{fm},W_{ut},%P_{fe},%P_{fm},%P_{ut}
de Wilde, 1980a,b	114	110	W_u,W_{fe},W_{fm},W_{ut},P_{fe},P_{fm},P_{ut}
Shields and Mahan, 1983	120	0 - 105	W_u,P_u,L_u
Noblet et al., 1985	104-139	51 - 102	W_u,W_{fe},W_{fm},W_{ut},P_u,P_{fe},P_{fm},P_{ut}, H_u,H_{fe},H_{fm},H_{ut},L_u,L_{fe},L_{fm},L_{ut}

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‡ W=weight, P=protein, L=lipid, H=water; with subscripts $_{fe}$=fetuses, $_{fm}$=fluids/membranes, $_{ut}$=empty uterus, $_{u}$=total gravid uterus. NA= not available

Table V.2. Equations for weight and composition of uterus and components through pregnancy.

Component	Equation	Number in text
Fetuses		
	$W_{fe} = LS.(e^{8.496-9.494\ e^{-0.017tg}}) / \{1+(4.83/Ei)-(4.55/Ni)\}$	1.
	$P_{fe} = e^{(7.367-4.97\ e^{(-0.00026\ Wfe)})}$	2.
	$\ln(H_{fe}) = 0.09687 + 0.9697 \ln(W_{fe})$	3.
	$A_{fe}(\%) = 1.817 + 0.00016\ W_{fe}$	4.
Fluids and Membranes		
	$W_{fm} = W_{fe}\ \{48.677\ e^{(-0.0415\ tg)}\}$	5.
	$P_{fm} = W_{fm}\ \{0.0087\ e^{(0.0146\ tg)}\}$	6.
	$H_{fm} = P_{fm}\ \{78.97\ e^{(-0.001\ tg)}\}$	7.
	$L_{fm} = LS\ \{1.6\ e^{(0.0075\ tg)}\}$	8.
Uterus		
	$W_{ut} = 442.03\ e^{(0.0273\ tg)} - 44.69\ e^{(0.0427\ tg)}$	9.
	$P_{ut} = 20.924 + 0.0993\ W_{ut}$	10.
	$H_{ut} = 34.46 + 0.847\ W_{ut}$	11.
Mammary		
	$W_{mm} = 1107.3 + 3521\ e^{(0.118\ tl)}$	12.
	$P_{mm} = 117.15\ W_{mm}^{\ 0.8915}$	13.
	$H_{mm} = 365.4\ e^{1.2838\ \ln(Wmm)}$	14.
	$L_{mm} = 460.0\ W_{mm}^{\ 0.6955}$	15.

NB: Where lipid or ash are not specified, they have been calculated by difference. For symbols see text and table V.1.

Table V.3. Comparison of rates of nitrogen accretion in the total gravid uterus calculated from equations derived by Noblet et al., (1985), and equations reported herein (predicted).

Daily Intake				Rates of Nitrogen accretion			Uterine Weight	
Energy (MJME)	Protein (gCP)	Litter Size	Day of Gestation§	Measured† (g/d)	Calculated‡ (g/d)	Predicted (g/d)	Measured (kg)	Predicted (kg)
Noblet et al., (1985):								
20	35	11	51	0.55	1.76	0.99	6.5	5.8
20	35	10	79	2.63	3.04	3.09	15.2	12.3
20	35	12	102	4.31	6.24	6.30	20.2	18.5
30	65	13	53	0.85	2.08	1.28	8.5	7.6
30	65	11	72	1.81	3.84	3.08	14.0	13.3
30	65	13	103	7.22	8.16	6.95	24.5	22.4
Noblet and Etienne, (1987):								
27.6	45.4	9.5	65	-	2.70	2.13	9.7	8.9
27.6	45.4	9.5	101	-	6.00	6.03	15.8	16.2
27.6	45.4	9.5	108	-	7.00	5.70	16.4	17.6
32.7	50.5	12.4	36	-	1.30	0.86	2.0	3.5
32.7	50.5	12.4	72	-	4.00	3.54	15.4	13.0
32.7	50.5	12.4	105	-	9.70	5.40	23.0	21.3

§ Day of slaughter

† Measured by dissection

‡ Estimated from equations derived by Noblet et al., 1985

Table V.4. Comparison of maternal protein accretion rates (g/d) as calculated by equations of Noblet et al., (1985) and equations presented in this chapter.

Sow Liveweight		Day of	Protein accretion		Lipid accretion	
Measured	Predicted	Balance	Measured	Predicted	Measured	Predicted
(kg)	(kg)	¶	(g/d)	(g/d)	(g/d)	(g/d)
Close et al., (1985):						
120	128	47	23.0	38.7	92.0	76.3
146	141	75	49.2	29.3	48.0	60.3
155	156	97	24.1	15.0	-49.6	42.3
139	148	49	32.5	54.3	271.0	189.7
147	165	68	49.2	49.9	140.0	161.3
200	192	98	25.4	34.2	90.3	112.6
Noblet and Etienne, (1987):					Live weight gain (g/d)	
164	169	65	45.6	60.8	530†	599.6‡
184	192	101	55.6	46.2		519.1
189	197	108	57.5	45.3		494.5
168	173	36	70.0	71.6	607	718.5
194	197	72	48.7	59.6		693.7
219	223	105	51.2	47.4		606.3

† Average daily gain over gestation

‡ Averages for whole gestation are 537.8 and 672.8 respectively

¶ Mid-range of 7 day balance period

Table V.5. Comparison of total protein accretion by nitrogen balance and model prediction - data not used in parameterisation of model equations.

Sow	Daily intake		Litter	Total protein accretion		Protein in utero	
Live weight	Energy	Protein	Size	Measured	Predicted	Measured	Predicted
(kg)	(MJDE)	(gCP)	born	(g/d)	(g/d)	(kg)	(kg)
Pike (1970):							
140	H C L‡	High	15.3	61.1†	53.5†	2.5	2.1
140	C C C	High	12.7	66.2	46.8	2.1	2.2
140	L C L	High	13.7	79.2	59.2	2.4	2.1
140	H C L	Low	15.0	37.8	22.8	2.8	2.2
140	C C C	Low	13.3	47.5	34.8	2.1	1.9
140	L C H	Low	11.7	29.3	33.0	2.4	2.1
Miller et al (1969):							
158	25§	114	10.0¶	27.8	32.9	-	-
158	25	171	10.0	64.8	46.8	-	-
158	25	228	10.0	76.8	59.4	-	-
158	25	285	10.0	95.0	72.4	-	-
158	25	342	10.0	96.3	79.7	-	-

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† Maternal protein accretion

‡ L,C,H respectively for Low protein intake was Pi=202,302,403 and Ei=24,36,48

L,C,H respectively for High protein intake was Pi=355,532,709 and Ei=25,37,49

§ Assumed energy intake

¶ Assumed litter size

Table V.6. Comparison of model predictions of protein and lipid accretion in maternal and uterine tissue with slaughter trial data, not used in parameterisation of model equations.

Daily intake		Protein accretion				Lipid accretion				Uterus weight	
		Total		Gravid		Total		Gravid			
Energy	Protein	Meas	Pred	Meas†	Pred	Meas	Pred	Meas†	Pred	Meas	Pred
(MJDE)	(gCP)	g/d)	(g/d)	(g/d)	(g/d)	(g/d)	(g/d)	(g/d)	(g/d)	(kg)	(kg)
19.7	240	36.0	45.3	18.1	14.8	-20.4	37.8	1.4	3.7	22.1	19.8
26.2	320	44.0	56.7	15.7	15.2	27.0	114.0	1.3	3.8	19.4	20.3
32.8	400	68.0	63.3	21.2	15.4	140.0	186.8	2.0	3.8	24.8	20.1
45.9	560	92.2	80.2	20.4	15.6	280.0	308.8	2.0	3.9	23.7	20.9
46.6	672	102.6	87.0	20.6	16.5	271.0	331.3	2.2	4.4	26.8	22.3

Source: Walach-Janiak et al., 1986. Sows were mated at 117 kg LWT and 240 days of age, and slaughtered at 112 days of gestation.

† Assumes zero at day zero, hence slight over estimation.

Figure V.1 Growth of the components of the gravid uterus over gestation

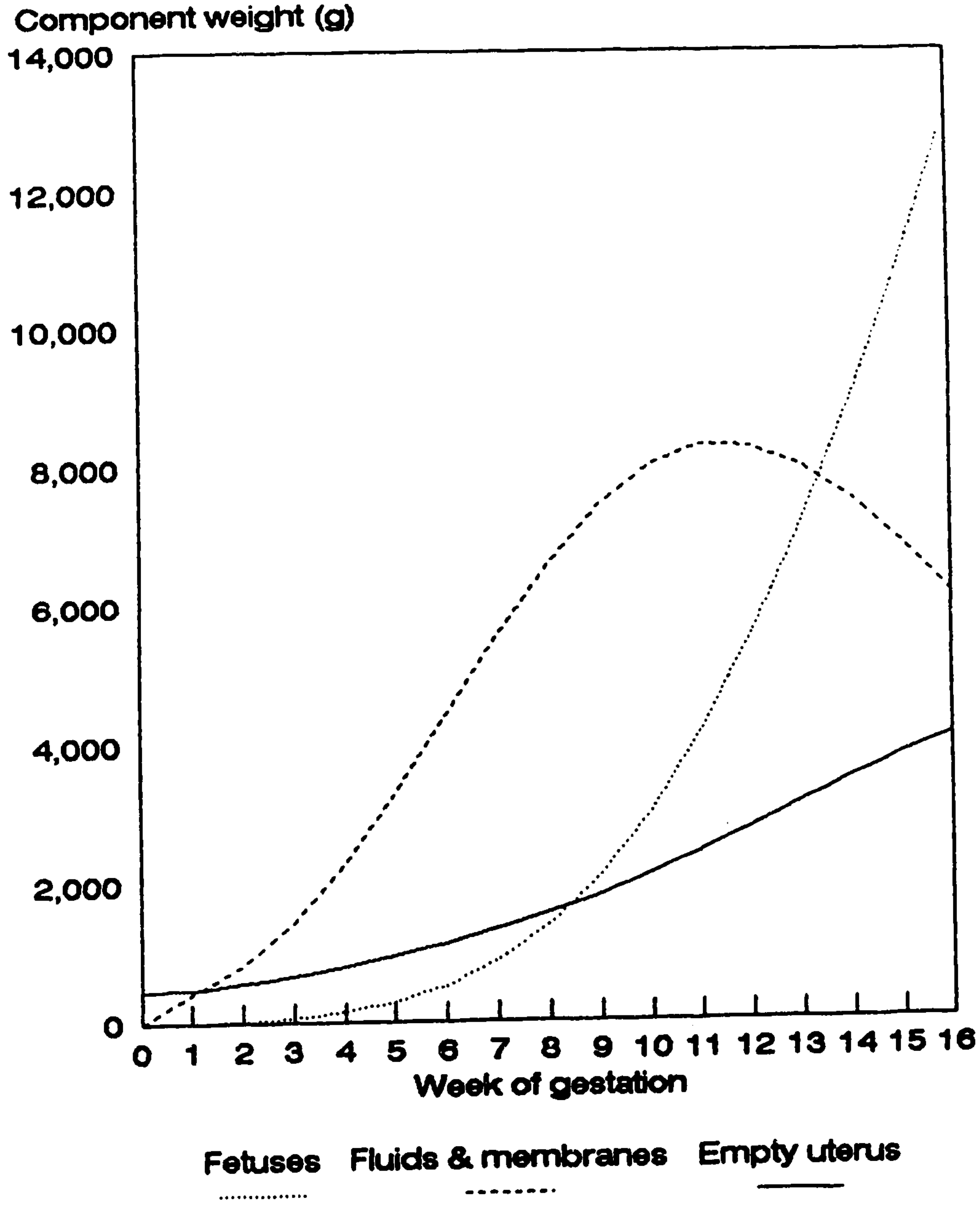


Figure V.2 Growth of fetal components over gestation

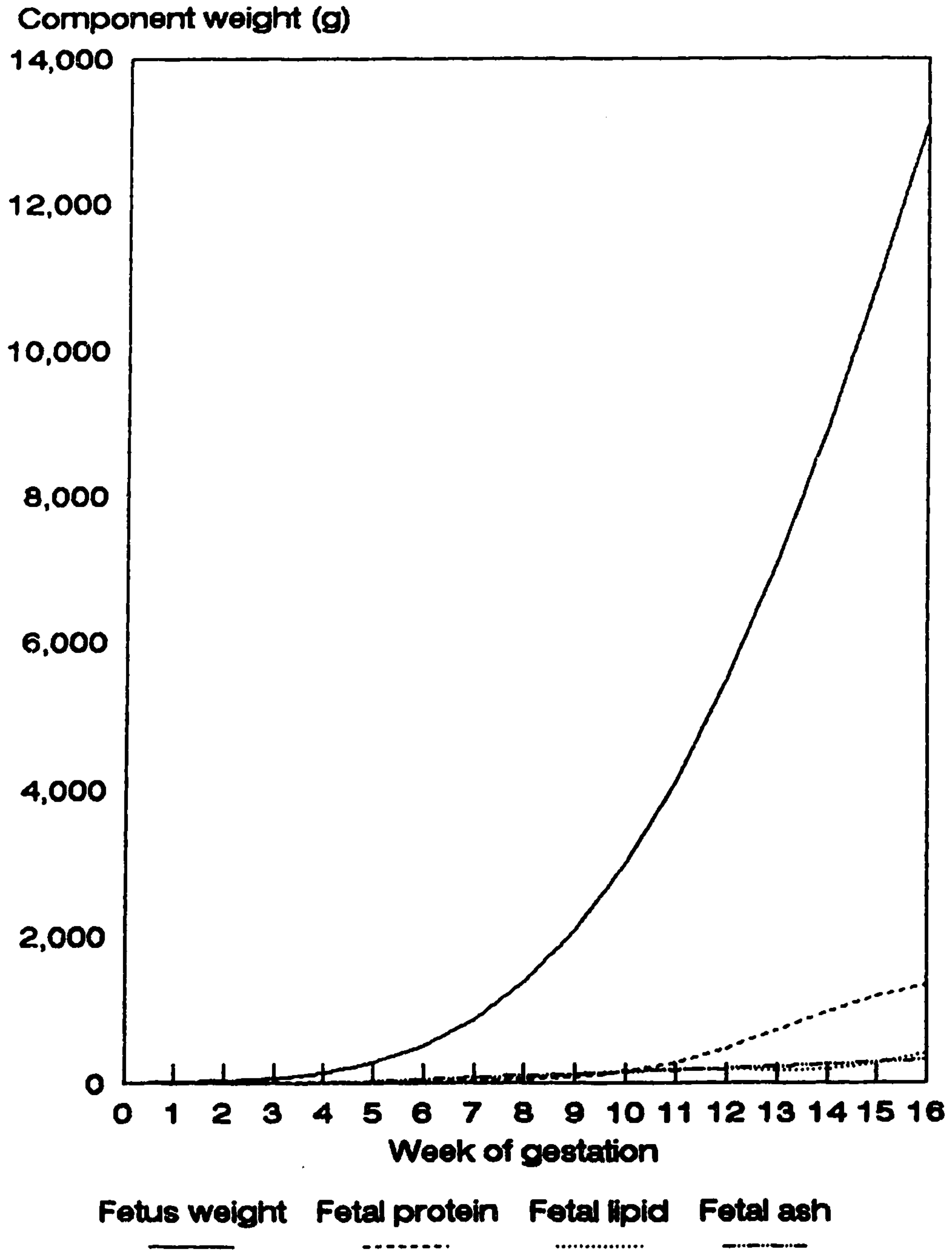
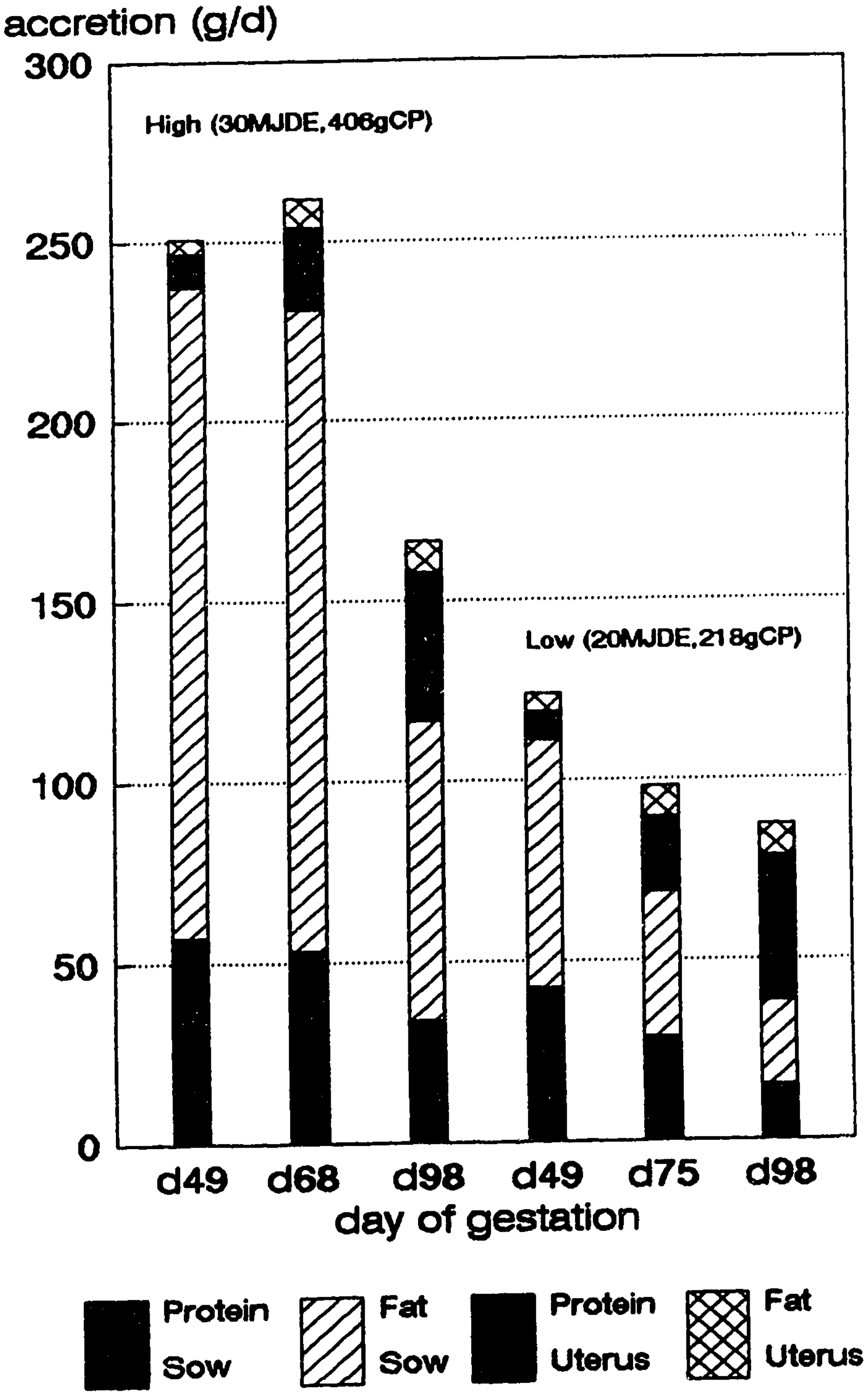


Figure V.3 Model predictions of daily rates of protein and lipid accretion in sow and uterus at high and low daily feed intakes



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VI. MODELLING THE REPRODUCTIVE RESPONSE OF SOWS TO NUTRIENT INTAKE. MILK YIELD, MILK COMPOSITION AND BODY COMPOSITION DURING LACTATION[1].

A. Introduction

The lactating sow, like the dairy cow in early lactation is in a highly productive and often catabolic state, where feed intake can seldom meet her nutrient requirements. The duration of lactation in the sow is short relative to the reproductive cycle as a whole but is probably the most vital time period in relation to overall reproductive efficiency. Excessive maternal tissue mobilisation during lactation has been linked to extended rebreeding intervals (Mullan and Williams, 1989; King and Williams, 1984), and has also been associated with effects on ovulation rate (Hardy and Lodge, 1969).

Live weight changes during lactation do not appear to be consistently related to the interval from weaning to mating (Reese et al., 1984; O'Grady et al., 1975) and it has been argued that hormonal changes necessary for estrous may be linked to body fat mobilisation (Whittemore et al., 1980; 1988) or body nitrogen balance (Brendemuhl et al., 1989; 1987; King and Dunkin, 1986b; Reese et al., 1982). Body compositional changes of lactating sows are difficult to establish since carcass evaluation is costly (King et al., 1986) and body water measurements may be biased because of changes in the relationship between protein and water during lactation (Shields and Mahan, 1983).

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[1] A version of this chapter has been submitted for publication: Walker, B., and Young, B.A. 1990. Livestock Production Science.

Measurements of energy and nitrogen balance in lactating sows will be influenced by current feeding strategy, previous body compositional changes and a number of reproduction variables (milk yield, litter size, parity, day of lactation). Although milk production exerts high demands on the sow, high intakes of protein and energy in excess of the projected requirements (ARC, 1981) may result in negative nitrogen and energy balances (King and Dunkin, 1986b; Verstegen et al., 1985).

Dynamic simulation modelling provides a tool to incorporate the complexities of sow response to nutrient intake. Presently, modelling efforts on the lactating sow have been limited and are restricted to a biochemical based research model (Close and Pettigrew, 1990) and an empirical model combining the growing and reproducing pig (Black et al., 1986). Considerable difficulties arise in sow modelling as a consequence of the complexities of dynamic change in, and limited information on, compositional changes in maternal tissue and milk, hence a continuous model of the reproducing sow does not yet exist.

The purpose of this chapter was to develope predictive equations for milk production in the sow, in order to evaluate the dynamic changes in maternal body composition through lactation. Ultimately this was required as an integral component of the complete model and to evaluate the link between nutritional regimens and reproductive performance, in order to provide support and insight to recommended feeding strategies for sows.

B. Approach and Analysis

The system of partitioning protein and energy intake in the lactating sow was that of the dry sow (Walker and Young, 1990a) with the following hypotheses added;

1. Milk yield is the result of a balance of forces - the suckling demand of the litter and the resistance to mobilise excessive sow body reserves in the face of a deficit in dietary supply.
2. Requirements for milk protein and energy are met from the most readily available nutrient pool and thus occur at maximal biological efficiency for these processes. Theoretical efficiencies for protein and energy utilisation for milk were taken to be 0.82 and 0.72 respectively (Baldwin, 1980).
3. Nutrients derived from maternal tissue enter the available pool at a greater efficiency than feed nutrients and are therefore used for milk with greater overall efficiency.
4. Priority for available nutrients is to milk followed by support processes, (which are dependent on the level of sow productivity), protein accretion, and lipid accretion. Protein mobilisation was calculated from the same function as protein accretion, relative to available protein and energy.
5. The carry over effects of gestation feed intake are effected through the different body composition consequent upon them.
6. Piglet growth is predicted from milk nutrient output, (no creep feed being provided) and not vice versa.
7. Support costs for the lactating sow follow the same relationships derived in the dry and pregnant sow, as described in Chapter IV (Walker and Young, 1990a). Energy support costs are related to body protein mass and net synthesis of protein (protein accretion plus protein synthesis

in milk), while protein support costs are related to body mass and level of intake.

Sources of data used in derivation of milk yield and composition equations are listed in Table VI.1., some of these data sets were also utilised in the derivation of piglet growth. Calculated sow protein and energy retentions (or mobilisation) were compared with measured values (Mullan and Williams, 1989; Verstegen et al., 1985; King and Dunkin, 1986b) to further modify model parameterisation. The simulation equations were then tested under various scenarios and compared to experimental data. All equations were derived using SAS (SAS Inc., Cary. NC) and evaluated on the basis of non linear r^2, residual sum of squares, and significance of coefficients. Finally model predictions were tested against data not used in the parameterisation of model equations (Brendemuhl et al., 1987; 1989).

C. Results

Milk Production: Actual milk yield was determined as the difference between the maximum yield and the limit of nutrition and body reserves. Daily maximum yield (MY;kg/d) was calculated for each parity (1, 2 and 3+) on the basis of litter size and day of lactation. This was best achieved using the functional form; $at_1.e^{-ct_1}$ (where t_1=day of lactation), and data selected on the basis of highest yield for any particular day of lactation for sows with high dietary nutrient supply. Parity 1 maximum yield curve was on average 20% lower than other parities and much flatter (Figure VI.1), but it should be noted that the maximum daily feeding level provided to gilts (815g CP, 63.2 MJ DE) was considerably lower than to sows (1244g CP, 73 MJ DE). Since most experiments involved controlled feed allowances, it is unclear whether there was a real difference in the appetite of gilts and sows and therefore a genuine parity restriction on maximum milk yield.

The differences between parity 2 and older sows was small; parity 2 milk yield peaked earlier and declined sooner than parity 3+. For a litter size (LS) of 9, the peak yield (kg/d) and its occurance for parity 1, 2 and 3+ was 7.32 on day 11, 9.67 on day 17, and 9.18 on day 27, respectively. Litter size was included in the relationship as a logarithmic function on maximum yield, hence the increment in milk yield diminished with increasing LS (Figure VI.2).

$$MY_n = \frac{a.\ln(LS)\ \{b + c.t_1^{\,d}\ e^{\,(-f.t1)}\}}{\{1 + g.[(80-E_i)/80] + h.[(1200-P_i)/1200] - j.(Gg/Wi)\}} \quad \ldots \text{VI.1.}$$

Where MY_n = Milk yield; kg/day (n=parity 1, 2 and 3+), LS= Litter size, t_1= day of lactation, E_i= Energy intake (MJDE/d), P_i= Protein intake (g/d), Gg= Gestation total weight gain over 115 days (kg), Wi= Weight on day 1 lactation. The coefficients a through j, r^2 and RSS for parity 1, 2 and 3+ are given in table VI.2a.

The response of milk production (equation VI.1) to protein and energy intakes below that required to meet maximum yield was modelled in a way approximating Michaelis-Menton kinetics (Gill et al., 1990a). The level of nutrient intake was then expressed relative to maximum intake in the available data set (Ei=80MJ/d, Pi=1200g/d) such that, in general, the lower the intake the larger the fractional difference and the greater the denominator becomes, thereby reducing milk production below maximum. It was assumed that at levels of intake greater than the maximums set in Equation VI.1 no further increase in milk yield would be observed. It can be seen from the coefficients in Table VI.2a that protein intake had a greater effect on milk yield than energy intake, and the effect became more marked from parity 1 through 3+. The coefficients for Ei were not significant and in parity 2 the effect of Ei was opposite to that of Pi. The interaction term between Ei and Pi was not significant for any of the equations.

It is interesting to note that a reduction in feed intake of 50% had a relatively larger effect on parity 3+ sows than on gilts (Figure VI.3). Presumably this occured because maximum milk yield in gilts was achieved at a lower feed intake (70% less Pi, 84% less Ei) than sows. Thus a 50% reduction from sow maximum intake is actually more equivalent to a 20 to 35% reduction for gilts.

Estimates of sow body reserves were required in order to establish how sow reserves can supplement a deficit of nutrient intake, in supporting milk production. Gestation weight gain relative to sow weight at the beginning of lactation (Gg/Wi) was therefore established as an indirect measure of sow condition, and was found to be significant in parities 1 and 3+. The large coefficient of parity 3+ sows would indicate that sows gaining more in gestation utilised body reserves to maintain milk yield closer to the maximum when dietary intake would otherwise limit production. Unfortunately, body composition data were not available on the sows used to determine milk production (Table VI.1), hence this could not be tested.

Milk composition: With the advancement of lactation the protein content in milk (g/kg) followed an inverse polynomial pattern and the propotions of energy, dry matter and fat plus lactose were relatively constant. As a consequence of the relatively constant milk composition, log-linear responses of total secretion of protein (P_{milk},g/d), energy (E_{milk},MJ/d) and dry matter (DM_{milk},g/d) were derived from milk yield (equations VI.2, VI.3 and VI.4, Table VI.2b; all had $r^2>0.999$). The amount of fat plus lactose was determined from the difference between milk DM and P, assuming milk to be 0.9% ash.

It can be seen from the equations in table VI.2b, that an increase in protein intake relative to energy intake would increase milk protein content, but an increase in energy intake alone may decrease the concentration of energy and dry matter in milk. This is more a result of the ratio of energy to protein rather than absolute amounts of dietary protein and energy.

Piglet growth: The linear fit of milk intake per pig (MI;g/d) versus average piglet gain (Pig_{gain};g/d) was quite poor ($r^2=0.589$) and the variation at all levels of intake was large. The prediction was based on data where no creep feed was provided. The poor linear fit may be partially accounted for by the decrease in milk yield from about day 20 of lactation, while piglet growth generally shows a linear increase over time (age). For the period 1 to 41 days piglet growth was curvilinearly related to age, with additional variation in growth rate being accounted for by variation in milk intake (Equation VI.5, Table VI.2b; $r^2=0.9828$, RSS=332). The inclusion of milk protein, dry matter or energy intake per piglet did not significantly improve the prediction. Feeding creep in early lactation (d12 to 21) may increase piglet gain by 30 to 50 g/day but later in lactation creep feed showed little effect beyond the highest gains attainable from milk. It may be that creep feed can supplement low milk intake in early lactation, but becomes more of a substitute for milk in late lactation.

Maternal tissue changes: The scheme of nutrient partitioning between various processes in the lactating sow has been depicted in the context of a dynamic model, as presented in the first paper of this series (Walker and Young, 1990a, Figure IV.1). The designated 'available pools' of energy (Ea;MJ/d) and protein (Pa;g/d) become important in the lactating sow since the pool is common to food and tissue nutrients in its accessibility to production processes. Hence nutrients from food enter the pool with a different efficiency than nutrients from mobilisation of body tissue. Available nutrients are therefore the precursors of biochemical processes and the efficiency of use is a direct consequence of those processes. In the present model, energy and protein from the available pool were first allocated to milk production with the theoretical efficiencies of 0.72 and 0.8, respectively. Protein mobilisation was then determined simultaneously with protein support costs, (from Pa and Ea after milk production). If it was estimated that body protein needed to be mobilised to meet milk protein production, the mobilised protein-energy also reduced the non protein energy requirement for milk, thereby reducing the Ea required from dietary sources. Body protein was estimated to be mobilised with a high efficiency and was therefore used for milk protein (0.88) more efficiently than was feed protein (0.8). Similarly body energy mobilised was utilised with higher efficiency (0.8) than feed energy (0.72). Any protein available after protein support costs and retention, was assumed to be deaminated and supplied 11.5 kJ/g of energy (Whittemore and Fawcett, 1976) to the available energy pool.

Ea after milk production was utilised to meet energy support processes which was dependent on rate of protein retention in the sow and protein secretion in milk, and body protein mass. The energy cost of protein mobilisation was taken to be one quarter the cost of accretion (Gill et al., 1990b). Energy mobilised from tissues was estimated to enter the available pool with an efficiency of 0.9, and energy accretion in fat and protein was assumed to require 54.6 and 53.5 kJ/g, respectively (Walker and Young, 1990a).

The available pools of food nutrients were initially assumed to be equivalent to the daily intakes of metabolisable energy (MEi;MJ/d) and digestible crude protein (DCPi;g/d). At given ME and DCP intakes, where protein and lipid mobilisation (or retention) was known (Verstegen et al., 1985; King and Dunkin, 1986b; Mullan and Williams, 1989), the true availability of nutrients could be calculated. Where these values differed from ME and DCP intake, a conversion factor was calculated to find Ea and Pa. The calculated difference was negligible at low nutrient intakes similar to those given to pregnant and dry sows, but became large at high intakes of ME and DCP or with imbalance of ME to DCP ratio in the diet. For the purposes of predicting maternal body tissue changes, the factor associated with truly available nutrients was considered to be the cost to the sow of assimilation and processing large amounts of food nutrients. The availability of ME was also reduced with high energy to protein ratios in the diet (DEi/Pi) and in animals with heavier initial live weight (Equation VI.6, r^2=0.997, RSS=0.997). The cost of protein (N x 6.25) assimilation increased curvilinearly with

Pi per kg body weight, levelling at high intakes, and also increased with high energy to protein ratios in the diet (Equation VI.7, r^2=0.972, RSS=545).

$$Ea = MEi\{1.3572 - 0.02617(DEi^2/Pi) - 0.00278\,Wi\} \qquad \ldots\ VI.6.$$

$$Pa = DCPi - 6.25\{-69.75 + 36.43(Pi/Wi) - 3.1(Pi/Wi)^2 + 4.36(DEi^2/Pi)\} \qquad \ldots\ VI.7.$$

Within the data used to parameterise equations VI.6 and VI.7, Ea ranged from 0.95 to 0.75 of MEi and protein costs ranged form 37 to 450g for Pi between 332 and 1244g/d. The efficiency of conversion of Pi to Pa therefore ranged between 0.85 and 0.57, though in situations of high DEi with moderate or low Pi the efficiency was as low as 0.3. The consequences of the changes in availability of nutrients at different intake, levels can be seen in the comparison of actual and predicted protein and lipid mobilisation data (Table VI.3). At the same level of intake fat sows mobilised more protein and more lipid from body tissues, with an apparently greater water to protein ratio in their lean. Increased DCPi at fixed MEi appeared to spare some body protein mobilisation, while increased MEi at fixed DCPi may spare body lipid mobilisation depending on the ratio of energy to protein. Increasing both MEi and DCPi reduced weight loss but all sows in the test data sets still mobilised lipid and most mobilised protein, even at the highest intakes (Table VI.3, Figure VI.4). Predicted values of protein and lipid mobilisation followed similar patterns of response to actual data, and live weight change predicted from tissue mobilisation reasonably approximated the actual values (Table VI.4) for data sets not used in the parameterisation of model equations.

Calculated lipid to protein ratio (Lr:Pr) in mobilised tissue ranged between 1.1:1 and 4.1:1, except for the values at very high protein intakes, where protein mobilisation was very small relative to fat mobilisation (ratio as high as 15.6:1). Experimentally determined values for Lr:Pr ranged between 2.1 and 5.2, with the same exceptions as in the predictions. Water to protein ratio (Hr:Pr) in mobilised tissue calculated from actual weight changes (g/d) ranged between 1.5 and 6.9, though excluding the extremes data for the Lr:Pr ratio, the range was only 3.2 to 3.9. For model calculations of live weight change (g/d) in the sow, a constant Hr:Pr was assumed (3.5) and is consistent with body composition data for lactating sows derived by Kotarbinska (1983). This assumes that any additional water changes in the sow occur as a consequence of mammary development or regression.

<u>Uterine resorption:</u> An exponential decay curve (Equation VI.8) was used to describe the resorption of the uterus following parturition. Resorption of the uterus could provide a relatively small amount of amino nitrogen and energy to the available pools in the initial stage of lactation. In contrast to uterine sources of P and E, no account was taken of mammary resorption since development was assumed to occur in late gestation and remain stable through lactation (Walker and Young, 1990b), and no data were available for mammary regression.

$$W_{ut} = 529.67 + 5041.2\, e^{(-0.2773\, t1)} \qquad \ldots \text{VI.8.}$$

Where W_{ut} is the weight of the degenerating uterus in grams and t_1=day of lactation, $r^2 = 0.997$, RSS=137986. The chemical composition of uterine tissue was assumed to follow the relationships described in the pregnant sow (Walker and Young, 1990b).

D. Discussion

The lower maximum milk yield curve of gilts and the smaller reduction in yield with a decrease in food intake, relative to sows, corresponded to the lower feeding level imposed on gilts, either voluntarily or experimentally, relative to sows. The ad libitum intake of gilts may be relatively low in practice (King and Williams, 1984) and therefore, although milk yield is lower than in sows, body tissue losses are large. It is not clear how much the drive to achieve growth in maternal tissue of the gilt affects the maximum curves derived, but delay of mating until heavier body weights does lead to higher milk production in the first parity (O'Grady et al., 1973; 1975).

The greater predicted responsiveness of milk yield to protein intake than energy intake is in agreement with literature reports (Mahan et al., 1971b; King and Dunkin, 1986b). The reason for this is unclear but it may be that as increased protein intake stimulates milk yield, any deficit in energy can be readily met from the body. In the case of a high energy to protein ratio in the diet, protein will limit milk yield and may be less readily drawn from body stores. Furthermore, for any kg of body tissue mobilised there would usually be more available energy than protein. Though, in the present analyses, energy intake was not a significant variable in determining milk yield, the ratio of energy to protein intake appeared to be important. This ratio was also of importance in determining the secretion of total milk protein and milk energy, via milk yield, since composition appears to be relatively unresponsive to nutritional variations. The increasing responsiveness of milk yield to protein intake with parity may be somewhat exaggerated by the inclusion of data for parity 3+ sows which had been on restricted feeding regimens for a number of parities (O'Grady et al., 1973; 1975; Greenhalgh et al., 1977; 1980).

The effect of sow body reserves on milk yield could be better established with more data on body composition since weight and backfat measurements are not likely to correlate well with total fat and protein, and body composition at the end of pregnancy can vary greatly (ARC, 1981). In addition, the composition of mobilised tissue appears to be quite variable and diet dependent (Brendemuhl et al., 1989). Variation in composition of weight loss may also relate to priority of utilisation of different labile reserves (Brendemuhl et al., 1989), and dietary availability of nutrients. The representation of body reserves used in the present model is a static and relatively unreliable approximation of available body stores (Gg/Wi), and would be greatly enhanced if a better estimate of body composition were available. However, with known or predicted initial composition, the model provides an indication of the dynamic changes in body stores over the reproductive cycle.

Variation still exists in estimated milk yield from the present equations, despite attempting to account for the most significant variables, possibly reflecting problems in methods of milk estimation. The evaluation of milk production from piglet gain, and vice versa, have limitations since estimates of both milk yield and composition may vary depending on technique used (Mahan et al., 1971c; den Hartog et al., 1984; 1987; Speer and Cox, 1984) as well as day of lactation (van Kempen et al., 1985; Noblet and Etienne, 1986). Furthermore, Lewis et al., (1978) showed that piglet growth does not exhibit a very strong relationship with milk yield across published data sets, whereas individual experiments have reported correlations in the range 0.76 (Aherne and Speer, 1974; White et al., 1984). Noblet and Etienne (1989) recently reported high correlations (r^2=0.9) of piglet body composition to milk yield and composition. Estimates of milk conversion to piglet gain are also highly variable (range 3.12 to 4.7g milk/g piglet gain). Analysis of a large number of data sets (equation VI.5) indicated that piglet growth is largely a function of age. However, it appears likely that low milk production can be supplemented by creep feed in early lactation to achieve similar gains to that possible in higher producing sows. Difficulties in obtaining reliable prediction of piglet gain from milk production probably arise from additional, uncontrolled variables such as disease, environment and teat function.

The system of priorities for nutrient utilisation in the present simulation model differs from the conventional feeding systems (ARC, 1981) in the assignment of nutrients to milk with high priority and efficiency, and the existence of 'available' nutrient pools. In addition the model utilises the concept of variable support costs rather than fixed maintenance (see Walker and Young, 1990a) and maintains the same relationship between Pa, Ea, LWT and Pr under conditions of body protein mobilisation. Furthermore, the available pools are common to both feed and body nutrients and therefore allowed the establishment of an extra level of feed nutrient processing, or inefficiency. The increasing inefficiency of dietary nutrient use with increasing intake elucidated by the model was assumed to be associated with assimilation, processing and absorption of nutrients. The experimental evidence in support of this concept arises from observations of reduced apparent digestibility of diets with increasing intake (van Kempen et al., 1985; Mullan and Close, 1989) and measurements of the protein synthetic rate and oxygen consumption of the viscera at different feeding levels (Gill et al., 1990b,c; Ferrel and Koong, 1987). In addition, increased heat production with feeding level has been observed and previously called 'diet induced thermogenesis' and 'heat increment of feeding' (Webster, 1981). Other processes often included in 'maintenance costs' are known to increase at high feeding levels, eg. substrate cycling (Summers et al., 1986). The alternative accounting system, commonly used in the literature, would suggest that these increased costs be incorporated in the inefficiencies of protein accretion rather than a component of 'maintenance' or energy support costs. It is still arguable to which process these increments should be accounted, and which processes actually or theoretically change. It is conceivable that the reported changes in partitioning are unique to the catabolic state of lactating animals and involve changes in the underlying relationships between Pr and Pi, Ei and LWT. Similar scenarios have been described in the modelling of cattle (France et al., 1987) and the lactating sow. It will likely prove very difficult to separate and/or measure the precise changes occuring in the lactating sow at high nutrient intakes.

Accounting for variation in availability of nutrients for lactation and support processes before these demands have been met assumes that the processing cost is borne by the sow and that these processes occur at a constant efficiency. In contrast, the conventional empirical estimates of partial efficiency of energy use for 'maintenance' are constant, and for milk production vary (0.62 to 0.79; Verstegen et al., 1985; Noblet et al., 1990). Partial efficiencies of nutrient use obviously depend on the assumptions and methods used in their derivation.

As a consequence of high productivity and assumed greater inefficiencies of assimilation, sows on high feed intakes still mobilised body tissues, despite intake being three times that required for milk production alone. It would appear that the catabolic state of sows during early lactation is difficult to avoid and enforced mobilisation appears inevitable (ARC, 1981), which brings into question the viability of feeding excessive amounts of dietary ingredients, in order to maintain body reserves. Of particular importance is the response of tissue losses to variations in the ratio of energy to protein in the diet, specifically the ability of high protein levels to promote greater lipid mobilisation (Noblet and Etienne, 1987) and reduce protein mobilisation. Imbalances of energy relative to protein appear to reduce the efficiency of utilisation of dietary protein and energy, but reduce the extent of lipid mobilisation. It is still necessary to determine the most desirable compositional changes in the sow in regard to subsequent reproductive performance, in order to attain the desired response through dietary manipulation.

The trend and accuracy of model predictions is encouraging and differences in absolute amounts of tissue mobilisation were relatively small considering the variation within and between actual data sets. Rates of protein and fat mobilisation averaged over long time durations, eg. 28 days, were not indicative of some more important fluctuations occurring at different stages of lactation. Also values of lipid mobilisation calculated indirectly in data sets will be dependent on the method of calculation used. Two factors for consideration in early lactation are; the problems associated with achieving high sow feed intakes, and the possibility for nutrients to be derived from uterine resorption. Both factors may contribute to the observed rapid flush of nitrogen excreted in the urine immediately following parturition (de Hovell et al., 1977b).

Ratios of lipid to protein and water to protein mobilised in sow tissue appeared to vary widely, though some of the extreme variance could be a consequence of inaccuracies in measurement of values close to protein or energy balance. It is possible that the ratio of water to protein (Hr:Pr) may vary, depending on the source of the tissue being mobilised, since mammary tissue contains a higher proportion of water than maternal tissue. Hence, the variance in Hr:Pr from carcass composition data for pregnant (early, 3.2 and late, 3.4), lactating (3.6) and dry (3.2) sows (Kotarbinska, 1983; Mullan and Williams, 1989) could be explained by the development of the mammary gland. Separating mammary tissue from the sow carcass therefore allows the use of a constant ratio of Hr:Pr for maternal tissue. This is supported to some extent by the narrow range in carcass water to protein ratios (2.9 to 3.3) of sows at mating, and at weaning parity 1 and 4, reported by

Whittemore and Yang (1989), for body protein contents ranging from 19.8 to 42.5. Residual differences in H:P ratio may reflect the source of tissue mobilised eg. visceral and muscle protein.

The present observations illustrated the importance of the balance of energy and protein in the diet to milk yield and sow composition changes. The simulation model also supports the contention that to a limited extent it may be more economical to utilise sow body reserves during lactation than to attempt to maintain them. Also, depending on which parameters of tissue mobilisation are linked to rebreeding interval, the composition of weight loss and therefore reproductive performance of sows could be manipulated through dietary means.

Table VI.1. Data sources used in the calculation of milk composition and production.

Source	Parity†	Day of lactation‡
de Hovell & McPherson 1977	1,2	21
& de Hovell et al 1977a		
den Hartog, et al., 19[illegible]	[illegible], +	17, 19
den Hartog, et al., 19[illegible]	[illegible]	12, 26
King and Dunkin, 1985a,b	1	14
Noblet and Etienne 1986,1987	1	8, 17
Mahon et al., 1971a,b,c	1,2	13, 16, 21, 24, 29
Noblet and Etienne, 1989	1	3, 13
O'Grady et al., 1973,1975	1,2,3+	24, 41
Harkins et al., 1989	2	10, 16, 22, 28
Van Kempen et al., 1985	2	5, 10, 15, 20, 25
Verstegen et al., 1985	2	11, 22
White et al., 1984	2	14, 21
Aherne and Speer, 1974	3+	8, 17
Boyd et al., 1982	3+	9, 18
Greenhalgh et al., 1977,1980	3+	25, 41

Table VI.2a. Coefficients by parity of parameters for milk yield prediction, as given by equation 1 in text.

Parity	a	b§	c	d	f	g	h	i	RSS	r^2
1	0.46	3.75	1.44	0.64	0.057	0.133	0.36	0.467	15.3	0.989
(SE)†	(0.01)¶	(-)	(0.78)	(0.35)	(0.02)	(0.17)	(0.16)¶	(0.224)¶		
2	0.46	4.50	0.22	1.69	0.098	-0.095	0.90	0.095	10.1	0.987
(SE)	(0.02)¶	(-)	(0.39)	(0.54)¶	(0.03)¶	(0.25)	(0.18)¶	(0.428)		
3+	0.45	4.00	0.33	1.41	0.072	0.812	2.45	6.861	28.9	0.975
(SE)	(0.02)¶	(-)	(0.33)	(0.49)¶	(0.02)¶	(0.51)	(0.48)¶	(1.945)		

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† Asymptotic standard error of coefficient

‡ RSS= residual sum of squares, r^2= non-linear regression fit

¶ significant ($P<0.05$)

§ Intercept (at day=0) fixed iteratively

Table VI.2b. Equations developed for milk composition and piglet gain.

Component	Equation	Number in text
Protein (g/d):	$P_{milk} = e^{\{4.13 + 0.897\ln(MY) + 0.00011Pi - 0.0113(Ei2/Pi)\}}$	2.
Energy (MJ/d):	$E_{milk} = e^{\{1.474 + 1.067\ln(MY) - 0.0119(Ei2/Pi)\}}$	3.
Dry matter (g/d):	$DM_{milk} = e^{\{5.1662 + 1.0737\ln(MY) - 0.00167Ei\}}$	4.
Pig gain (g/d):	$Pig_{gain} = age\ \{74.237\ e^{-0.1874age} + 0.000973\ MI\}$	5.

Table VI.3. Actual versus predicted protein and lipid mobilisation in lactating sows in response to varying protein and energy intakes.

Source	Parity	Period†	Daily intake		Daily tissue mobilisation			
Sow live weight			Protein	Energy	Protein(g/d)		Lipid(g/d)	
(kg)					Measured	Predicted	Measured	Predicted
Mullan and Williams, (1989b)								
127	1L‡	1-31	332	27	125	149	559	507
126	1L		739	66	66	11	14	+62
170	1H		332	27	163	128	826	698
171	1H		513	46	132	108	516	416
King & Dunkin (1986b)								
148	1	1-28	511	45	126	110	-	319
147	1		703	45	72	95	-	380
145	1		508	60	89	82	-	70
147	1		815	63	69	44	-	134
Verstegen et al., (1985)								
157	2	7-14	1025	60	+9	27	413	422
159	2		531	31	182	146	616	590
152	2	18-25	1244	73	+58	+43	300	519
132	2		550	33	221	173	467	582

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† Days of lactation over which tissue mobilisation was calculated

‡ L=gilts fed low feed intake in pregnancy, H= high pregnancy feed intake

Table VI.4. Comparison of predicted live weight change over lactation with data not used in parameterisation of model equations.

Daily intake		Lactation weight change§			Protein mobilised
Energy (MJDE)	Protein (gP)	Measured-87† (kg)	Measured-89‡ (kg)	Predicted (kg)	Predicted (g/d)
33.5	380	26.1	34.2	33.7	159.2
66.9	380	18.9	31.8	22.0	154.9
33.5	760	20.0	29.9	34.5	130.5
66.9	760	3.7	11.5	13.0	76.2

† Brendemuhl et al., 1987

‡ Brendemuhl et al., 1989

§ Sow live weight was 164 to 174 kg, litter size = 10, lactation length was 28 days

Figure VI.1 Derived maximal milk yield curves for parity 1, 2 and 3+ sows over lactation

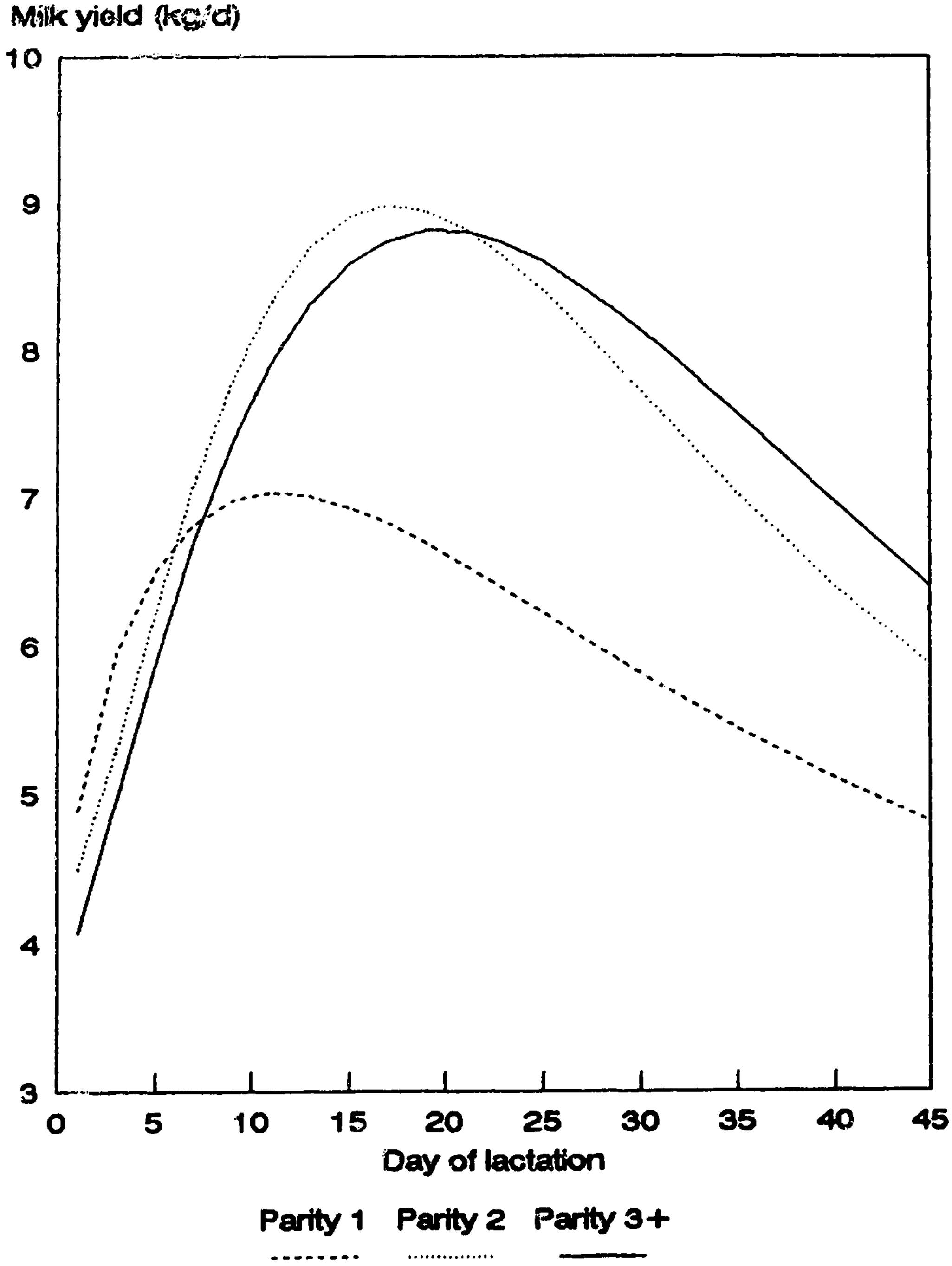


Figure VI.2 Influence of litter size on the maximum milk yield curve of parity 2 sows

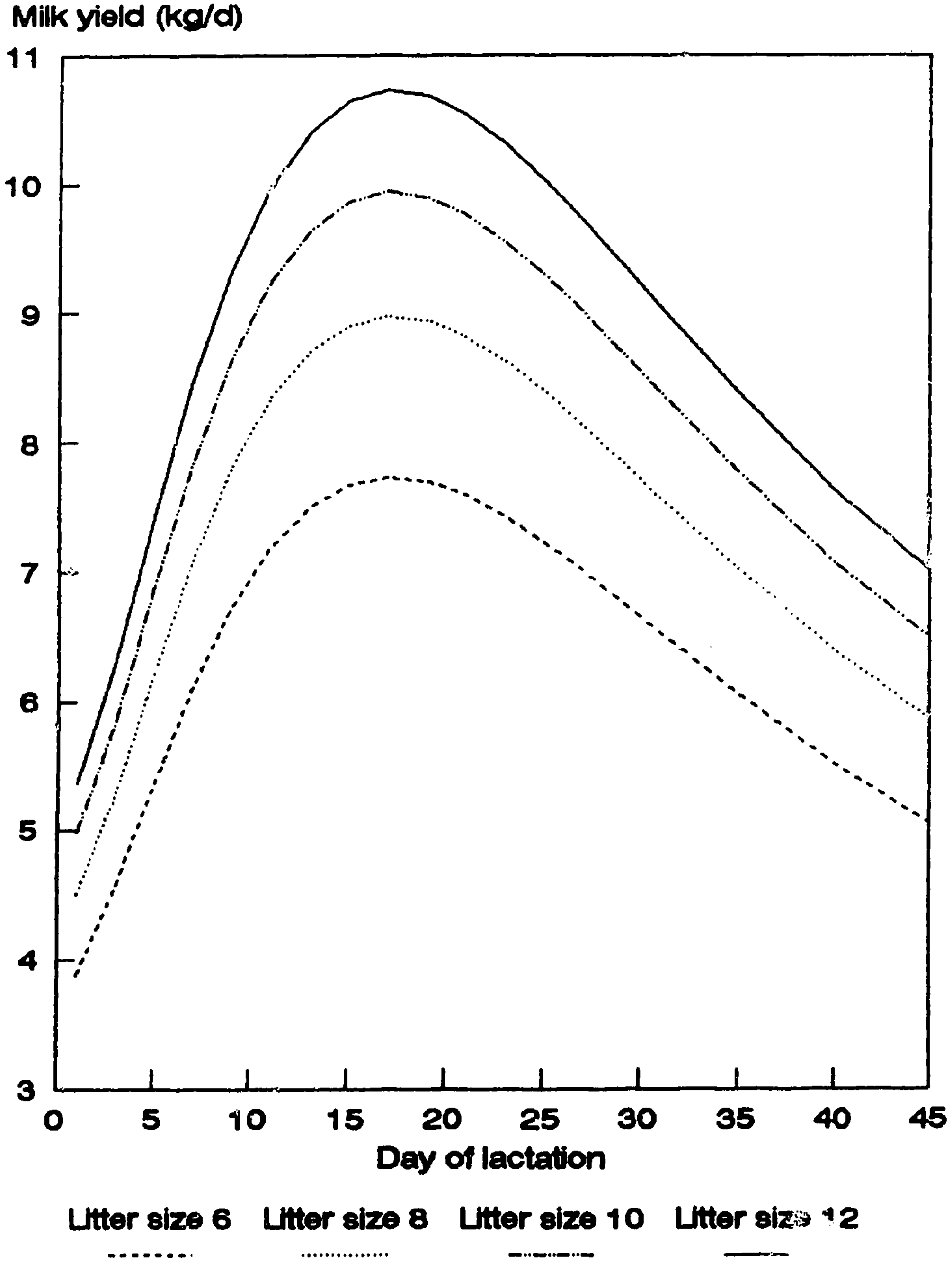


Figure VI.3 Effects of a 50% reduction below feed intake (0.5FI) for maximum milk yield on parity 1 and 3+ sows (LS=8)

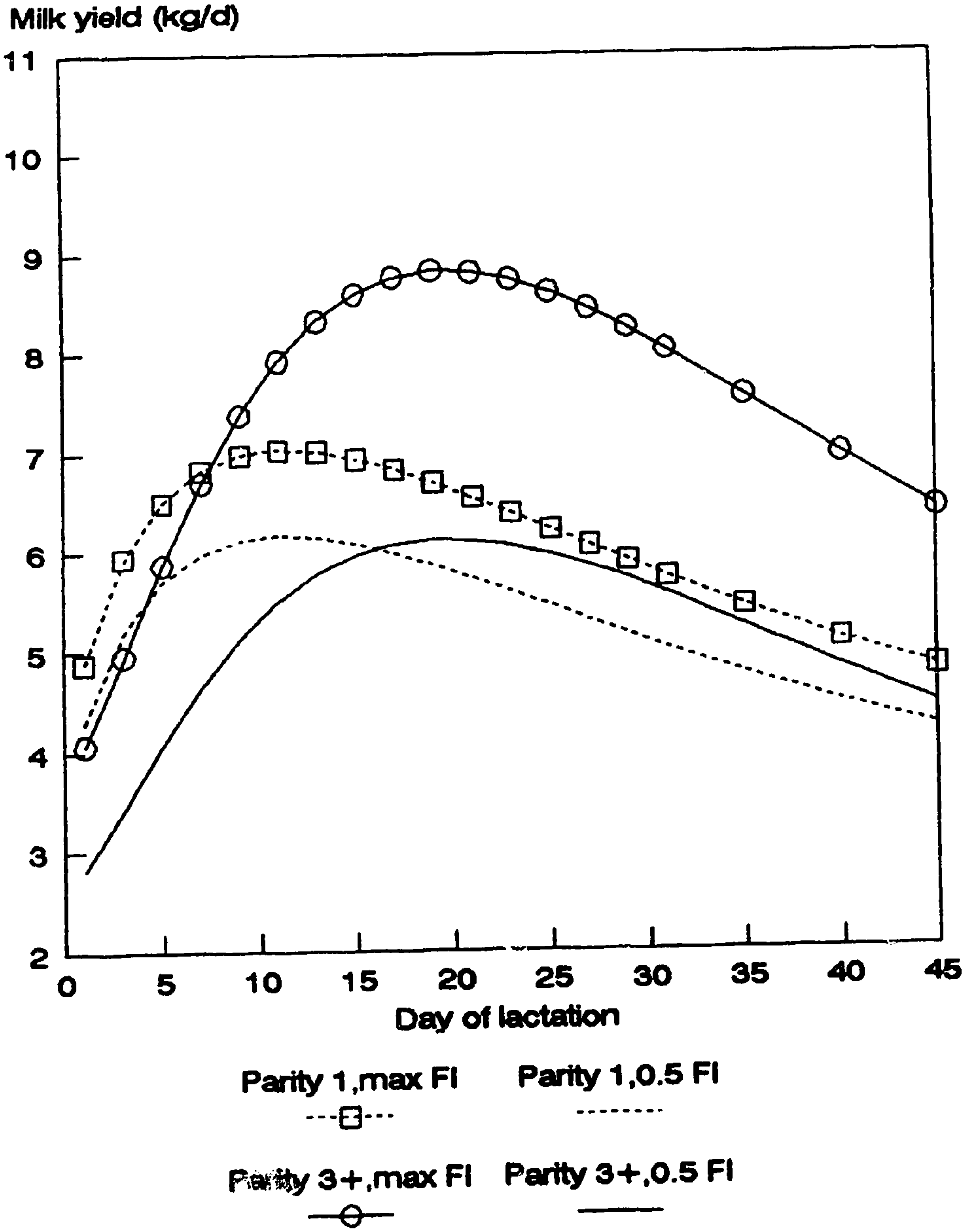
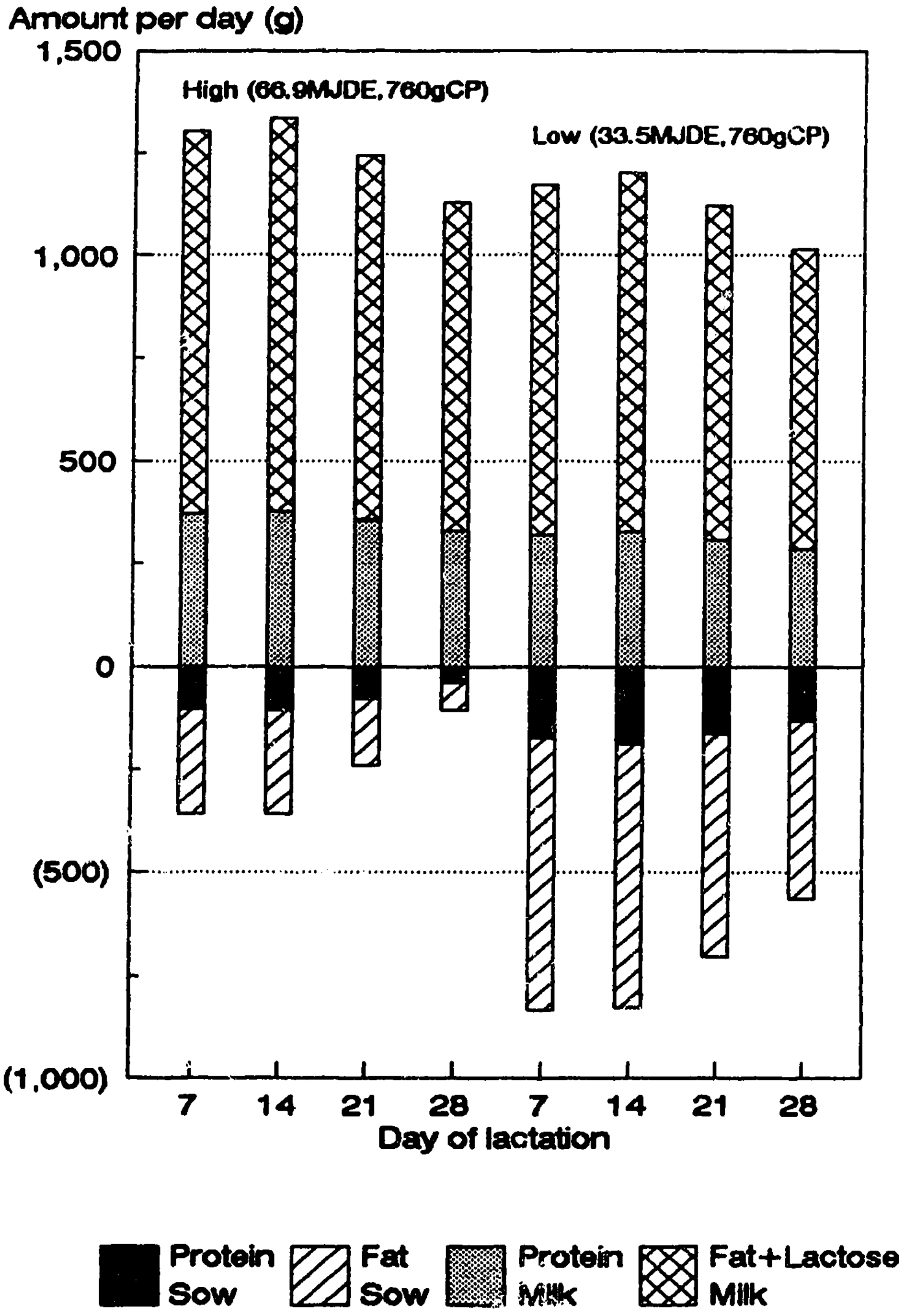


Figure VI.4 Partitioning of protein and lipid between maternal tissues and milk for sows on a high or low feed intake over a 28 day lactation



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VII. THE LINK BETWEEN NUTRITIONAL STATUS AND REPRODUCTION

A. Introduction

A large number of factors are known to be involved in determining the weaning to estrous interval in sows (Fahmy, 1981; King, 1987), some of which are related to management and genetic potential, but a large number of observed responses may be related directly or indirectly to nutrition.

Recommended feeding strategies have, in the past, allowed for the utilisation of maternal body reserves during lactation, to support milk production, on the assumption that tissue mobilisation would be predominantly lipid. With selection toward maximising lean tissue growth rates, and the introduction of gilts to the reproductive cycle at earlier ages, reproducing sows have fewer reserves with which to buffer nutritional inadequacies (Williams, 1985). 'Thin sow syndrome' has been of concern for a number of years (de Hovell et al., 1977) and the incidence of reproductive failure as a consequence of poor body condition has increased with the developments in genetic selection for lean market pigs. To this end, a large volume of research has been, and continues to be, directed at comprehension of the link between nutritional status of the sow and her reproductive performance.

Early studies have focused on the correlation between live weight loss over lactation and return to estrous or weaning to mating interval (King et al., 1983; King and Williams, 1984). Live weight alone is not necessarily a good indication of body composition or a reliable predictor of reproductive performance since animals of different body composition (Esbenshade et al., 1986; Whittemore and Yang, 1989) and experiencing different weight changes over lactation (Eastham et al., 1988) may exhibit no difference in reproductive efficiency. Conversely, sows showing similar patterns of weight change in lactation may display differences in subsequent reproductive performance (Reese et al., 1984).

Evidence of a link (negative correlation) in humans between energy status, body fatness, and plasma gonadotrophin levels gave rise to attempts to link fatness levels in swine to rebreeding interval (Kirkwood and Aherne, 1985). The hypothesis behind the importance of fat is based on the fact that adipose tissue metabolises and stores sex steroids, which are lipophilic, and may therefore influence the levels of estrogen and progesterone circulating in the blood. Fatness at parturition and backfat changes over lactation have been linked to return to estrous interval in the sow (Yang et al., 1989; Whittemore et al., 1988; King et al., 1984). Estimation of body fatness by deuterium oxide dilution in conjunction with P_2 backfat thickness measurement has failed to provide an accurate indicator of return to estrous interval in the sow (Johnston et al., 1989).

It is evident that the metabolic link between nutritional status and hormonal response is of greater complexity than can be measured by live weight or backfat thickness. Mullan and Williams (1989) demonstrated that the body compositional changes occuring in sows on different nutritional regimens were more closely linked to return to estrous. Other body components which have been suggested to be of importance to reproductive performance include rates of protein mobilisation and changes in blood metabolites (Jones and Maxwell, 1982; King et al., 1986b; [illegible]lemuhl et al., 1987). Rates of tissue mobilisation and accretion and hormonal responses are dynamic functions and are therefore difficult to measure. Recent hormonal studies have focused on the period just prior to and post weaning as being important indicators of luteinising (LH) and follicle stimulating (FSH) hormone status (Shaw and Foxcroft, 1985; King and Martin, 1989). It is therefore important to understand the metabolic changes leading up to this period and during it, in order to be able to evaluate the mechanisms involved.

In addition to the onset of estrous, nutrition during pregnancy, lactation and between weaning and mating have variously been linked to differences in ovulation rate (Hardy and Lodge, 1969; den Hartog and van der Steen, 1981; King and Williams, 1984) and litter size (Brooks and Cole, 1972; Jones and Maxwell, 1982; King et al., 1983; King and Dunkin, 1984a,b).

The purpose of this chapter was to evaluate the link between the compositional changes predicted by the model (chapters IV, V and VI) and subsequent reproductive performance (weaning to mating interval), in order to allow predictions across parities and consideration of parity to parity interactions.

B. Approach and Analyses

Data on reproductive performance (weaning to estrous, conception or mating intervals, and percentage of sows returning to estrous) were collated from the literature, for lactating sows receiving known quantities of dietary energy and protein (Table VII.1). The data were analysed for linear and non-linear relationships of reproduction with live weight and backfat thickness at the beginning of, end of, and change over, lactation. Relative change in weight and backfat were also examined, as were level of feed (energy and protein) intake. In addition, daily rates of protein and lipid mobilisation or deposition were calculated, where these were not measured experimentally, by the model described in chapters IV, V and VI. Predictions of tissue changes were tested for validity through comparison of the resultant live weight change with that observed experimentally. Functions were fitted using SAS (Cary Inc) on the basis of r^2, residual sum of squares (RSS) and coefficient significance.

C. Results

Live weight at any particular time point, and total live weight change over lactation were poor predictors of weaning to mating interval (WMI;days), as were backfat thickness (P_2) and P_2 changes over lactation. Some of the variation in P_2 values may have been due to the differences in location of measurements between British and Australian data. Relative weight change (lactation weight change/weight on day 1 of gestation; δLWT/LWTi) was curvilinearly related to WMI, and negatively related to percentage of sows in estrous by day 8 following weaning at 28 to 32 days post-farrowing (Equation VII.1, $r^2=0.964$, RSS=2566), though both varied widely. The function was also insensitive to compositional differences in weight loss (Table VII.2).

$$\begin{array}{ll}\%\text{estrus by d8} = 89.71 - 247.6\ (\delta LWT/LWTi) & \quad \ldots\ \text{VII.1.} \\ \qquad\qquad\qquad\quad (\pm 5.38)\quad (\pm 33.37) & \end{array}$$

Calculated and measured rates of protein mobilisation were more closely related to WMI and % return to estrous than rates of lipid mobilisation, since lipid mobilisation is the more variable parameter. Rates of mobilisation relative to LWT did not improve the prediction of reproductive performance above that provided by the average rates of mobilisation (averaged over the lactation period). WMI was exponentially related to average protein mobilisation rate (Pmob,g/d), the average being a reflection of the total protein change over lactation (Equation VII.2, $r^2=0.967$, RSS=220.5). Both coefficients of the response were significant ($P>0.01$), and the relationship was not improved by the inclusion of parameters relating to live weight, P_2 or lipid mobilisation rates. Where protein mobilisation was close to zero or where protein accretion occured the minimum interval to mating was just over one week (Figure VII.1).

$$\underset{(\pm 1.32)}{\mathrm{WMI} = 8.937}\ \underset{(\pm 0.0011)}{e^{(0.0066\,\mathrm{Pmob})}} \qquad \ldots\ \mathrm{VII.2.}$$

Rate of protein mobilisation at the end of lactation or averaged over the period of lactation was taken to reflect body protein changes, and hence changes in circulating metabolites in the blood, which may influence hormonal response. Luteinising hormone changes may be more closely related to reproductive performance, but measurements of LH changes were not available for the data sets used in this analysis. In addition, it may prove to be more fruitful from a modelling approach to monitor some other metabolite which is representative of sow body status and directly or indirectly linked to hormonal response eg, glucose or insulin. The relationship between protein mobilisation and measured or predicted reproductive performance is illustrated in Table VII.2.

D. Discussion

Analyses of the limited data available indicated that live weight and lipid changes over lactation were generally unreliable in the prediction of subsequent reproductive performance, though to a limited extent they will reflect the changes in protein mobilisation which appeared to be of importance. The increase in WMI with increasing body protein mobilisation was initially demonstrated experimentally by King and Dunkin (1986b) and is in agreement with the observations of Brendemuhl et al., (1987). Variation in energy to protein content in the diet resulted in considerable differences in protein mobilisation rates, and low WMI was associated with high lactation protein intake or combined high energy and protein intakes. This offers possibilities for the control of reproductive efficiency through dietary manipulation. The importance of protein in determining reproductive performance has been demonstrated previously through linear regression (King, 1987) for body protein content, protein loss and protein intake (r^2=0.63 to 0.68). The response of multiparous sows is reportedly much less than primiparous sows (Reese et al., 1982), possibly due to their higher total body protein content or differences in the extent of protein mobilisation.

The minimum number of days for WMI (8.9) is slightly greater than the time required for uterine resorption and though it is possible to rebreed sows within 4 to 5 days (Reese et al., 1982) the data used herein considers only gilts. Gilts are known to have a characteristic delayed return to estrous, but with good conditions of nutrition and management a large percentage of animals may exhibit estrus by day eight post weaning (Table VII.2). In addition it was assumed that conception occured at mating and that once estrus occured ovulation rate (number of ova shed) was not influenced by lactation weight nor change in body composition (King and Dunkin, 1986a,b). Ovulation rate has been shown to be increased in some instances by increasing feed intake (flushing) after weaning (King and Williams, 1984; Hardy and Lodge, 1969) but the response is variable and likely to be dependent on ovulation rate being suppressed initially by nutrition (Williams, 1985; Kirkwood and Aherne, 1985).

Litter size appears to be fixed at the beginning of pregnancy since it is generally not influenced by feed intake during pregnancy (Jones and Maxwell, 1982) or lactation (King et al., 1983). Some evidence exists to support a response in litter size to feed intake between weaning and mating (Brooks and Cole, 1972), which is probably a direct relationship to ovulation rate. Until better information becomes available litter size had to be assumed to be related to parity and age at first mating (Black et al., 1986), which in turn are likely to be a direct consequence of differences in ovulation rate. Embryonic survival is a variable influenced by a large number of factors (Bennet and Leymaster, 1989).

It is evident from the literature that rate of protein mobilisation is unlikely to be the only factor controlling reproductive response to nutrient intake, and it is most likely that there are a number of metabolic parameters interacting with pituitary-hypothalamic function. It is not clear what mechanisms would be available for monitoring body protein status (King, 1987) but catabolism of labile protein reserves appears to somehow influence LH secretion, through release of gonadotrophic hormone from the hypothalamus. Circulating levels of LH appear to be important in determining the return to ovarian activity in a number of domestic species. King and Martin (1989) have speculated on the mode of action of dietary and body protein on LH secretion, and have demonstrated that sows fed low protein in lactation lower LH levels (pulse interval and amplitude) 20 hours prior to and after weaning, and higher WMI than sows on a high protein diet. It is postulated that LH secretion from the pituitary is limited by gonadotrophic hormones which are peptides, released from the hypothalamus, and may be influenced by body protein status, but possibly also by a combination of other metabolite concentrations eg. glucose and insulin.

Irrespective of the ultimate mechanisms involved, the present analyses illustrated a direct response of rebreeding interval to rate of body protein mobilisation.

Table VII.1. Data sources used in the evaluation of weaning to mating interval.

Source	†Live weight range (kg)	Lactation length (d)	Data given ‡
Mullan & Williams 1989	126-171	31	δLWT,δP_2,Pmob,Lmob,WMI,%E
King & Williams 1984	144	32	δLWT,δP_2,WMI,%E
King et al., 1983	142-144	26	δLWT,δP_2,WMI
Reese et al., 1982	-	28	δLWT,δP_2,%E
Reese et al., 1984	-	28	δLWT,δP_2,%E
Brendemuhl et al., 1987	164-174	28	δLWT,δP_2,%E
King & Dunkin, 1986a	151-155	28	δLWT,δP_2,Pmob,WMI,%E
King & Dunkin, 1986b	145-148	28	δLWT,δP_2,Pmob,WMI,%E

‡ δLWT-live weight and change over lactation, δP_2-P_2 backfat and change over lactation (measured at the last rib between 45 and 80mm from the midline). Pmob-protein mobilisation (g/d), Lmob-lipid mobilisation (g/d), WMI-weaning to mating interval, %E-percentage of sows returning to estrous by given time.

† Live weight of sows on day 1 of lactation

Table VII.2. Changes in reproductive performance of sows with variation in dietary protein content; measured and predicted values.

Daily intake		Weight change		Mobilisation	Reproductive response	
Protein	Energy	over lactation		of protein	‡WMI (% estrous by d8)	
(g/d)	(MJDE/d)	(Kg)	¶LWTi(kg)	(g/d)	Measured	Predicted
Mullan & Williams, (1989)						
332	27	30.2	127	125	23 (33)	20.4 (30.8)
739	66	3.6	126	66	14.5(62)	13.8 (82.6)
332	27	45.4	170	163	21.3(29)	26.2 (23.6)
513	46	30.7	171	132	14.2(53)	21.3 (45.2)
King & Dunkin, (1986b)						
511	45	21.8	148	126	18.6(23)	20.5 (53.2)
703	45	20.8	147	72	12.9(64)	14.4 (54.6)
508	60	17.8	145	109	17.6(41)	18.4 (59.3)
815	63	9.6	147	45	12 (59)	12.0 (73.5)
Brendemuhl et al., (1987)						
380	35	34.2	168	†159	- (66)	25.5 (39.3)
380	70	31.8	174	†155	- (60)	24.8 (44.4)
760	35	29.9	173	†130	- (77)	21.1 (46.9)
760	70	11.5	164	† 76	- (87)	14.8 (72.4)

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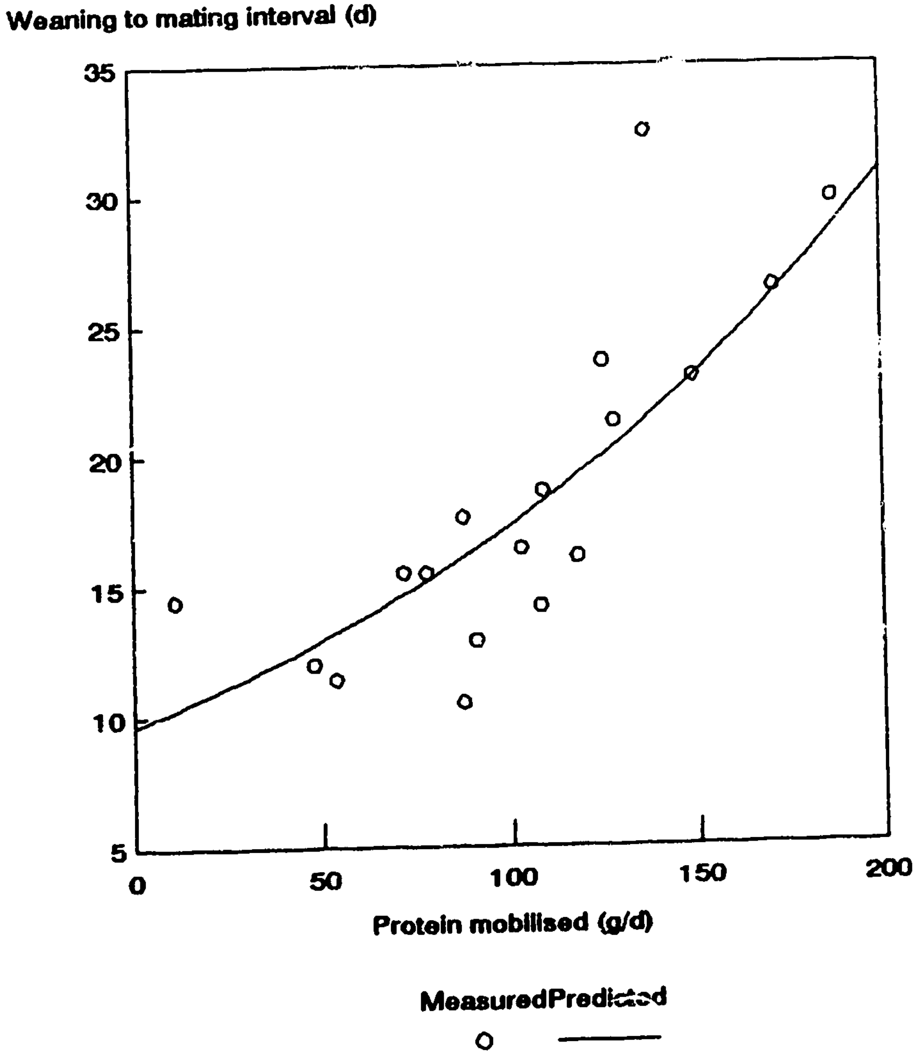
† Calculated rate of mobilisation from simulation.

‡ Weaning to mating interval in days (% of sows in estrous by 8 to 10 days)

¶ LWTi- live weight on day 1 of lactation.

Figure VII.1 Measured and predicted response of weaning to mating interval to average protein mobilisation over lactation.



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VIII. THERMOREGULATORY BALANCE AND PREDICTED FEED INTAKE

A. Introduction

The issues of thermoregulation and feed intake are dealt with together in this chapter to take account of the interrelationships of the thermal demand from the environment on metabolic heat production, feed intake and sow productivity. Under conditions of restricted feeding, changes in the thermal environment will most likely result in changes in heat production, or behavioral responses to modify heat exchange with the environment, and therefore may influence the estimated partial efficiency with which feed is utilised for production. This scenario is most likely to occur in growing finishing pigs with low cold tolerance or in dry and pregnant sows which are fed at restricted levels.

In the lactating sow, a different situation generally exists, where the key to maximum production is to stimulate maximum feed intake. Voluntary feed intake during lactation tends to lag behind the increased requirements for milk production, and in practice problems occur in attaining intakes sufficient to prevent excessive body tissue mobilisation. Some factors which may be of significance in determining *ad libitum* feed intake during lactation include the high metabolic heat production of highly productive animals, and their low heat dissipation capacity under warm environmental conditions. An imbalance between heat production and environmental thermal demand may therefore result in reduced feed intake in the lactating sow and pigs housed in warm or tropical environments (Christon, 1988), in contrast to an increase in feed intake observed in pigs housed in cold conditions (Close and Mount, 1978).

In addition to the importance of thermal balance in determining feed intake, a large number of factors have been implicated in the control of appetite and feeding behaviour (Forbes, 1986; 1988). These have been divided into physical and metabolic control of feed intake (Forbes, 1977a). The absolute level of feed intake will ultimately be a product of the physical factors controlling meal size (gut fill, passage rate), the metabolic parameters influencing feeding frequency (blood levels of glucose, insulin, peptides, catecholamines or ketones) and the neural feedback mechanisms with the brain's satiety centres (Forbes, 1988).

At the empirical level, prediction of *ad libitum* feed intake has generally been based on the assumption that animals eat to meet their energy requirements ie. for 'maintenance' plus productive processes (ARC, 1981). This approach tends to assume a value of 'maintenance' relative to live weight, and a fixed growth rate and composition (ARC, 1981; Phillips and MacHardy, 1982), or a general growth function to 'mature' weight (Parks, 1972; Headley et al., 1961, Kanis and Koops, 1990). Modelling of growth in pigs has provided a tool for more accurately estimating total energy requirements (Emmans, 1986; Black et al., 1986) and therefore predicting dietary energy intake. In addition, ruminant models have attempted to include the limitations imposed by gut capacity, visceral fatness, uterine growth (Forbes, 1977b), and dietary factors (Young, 1983).

Once nutrient requirements can be established, an animals metabolic heat production should be a direct function of productivity, and heat balance (the difference between body heat loss and heat production) can be determined by environmental (temperature, air velocity, humidity) and animal (insulation, behaviour) factors (Mount, 1972; Curtis, 1983). In turn, body heat balance, or imbalance, will influence dietary intake and nutrient utilisation, hence there is a close interrelationship between an animals ability to thermoregulate and feed intake. The purpose of this chapter was therefore to evaluate these interrelationships (of thermal balance and gut capacity) in the context of the reproducing sow model, and to establish a means of predicting feed intake by the sow, where *ad libitum* feeding is practiced.

B. Analysis and Approach

Calculation of sow heat production - Total heat production was taken to be the sum of all the heat producing processes involved in nutrient partitioning, described in the previous chapters (II to VI). Under thermoneutral conditions, total heat production (Hp, MJ/d) was therefore the sum of the energy use for support costs (Es_T), plus the metabolic costs (inefficiencies) of uterine tissue accretion (Hp_u), milk production (Hp_l), maternal tissue accretion (Hp_t), and nutrient processing to the available pools (Hp_a), equation VIII.1.

$$Hp = Es_T + Hp_u + Hp_l + Hp_t + Hp_a \qquad \text{... VIII.1.}$$

Hp from Es_T was considered to be equivalent to energy used for support costs and dissipated as heat, Hp_u was taken to be the sum of the inefficiencies of protein and lipid accretion (0.0299 and 0.0167 MJ/g, respectively) in uterine and mammary tissues. Hp_t was similarly calculated from rates of protein and lipid accretion, or protein and lipid mobilisation (0.007 and 0.0035 MJ/g, respectively). Hp_l was calculated from the sum of the energy costs of energy and protein secretion in milk ($0.28\ E_{milk} + 0.0026\ P_{milk}$), as derived from the equations in chapter VI. The use of protein in the assimilation of dietary protein and energy to the available pools (Chapter VI) was assumed to require energy since the protein would ultimately be deaminated and the nitrogen excreted with energy in the form of urea. The process therefore required 0.012 MJ of energy per gram of protein deaminated (Whittemore and Fawcett, 1976), which was derived from the associated energy costs of nutrient assimilation; the remaining energy was assumed to be dissipated as Hp_a. Metabolic heat production of pigs outside their zone of thermoneutrality was estimated following determination of the lower and upper critical temperatures (LCT and UCT, respectively) and the rate of heat loss to the environment (°C still air equivalent).

Calculation of sow heat loss - Heat increment or decrement required outside thermoneutrality was calculated by two approaches; (i) by calculation of LCT and UCT relative to environmental temperature, and hence change in thermoregulatory Hp required per degree difference (temperature gradient), or (ii) directly from calculation of the thermal demand of the environment.

(i) **Temperature gradient**: The LCT of sows was calculated either as a direct relationship to Hp (ARC, 1981; Equation VIII.2a) or with consideration of the thermal resistance (or insulative capacity) of the animal and environment (Bruce and Clark, 1979; Equation VIII.2b). UCT was calculated from the equation of Black et al., (1986; Equation VIII.3), developed on the principles applied to LCT in Equation VIII.2b (Bruce and Clark, 1979).

$$LCT = 63 - 0.06\ LWT - 0.067\ Hp \qquad \ldots\ VIII.2a.$$

Where Hp is in $kJ/kg^{0.75}/d$

$$LCT = Tb - \frac{Qn\ (Ra + Rt) - Qe\ Ra}{A\ (1 + Af\ (Ra - Rf/Rt + Rf))} \qquad \ldots\ VIII.2b.$$

Where Tb=body temperature (39 °C)
Qn=thermoneutral Hp (Watts; 1MJ/d=11.568 W)
Qe=evaporative heat loss = Ql+Qs = $A(18 + 91/LWT^{0.33})$ and the ratio of respiratory to skin losses (Ql:Qs) is assumed to be 50:50 in cold, 67:33 in warm conditions, without consideration for changes in humidity or extra water cooling.
Ra=thermal resistance of air (0.136 to 0.179 $°Cm^2/W$, in cold or hot temperatures, respectively)
Rt=thermal resistance of pig tissue (0.104 to 0.0267 $°Cm^2/W$, in cold or hot temperatures, respectively)
Rf=thermal resistance of floor (0.021 to 0.148 $°Cm^2/W$, for concrete or straw, respectively)
A =total surface area of pig = $0.09\ LWT^{0.67}$
Af=proportion of area of pig in contact with floor (0.2)

Additional assumptions are that the sow is individually housed, on concrete with straw bedding, and variations in the thermal resistances account for changes in skin temperature (32 to 39 °C), and tissue resistance with environmental temperature (hot or cold, for UCT and LCT, respectively). Other factors, eg. air flow rate, humidity and contact with other pigs, have been omitted for simplicity.

$$UCT = Tb - \frac{(Qn - Ql\ (Ra + Rt) - Qs\ Ra)}{(A\ (1 + Af\ (Ra - Rf/Rt + Rf))\ )} \qquad \ldots\ VIII.3.$$

The equations utilised here, and the assumptions stated above, were derived from published equations, and developed from functions considering radiative, conductive, convective and evaporative heat exchanges (Mount, 1972; Bruce and Clark, 1979; Curtis, 1983; Black et al., 1986). Extra thermoregulatory heat demand (kJ/kg$^{0.75}$/d/°C) below LCT was then estimated as a constant value (EHp) per degree difference between LCT and environmental temperature (LCT - Ta) and added to the estimated thermoneutral Hp (Equation VIII.1). Table VIII.1 summarises a range of measured EHp values for sows taken from the literature, and values are comparable to those for growing finishing pigs.

ii) **Thermal demand**: Total heat loss (Q) from sows was alternatively calculated in direct relationship to the thermal demand of the environment, using the equations of Bruce and Clark (1979) and Black et al., (1986), for environments below LCT or above UCT respectively, (given in Watts and converted to MJ/d). The respective equations for LCT and UCT are derived by rearrangement of this function (Equation VIII.4), hence the parameters are those described above.

$$Q = \frac{(A\ (1 + Af\ (Ra - Rf/Rt + Rf)\ (Tb - Ta) + Qe\ Ra))}{(Ra + Rt)} \qquad \ldots \text{VIII.4.}$$

At temperatures greater than UCT the modified equation of Black et al., (1986) was used; where Qe is split between Qs on the numerator, and the addition of Ql to the denominator. The difference between heat loss and calculated thermoneutral heat production was taken to be the total increment or decrement in Hp.

Thermal modification of feed intake - In the case of a requirement for extra metabolic heat production (Q > Hp), it was assumed to be met with 100% efficiency from the available energy pool, or to lead to an equivalent increase in feed intake. Where Hp exceeded Q, feed intake was diminished, following an allowance for body temperature to increase to 40 °C on the basis of the heat capacity of the sow body (3.179 LWT; kJ/°C increase in core temperature). A reduction of 1.65 to 2.5 % / °C greater than UCT was used (NRC, 1987; Close and Mount, 1978) to decrease feed intake iteratively until Hp=Q.

Predicted feed requirements - Under conditions where feed is available *ad libitum*, and assuming water is also provided *ad libitum*, the energy and protein requirements of the sow were calculated on the basis of the drive to meet maximal production of reproductive tissue (Chapter V) or milk (Chapter VI), and maximal maternal tissue protein accretion (Chapter II). A minimal level of fatness was allowed for through a consistent ratio of lipid to protein accretion in gain (Lr:Pr of 2:1) to limit energy intake to a level below that considered to be excessive. This was achieved through a reversal of the model calculations, described in the respective chapters, at maximal rates of production, and feed intake as a whole (kg/d) was determined by the first limiting nutrient, with consideration given to diet digestibility and concentration. Hence, if total protein requirements exceeded the quantity of feed required to meet total energy requirements, the animal would eat to meet protein requirements for maximal production. In a similar manner, feed requirements to maintain energy and protein balance in maternal tissue could also be the designated goal, hence protein and lipid accretion in maternal tissue would be approximately zero, and total requirements would be lower.

Metabolic heat production of the sow was then calculated, along with the heat loss to the environment, by the methods described above.

The estimated feed consumption was then derived from the balance between predicted feed requirements and the modifiers of thermal balance and limitations of gut capacity.

Physical limitations on feed intake - Predictions of *ad libitum* feed or energy intake existing for growing pigs (ARC, 1981; Kanis and Koops, 1990) in relation to live weight, do not apply well to sows and limited information is available on the physical limitations of gut size and passage rate in monogastrics. The equation of Black et al., (1986) was used for dry and pregnant sows (Equation VIII.5), with a 25% modification to allow greater intakes during lactation (0.138 $LWT^{0.803}$).

$$FI_{max} = 0.11\ LWT^{0.803} + 0.11\ LWT^{0.803}\quad 0.025\ (LCT - Ta) \quad \ldots\ VIII.5.$$

It was assumed that this limit of gut fill would only be incurred where nutrient density was very low. In addition variable limitations were applied to the maximum rate at which feed intake could increase following an increase in predicted feed requirements (Forbes, 1977a) to allow gut hypertrophy.

C. Results

Model predictions of sow heat production at thermoneutrality compared well with literature values for dry, pregnant and lactating sows (Table VIII.2), though some values appeared a little high for sows in each category on very high levels of feed intake. In lactating sows, milk production and nutrient processing composed a large proportion of the estimated total heat production, and in all animals support costs made up the largest proportion. Heat production from uterine development was relatively small.

Lower critical temperatures predicted from the equation of ARC (1981) tended to be slightly higher than the experimental measurements of heat production would indicate for sows (Table VIII.3). Calculated LCT from the equations of Bruce and Clark (1979) were generally lower than measured values and much more responsive to productivity level, as a consequence of the inclusion of heat production in the equations. Values for extra thermoregulatory heat demand varied threefold in the literature, depending on the range of temperature over which the value was measured, live weight of pigs and feed intake level (Table VIII.1). EHp was lowest for animals on the highest feed intake. The use of a single, average value for EHp per degree below LCT, was therefore associated with relatively large errors in estimated total heat production in the cold. This may be a reflection of the fact that incremental heat production is possibly non-linear, because of the substitution effect of heat production from high feeding levels (high productivity) which compensated for the heat demand of the environment.

Values calculated for upper critical temperature were quite variable and relative to recommended house temperatures (comfort zone) for lactating sows, animals on high feed intake during lactation would be only a few degrees below the UCT (Table VIII.3). Conversely, thin, dry sows on low feed intakes may experience cold stress at similar temperatures. When compared to values of LCT predicted by a similar equation (Bruce and Clark, 1979) the estimated thermoneutral zone of sows was quite wide. Predicted values for heat loss below the LCT and above the UCT also varied widely between different feed intakes and at different environmental temperatures (Table VIII.4). The equation for temperatures below LCT, developed by Bruce and Clark (1979) predicted heat losses more closely approximating the measured heat productions in cold temperatures.

Predicted feed requirements, under non-limiting conditions, closely followed the increasing demands of pregnancy and lactation (Figure VIII.1), as expected, and appeared to be quite reasonable relative to observed *ad libitum* feed intake. Table 5, illustrates the relationship between reproductive state, predicted requirements and maximal physical limits. However, it appeared most likely that high heat production (as a consequence of high productivity and nutrient intake) could quite likely become a limiting constraint at the high predicted feed intake required for maximal production (comparing Tables VIII.2,3 and 5). Therefore, calculation of feed requirement for weight stasis may approximate a more realistic feed consumption for the lactating sow, without placing her outside the calculated thermoneutral zone.

A 1.5% maximum rate of increase in feed intakes, as applied in ruminants (Forbes, 1977a), would not allow intake to increase sufficiently rapidly in the lactating sow, in order to meet demands. The unlimited rate of increase was predicted to be 0.34 to 0.27 kg/d (5.0 to 3.1%) over the first 10 days of lactation, though this would allow intake to parallel demand. A limit of 3% was applied throughout, to reflect the more highly digestible diets of pigs.

D. Discussion

Prediction of sow heat production in the model was generally good, though overestimation at high intakes may have been correlated to some extent with the increasing assimilation and nutrient processing costs, though no consistent trend could be established. The equations available for prediction of LCT gave variable results and were either insensitive or overly sensitive to heat production (and also some factors of the thermal environment). In addition estimates of extra thermoregulatory heat production required below LCT are also variable, and influenced by animal and environment factors. EHp is a direct estimate of tissue thermal resistance and will therefore be influenced by environmental temperature, boundary layer factors and body fat content.

Estimates of heat loss, LCT, and UCT based on the physical principles of a black body (Bruce and Clark, 1979; Black et al., 1986) have obvious limitations, but do attempt to consider some of the factors which lead to variation in the experimental estimates of EHp. The experimental LCT for sows appeared to be somewhere between the values calculated by the different equations (ARC, 1981; Bruce and Clark, 1979). The combination of highly variable estimates of EHp and corresponding variation in estimated LCT would tend to result in large errors in predicted total heat loss/production. The calculation of total heat loss from the equation of Bruce and Clark (1979) at temperatures below LCT, and Black et al., (1986) at temperatures above UCT, provided the best means of estimating the required increment or decrement in heat production.

The low LCT and UCT values predicted for sows on high levels of intake, or highly productive, suggests that temperatures in the lactation barn can afford to be kept fairly cool, provided supplemental heating can sufficiently warm the piglets. Increases in feed intake can provide considerable amounts of heat production (Holmes and McLean, 1974) to combat low temperatures and it has been suggested that the efficiency of growth is increased at temperatures around LCT (Phillips and McHardy, 1982). The basis for this observation is that heat from production can supply part of the heat required for thermoregulation.

Environmental temperature has been reported to influence animal production in a number of ways; changes in body composition (Dauncy and Ingram, 1983; Close and Stainer, 1984; Le Dividich et al., 1987), rates of protein metabolism (Fuller, 1965; Lindsay et al., 1988) and digestive function (Kennedy et al., 1977). Most of the observed changes will likely be effected through the changes in nutrient availability consequent from the response of feed intake to thermal balance. The model will not, however, take account of changes in gut function and/or hormonal responses to temperature, or adaptive changes known to occur over a period of weeks exposure (Verhagen et al., 1987; Young, 1983). Similarly adaptive mechanisms are also important in estimation of the lag in feed intake in response to increased or decreased metabolic demand, and require further quantification in the monogastric. Another phenomenon which has proved difficult to quantify and model is the link between high pregnancy feed intake, and low lactation feed intake observed in the reproducing sow (Williams, 1985). High pregnancy feed intake tends to result in lower lactation feed intakes, possibly as a result of the catabolic nature of lactating sows, and the prefence for tissue mobilisation over feed utilisation in fat sows.

In conclusion, metabolic heat production at thermoneutrality can be reasonably predicted by the model. The change in heat production as a consequence of temperatures outside the zone of thermoneutrality was best estimated by use of Equation VIII.4 (Bruce and Clark, 1979; Black et al., 1986) which gave a direct estimate of heat loss to the environment. This required that LCT and UCT were calculated by the modified equations (VIII.2b and VIII.3, respectively) in order to determine which version of equation VIII.4 should be used, ie. in which zone the sow was operating. The resulting imbalance between heat production and heat loss then influenced either the nutrients available for production at fixed feed intake, or the predicted level of feed intake, under *ad libitum* conditions. Predicted feed requirements were then checked against physical limitations to give estimated feed consumption.

This method allowed for reasonable estimation of feed intake, in light of the large variation observed in experimental and practical measures of *ad libitum* feed intake, and the large number of variables known to influence feeding behaviour.

Table VIII.1. Sources of data used to evaluate the extra thermoregulatory heat demand of pigs from cold environments.

Source	Live weight and stage	(kg)	‡EHp (kJ/d/kg$^{0.75}$/°C)	Temperatures (°C)
Close & Mount 1978	Growing	21-38	18.9	10 - 30
Verstegen et al., 1971/73	Growing	25-30	7.4 - 11.3	8 - 20
Noblet et al., 1987	Growing	35-50	15.5	13 - 23
Le Dividich et al., 1987	Growing	30-97	8.9 - 19.5	12 - 28
de Hovell et al., 1977	Sow(Dry)	91-160	14.6 - 21.0	5 - 20
Verhagen et al., 1986/87	Sow(Preg)	160-195	8.6 - 22.0	11 - 24
Kemp et al., 1987	Sow(Preg)	160-197	10.2 - 20.7	12 - 24

‡ EHp = Extra thermoregulatory heat production required per degree temperature below LCT.

Table VIII.2. Model predictions of sow thermoneutral heat production as compared with experimental conditions.

Live weight	Experiment temp	Dietary intake		Heat production	
		Energy	Protein	Measured	Predicted
(kg)	(°C)	(MJDE)	(gCP)	(kJ/kg$^{0.75}$/d)	
160	18 Preg	22.5	230	475	470
185	18 Preg	27.7	283	474	523
91	20 Dry	12.6	134	485	478
162	20 Dry	18.1	192	469	447
96	20 Dry	19.9	211	505	551
162	20 Dry	26.6	282	466	541
150	18 Dry	20.6	252	429	469
180	18 Dry	27.3	335	449	486
185	18 Dry	41.1	504	470	584
185	18 Dry	34.2	419	462	554
230	18 Dry	41.1	504	421	597
230	18 Preg	41.1	504	452	621
175	18 Lact	59.6	646	707	841
176	18 Lact	43.5	686	634	694
154	18 Lact	49.1	769	682	682
150	18 Lact	27.4	423	542	619
172	18 Lact	46.4	769	721	692
186	18 Lact	31.1	480	531	649

Table VIII.3. Predicted values for lower and upper critical temperatures of dry, pregnant and lactating sows, relative to experimental temperature.

Live weight (kg)	Environmental temperature (°C)	Lower critical temperature† (°C)		Upper critical Temperature† °C
		ARC	Bruce&Clark	Black et al
160	18 Preg	21.6	16.9	26.3
185	18 Preg	20.1	14.1	24.2
91	20 Dry	25.0	25.2	32.1
162	20 Dry	21.8	16.9	26.3
96	20 Dry	23.3	23.8	31.3
162	20 Dry	22.0	17.1	26.4
150	18 Dry	25.2	20.4	28.4
180	18 Dry	22.0	16.0	25.4
185	18 Dry	20.3	14.3	24.3
185	18 Dry	20.9	14.8	24.5
230	18 Dry	20.9	12.8	22.4
230	18 Preg	18.9	10.7	21.2
175	18 Lact	5.1	2.0	17.8
176	18 Lact	9.9	6.1	20.0
154	18 Lact	8.1	7.0	21.2
150	18 Lact	17.6	14.7	25.4
172	18 Lact	4.4	1.8	17.8
186	18 Lact	16.2	10.6	22.2

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† Predictions from equations VIII.2a (ARC, 1981); VIII.2b (Bruce and Clarke, 1979); VIII.3 (Black et al., 1986)

Table VIII.4. Predicted heat loss to the environment below lower critical temperature and above the upper critical temperature for sows housed at different environmental temperatures.

			Heat production				
Live weight	Experimental temperature		Measured	Below LCT		Above UCT	
				At Te‡	At 15°C	At Te‡	At 30°C
(kg)	(°C)		(kJ/kg$^{0.75}$/d)	(kJ/kg$^{0.75}$/d)		(kJ/kg$^{0.75}$/d)	
160	24	Preg	418	469	801	117	183
160	21	Preg	443	426	687	117	218
160	18	Preg	475	497	687	117	248
197	23	Preg	465	324	587	92	152
185	21	Preg	464	382	615	99	182
185	18	Preg	474	446	616	99	210
91	20	Dry	485	687	1048	220	326
162	20	Dry	469	445	680	115	169
96	20	Dry	505	660	1007	207	307
162	20	Dry	466	445	680	115	169
90	5	Dry	853	1239	1057	223	330
168	5	Dry	768	776	662	110	162
91	5	Dry	809	1229	1048	220	326
171	5	Dry	746	766	653	108	159
150	18	Dry	429	522	720	125	267
180	18	Dry	449	455	628	102	217
185	18	Dry	470	446	616	99	210
185	18	Dry	462	446	616	99	210
230	18	Dry	421	378	523	77	163
230	18	Preg	452	378	523	77	163
175	18	Lact	707	570	747	105	155
176	18	Lact	634	568	745	105	154
154	18	Lact	682	629	825	122	179
150	18	Lact	542	643	842	125	185
172	18	Lact	721	577	757	107	158
186	18	Lact	531	543	712	98	144

‡ Te = environmental temperature used in experiment

Table VIII.5. Predicted feed intake required for maximum production or weight stasis in dry, pregnant and lactating sows.

Stage of cycle		Requirements for			Physical limit
(Live weight)		Energy	Protein	Feed ‡	on feed intake
	(kg)	(MJ/d)	(g/d)	(kg/d)	(kgDM/d)
Maximum growth:					
Lactation-mid	(205)	93.8	1098	7.21	9.82
Parity 1 sow	(160)	99.3	1149	7.60	8.09
Lactation-early	(200)	119.4	1384	9.18	9.68
Parity 1 sow	(170)	103.7	1201	7.98	8.49
Pregnancy-late	(198)	28.7	378	3.15	7.68
Pregnancy-mid	(143)	26.5	331	2.76	5.92
Dry	(120)	26.7	339	2.82	5.14
Weight stasis:					
Dry	(120)	18.2	150	1.46	5.14
Pregnant-early	(125)	18.6	161	1.49	5.31
Pregnant-late	(147)	21.9	243	2.03	6.05
Lactating-early	(160)	79.6	972	6.12	8.09
Lactating-mid	(160)	105.5	1259	8.11	8.09

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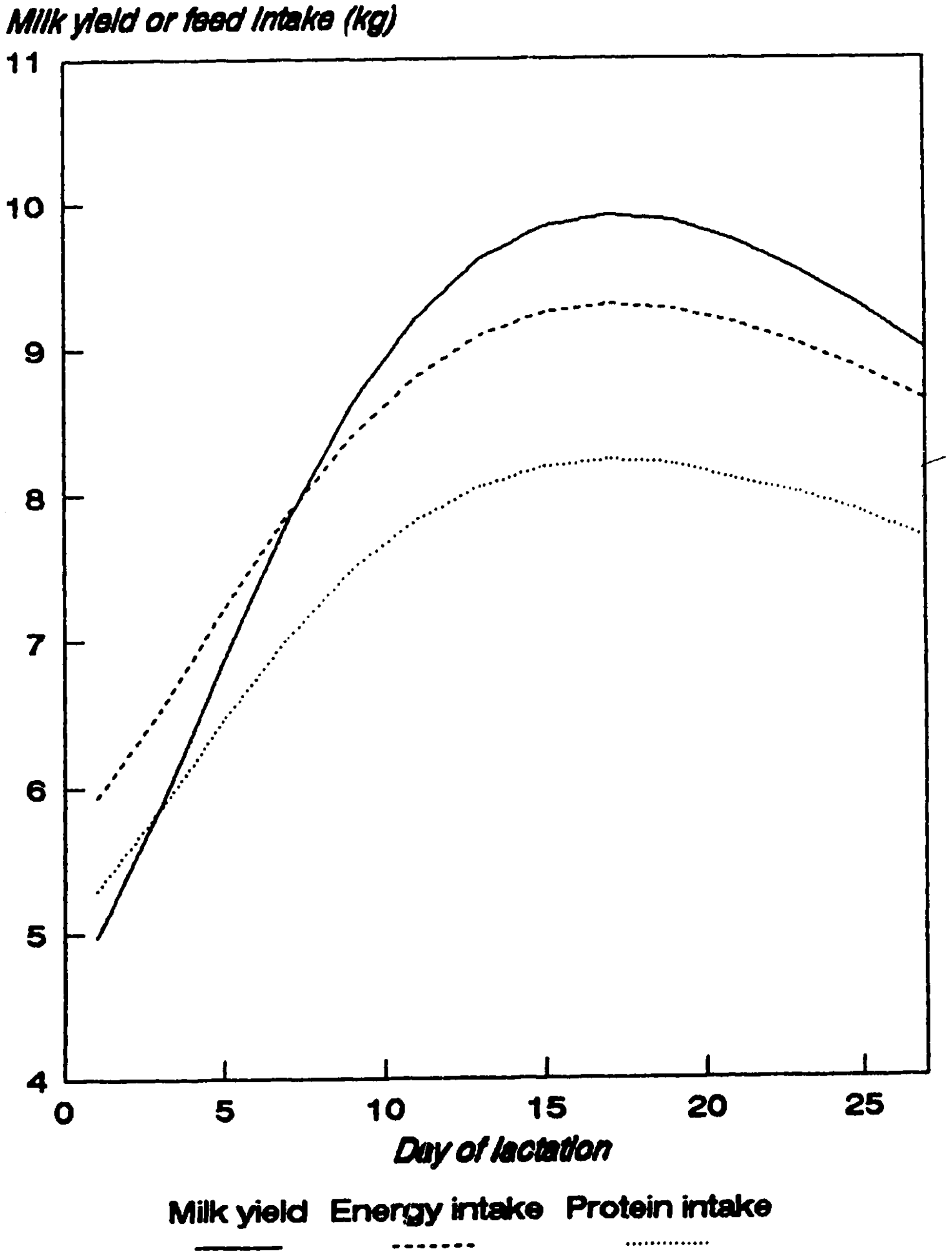
‡ Assuming the efficiency of conversion of dietary protein and energy to available forms of 0.7 and 0.85, respectively. Dry and pregnant sow diet taken to contain 12.5 MJDE/kg, 120gCP/kg and lactating sow diet to contain 13MJDE/kg and 170gCP/kg. Litter size was fixed at 10.

Figure VIII.1 Predicted feed requirements to meet milk yield over lactation.



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IX. GENERAL DISCUSSION

Modelling the reproducing sow required that a large volume of scientific research was scrutinised and compiled into one interactive medium, and therefore allowed critical examination of the existing knowledge base. The benefits of this process are many fold, but perhaps most important is the information which was found to be unavailable for modelling the sow, and the areas pinpointed in the model for further research effort. Numerous hypotheses were tested in the development of individual modules of the model, and further testing is possible with the complete model. The model also permits evaluation of nutritional strategies for parts of, or the whole, reproductive cycle, and allows for examination of nutritional manipulation of body composition and reproduction.

Some important concepts elucidated by the model, which require further experimental examination include the genetics of maximal rates of protein accretion and the body protein growth of older sows approaching 'maturity', both in reproducing and barren sows. In addition the relationship between rate of protein accretion and availability of protein and energy requires further elucidation, particularly at low nutrient intakes, or in the case of negative rates of protein accretion. The drive for protein accretion and the energetics of this process are central to partitioning in the model and better knowledge in this area for reproducing sows should be a priority in research programs, and is presently being investigated by Australian researchers (R.H. King, personal communication).

The concept of 'maintenance' has elicited lengthy discussion for decades and has been the focus of much experimentation. The sow model used the concept of support costs to allow for increased costs associated with the productive state, rather than assume a constant 'maintenance' with diminishing partial efficiency of productive processes. A great deal of uncertainty still remains as to the exact energy requiring processes accounted for in these estimates, or the processes which may change with a change in productivity. This is evident even in models of a greater level of complexity, where many energy requiring processes are individually accounted for, yet addition of a purely empirical 'maintenance' or 'fasting metabolism' is required to balance the accounts (Gill et al., 1990; France et al., 1986; Gill et al., 1984).

Body composition changes throughout the reproductive cycle are of prime importance in subsequent reproductive performance and could be reasonably predicted in the model. However, limited carcass data is available for reproducing sows to test this aspect, and more experimental measurements of rates of protein and lipid accretion in various body components are also required. In addition metabolic parameters of nutritional status must be monitored in order to provide better information on the link between nutrient balance and hormonal changes responsible for estrous activity. This is particularly important during lactation where the sow did not appear to utilise dietary protein and energy very efficiently. This may have been a consequence of the priorities and efficiencies of nutrient use built into the model, though it appears most likely a result of changes in the underlying physiology of the lactating animal. The sow would appear to have some mechanism to monitor the level of body tissue reserves and the extent of their mobilisation (King, 1987).

Ad libitum feed intake of lactating sows is probably one of the most important variables controlling performance in commercial sow herds, since selection of pigs for greater rates of lean tissue gain has inadvertently led to reduced *ad libitum* intake (Kanis and Koops, 1990). Feed intake is highly variable in practice and therefore remains difficult to predict, unless a more mechanistic approach can be developed. Little information is available on digesta passage rates, gut capacity and rate of metabolic adaptation to changes in feed intake in pigs.

Future modification of the sow model will likely require translation of nitrogen relationships to expression of amino acids relative to the concept of ideal protein, or lysine. It may also necessitate estimation of protein synthesis and breakdown rather than simply the balance of these which is accretion. Further quantification of the response of protein accretion to available amino acids and energy will be a corollary to this. The model will also require a better metabolic status indicator, for linkage with predicted reproductive hormone response.

In conclusion, some important lessons were derived from the modelling process. Firstly Animal Scientists need to better plan and report experiments in order that information generated will be applicable and useable in the context of the comprehension of systems as a whole. Secondly, analyses of data generated requires that we utilise more complex and appropriate mathematical interpretation. Simulation modelling provides a powerful tool to facilitate an integrated systems approach to Animal Science.

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X. APPENDIX 1. MODEL EQUATIONS FOR TURBOSOW

```
/*
   Calculation module for Turbo-sow
   VERSION 0.1 (pre-release)
*/
#include "sow.h"
#include "math.h"
int sowcalc(int mode)
{
/*
   INTEGER VARIABLES
*/
unsigned
 itemp,         /* temporary value */
 intrupt,       /* 0 -> not interrupted,  1 - calculations
interrupted */
 cur_state,     /* 0 = dry  4 = preg 8 = lact */
 day_cyc,       /* day of the current cycle */
 parity         /* current parity */
;
/*
   FLOAT VARIABLES
*/
float
 rtemp1,        /* temporary variables */
 rtemp2,
 livewt,        /* livewt in kgs at start of current day */
 dmi,           /* dry matter intake */
 ei,            /* energy intake */
 pi,            /* protein intake g/kg DM */
 pi_tot,        /* total protein intake g */
 dige,          /* digestibility of energy */
 digp,          /* digestibility of protein */
 hp,            /* heat production */
 pro_bdy,       /* body protein level in gms? */
 en_tot,        /* total intake energy */
 ni_tot,        /* total nitrogen intake */
 ni_dig,        /* digestible nitrogen */
 ni_av,         /* available nitrogen */
 ni_dec,        /* ni_dig - ni_av     */
 ni_deam,       /* additional nitrogen from deamination */
 en_dig,        /* digestible energy */
 en_av,         /* available energy */
 en_fec,        /* fecal energy */
 fet_wt,        /* weight of fetuses */
 fet_wt_p,      /* weight of fetuses (previous day)*/
 fet_pro,       /* weight of protein in fetuses */
 fet_pro_p,     /* weight of protein in fetuses (previous
day) */
 fet_water,     /* weight of water in fetuses */
```

```
fet_fat,       /* weight of fat in fetuses */
fet_fat_p,     /* weight of fat in fetuses (previous day)*/
fet_ash,       /* weight of ash in fetuses */
lwt_pregl,     /* liveweight on day 1 of preganancy */
lwt_lactl,     /* liveweight on day 1 of lactation */
memb_wt,       /* weight of membranes and fluids */
memb_wt_p,     /* weight of membranes and fluids (previous
day) */
memb_pro,      /* weight of protein in membranes and
fluids */
memb_pro_p,    /* weight of protein in membranes and
fluids (previous day)*/
memb_water,    /* weight of water in membranes and fluids
*/
memb_fat,      /* weight of fat in membranes and fluids */
memb_fat_p,    /* weight of fat in membranes and fluids
(previous day) */
ute_wt,        /* weight of uterus */
ute_wt_p,      /* weight of uterus (previous day)*/
ute_pro,       /* weight of protein in uterus */
ute_pro_p,     /* weight of protein in uterus (previous
day)*/
ute_water,     /* weight of water in uterus */
ute_fat,       /* weight of fat in uterus */
ute_fat_p,     /* weight of fat in uterus (previous day)*/
ute_ash,       /* weight of ash in uterus */
milk_yld,      /* milk yield              */
milk_en,       /* milk energy             */
milk_pro,      /* milk protein            */
milk_dry,      /* milk dry matter         */
milk_ash,      /* milk ash                */
milk_fat,      /* milk fat + lactose      */
pigl_gain,     /* piglet gain g/d/piglet   */
mamm_wt,       /* weight of mammary glands */
mamm_wt_p,     /* weight of mammary glands (previous day)
*/
mamm_pro,      /* weight of protein in mammary glands */
mamm_pro_p,    /* weight of protein in mammary glands
(previous day) */
mamm_water,    /* weight of water in mammary glands */
mamm_fat,      /* weight of fat in mammary glands */
mamm_fat_p,    /* weight of fat in mammary glands
(previous day) */
ni_ret_p,      /* retained nitrogen (predicted) */
ni_ret,        /* retained nitrogen (actual) */
pro_ret,       /* retained protein */
en_pr,         /* energy in retained protein */
en_pr_c,       /* energy cost of retained protein */
en_bm,         /* energy for background & machinery */
fat_ret,       /* retained fat */
en_fat,        /* energy in retained fat */
en_fat_c,      /* energy cost of retained fat */
```

```
 lwg           /* live weight gain */
;
/*
   mode  0  - reinitialize  (from day 0)
 MODE_INI
         1  - continue from point of interruption
 MODE_CON
         2  - continue from point with new initial values
 MODE_NEW
*/
intrupt = 0;
if (mode == MODE_INI || cur_day[cur_dset] == 0)
   {
   parity = drive[cur_dset][IPARITY - DRIVE];
   cur_day[cur_dset] = 0;
   mode == MODE_INI;
   rtemp1 = 1.0/log(drive[cur_dset][AGE - DRIVE]);
   rtemp2 = log(drive[cur_dset][ILIVEWT - DRIVE]);
   pro_bdy =  -103.4 + 396.58*rtemp1 + rtemp2*(32.07 -
118.37*rtemp1);
   store[cur_dset][cur_day[cur_dset]][LIVEWT] =
drive[cur_dset][ILIVEWT - DRIVE];
   if (drive[cur_dset][ISTATE - DRIVE] == 1)
      {
      flags[cur_dset][cur_day[cur_dset]] = PREGNANT;
      day_preg[cur_dset] = drive[cur_dset][IDAY - DRIVE];
      cur_state = PREGNANT;
      }
   else if (drive[cur_dset][ISTATE - DRIVE] == 2)
      {
      flags[cur_dset][cur_day[cur_dset]] = LACTAT;
      day_lact[cur_dset] = drive[cur_dset][IDAY - DRIVE];
      cur_state = LACTAT;
      }
   else
      {
      flags[cur_dset][cur_day[cur_dset]] = 0;   /* dry */
      day_dry[cur_dset] = drive[cur_dset][IDAY - DRIVE];
      cur_state = DRY;
      }
   }
else
   pro_bdy = store[cur_dset][cur_day[cur_dset]-1][PR];
if (mode != MODE_CON)
   store[cur_dset][cur_day[cur_dset]][LIVEWT] =
drive[cur_dset][ILIVEWT - DRIVE];
while (cur_day[cur_dset] <= drive[cur_dset][RUN_DAYS -
DRIVE] && intrupt == 0)
   {
   /*
     ______________________________________________
      Find the appropriate feed values - based on current
```

```
state
   ----------------------------------------
   */
   if (cur_state == PREGNANT)
      {
      day_cyc = day_preg[cur_dset];
      if (day_preg[cur_dset] <= drive[cur_dset][PREG1_CYC
- DRIVE])
         {
         dmi  = drive[cur_dset][DMI_P1 - DRIVE];
         ei   = drive[cur_dset][EI_P1 - DRIVE];
         pi   = drive[cur_dset][PI_P1 - DRIVE];
         dige = drive[cur_dset][DIGE_P1 - DRIVE];
         digp = drive[cur_dset][DIGP_P1 - DRIVE];
         }
      else
         {
         dmi  = drive[cur_dset][DMI_P2 - DRIVE];
         ei   = drive[cur_dset][EI_P2 - DRIVE];
         pi   = drive[cur_dset][PI_P2 - DRIVE];
         dige = drive[cur_dset][DIGE_P2 - DRIVE];
         digp = drive[cur_dset][DIGP_P2 - DRIVE];
         }
      }
   else if (cur_state == LACTAT)
      {
      day_cyc = day_lact[cur_dset];
      if (day_lact[cur_dset] <= drive[cur_dset][LACT1_CYC
- DRIVE])
         {
         dmi  = drive[cur_dset][DMI_L1 - DRIVE];
         ei   = drive[cur_dset][EI_L1 - DRIVE];
         pi   = drive[cur_dset][PI_L1 - DRIVE];
         dige = drive[cur_dset][DIGE_L1 - DRIVE];
         digp = drive[cur_dset][DIGP_L1 - DRIVE];
         }
      else
         {
         dmi  = drive[cur_dset][DMI_L2 - DRIVE];
         ei   = drive[cur_dset][EI_L2 - DRIVE];
         pi   = drive[cur_dset][PI_L2 - DRIVE];
         dige = drive[cur_dset][DIGE_L2 - DRIVE];
         digp = drive[cur_dset][DIGP_L2 - DRIVE];
         }
      }
   else
      {
      day_cyc = day_dry[cur_dset];
      dmi  = drive[cur_dset][DMI_D - DRIVE];
      ei   = drive[cur_dset][EI_D - DRIVE];
      pi   = drive[cur_dset][PI_D - DRIVE];
      dige = drive[cur_dset][DIGE_D - DRIVE];
```

```
     digp = drive[cur_dset][DIGP_D - DRIVE];
     }
  /*
    ------------------------------------------
    Get the current liveweight (at start of day)
    ------------------------------------------
  */
  livewt = store[cur_dset][cur_day[cur_dset]][LIVEWT];
  /*
    ------------------------------------------
    Initialize heat production
    ------------------------------------------
  */
  hp = 0;
  /*
    ------------------------------------------
          Total Energy intake Mj
    ------------------------------------------
  */
  en_tot = ei*dmi;
  /*
    ------------------------------------------
          Total Protein intake grams
    ------------------------------------------
  */
  pi_tot = pi*dmi;
  /*
    ------------------------------------------
          Total Nitrogen intake grams
    ------------------------------------------
  */
  ni_tot = pi_tot/6.25;
  /*
    ------------------------------------------
    Digestible energy
    ------------------------------------------
  */
  en_dig = en_tot * dige/100;
  /*
    ------------------------------------------
    Digestible nitrogen
    ------------------------------------------
  */
  ni_dig = ni_tot * digp/100;
  /*
    ------------------------------------------
    Available energy
    ------------------------------------------
  */
  en_av = en_dig*0.98*(1.357 - 0.0262 *
(en_dig*en_dig/pi_tot) - 0.0028 * livewt);
  /*
```

```
      ----------------------------------------
      Available nitrogen
      ----------------------------------------
    */
    ni_av = ni_dig - (-69.757 +
(pi_tot/livewt)*(36.434-3.009*(pi_tot/livewt)) +
4.3577*en_dig*en_dig/pi_tot);
    /*
      ----------------------------------------
      nitrogen decrement (difference between digestible and
available nitrogen)
      ----------------------------------------
    */
    ni_dec = ni_dig - ni_av;
    if (ni_dec < 0)
       {
       ni_av = ni_dig;
       ni_dec = 0;
       }
    /*
      ----------------------------------------
      Increment heat production for nitrogen decrement
      ----------------------------------------
    */
    hp += (en_dig*0.98 - en_av) - (ni_dec*0.075);
    /*
      ----------------------------------------
      Fecal energy = tot_en - dig_en
      ----------------------------------------
    */
    en_fec = en_tot - en_dig;
    /*
      ----------------------------------------
      Dry sow mammary gland mass (grams), uterus, and milk
      ----------------------------------------
    */
    if (cur_state == DRY)
       {
       mamm_wt    = 1107.3 ;
       mamm_pro   = 117.15*pow(mamm_wt,0.8915);
       mamm_water = 365.4*pow(mamm_wt,1.2838);
       mamm_fat   = 460*pow(mamm_wt,0.6955);
       milk_yld   = 0.0;
       milk_pro   = 0.0;
       milk_en    = 0.0;
       ute_wt     = 397.34;
       ute_pro    = 60.38;
       ute_water  = 294.98;
       ute_ash    = 3.97;
       ute_fat    = 38.01;
       }
    /*
```

```
    /*
      ─────────────────────────────────────
      Fetal calculations  (if pregnant)
      ─────────────────────────────────────
    */
     if (cur_state == PREGNANT)
       {
       if (day_preg[cur_dset] == 1)
          lwt_pregl = livewt;
       else
          {
          ute_wt_p = ute_wt;
          ute_fat_p = ute_fat;
          ute_pro_p = ute_pro;
          memb_wt_p = memb_wt;
          memb_fat_p = memb_fat;
          memb_pro_p = memb_pro;
          fet_wt_p = fet_wt;
          fet_fat_p = fet_fat;
          fet_pro_p = fet_pro;
          }
       fet_wt = drive[cur_dset][LS - DRIVE]*exp(8.496 -
9.494*exp(-0.017*day_preg[cur_dset]))/(1 + 4.83/en_dig -
4.55/ni_tot);
       fet_pro = exp(7.367 - 4.97*exp(-0.00026*fet_wt));
       fet_water = 1.1017 * pow(fet_wt,0.9697);
       fet_ash   = fet_wt * (.01817 + 0.0000016*fet_wt);
       fet_fat   = fet_wt - (fet_pro + fet_water + fet_ash);
       memb_wt   = fet_wt
*(48.697*exp(-0.0415*day_preg[cur_dset]));
       memb_pro  = memb_wt
*(0.0087*exp(0.0146*day_preg[cur_dset]));
       memb_water= memb_pro
*(78.97*exp(-0.0099*day_preg[cur_dset]));
       memb_fat  =
drive[cur_dset][LS]*(1.6*exp(0.0075*day_preg[cur_dset]));
       ute_wt    = 442.03*exp(0.0273*day_preg[cur_dset]) -
44.69*exp(0.0427*day_preg[cur_dset]);
       ute_pro   = 20.924 + 0.0993 * ute_wt;
       ute_water = 34.46 + 0.847 * ute_wt;
       ute_ash   = 0.01 *ute_wt;
       ute_fat   = ute_wt - (ute_pro + ute_water + ute_ash);
       milk_yld   = 0.0;
       milk_pro   = 0.0;
       milk_en    = 0.0;
       /*
          Add in mammary gland growth in after 60 days of
pregnancy
       */
       if (day_preg[cur_dset] > 59)
          {
          rtempl    = day_preg[cur_dset] -
```

```
(drive[cur_dset][PREG_CYC - DRIVE] + 1);
            mamm_wt_p = mamm_wt;
            mamm_wt   = 1107.3 + 3521*exp(0.118*rtemp1);
            }
        }
    /*
      -----------------------------------------
      Milk production calculations  (if lactating)
      -----------------------------------------
    */
    else if (cur_state == LACTAT)
        {
       if (day_lact[cur_dset] == 1)
          lwt_lact1 = livewt;
       if (parity == 1)
          {
          rtemp1 = 0.46*log(drive[cur_dset][LS -
DRIVE])*(3.75 +
1.439*pow(day_lact[cur_dset],0.6436)*exp(-0.059*day_lact[cu
r_dset]));
          rtemp2 = 1 + 0.133*(1 -
en_dig/80)+0.36*(1-pi_tot/1200) -0.4674*(1 -
lwt_preg1/lwt_lact1);
          }
       else if (parity == 2)
          {
          rtemp1 = 0.46*log(drive[cur_dset][LS -
DRIVE])*(4.5 +
0.215*pow(day_lact[cur_dset],1.689)*exp(-0.098*day_lact[cur
_dset]));
          rtemp2 = 1 - 0.095*(1 -
en_dig/80)+0.9*(1-pi_tot/1200) -0.0954*(1 -
lwt_preg1/lwt_lact1);
          }
       else
          {
          rtemp1 = 0.454*log(drive[cur_dset][LS -
DRIVE])*(4.0 +
0.33*pow(day_lact[cur_dset],1.407)*exp(-0.0717*day_lact[cur
_dset]));
          rtemp2 = 1 + 0.812*(1 -
en_dig/80)+2.45*(1-pi_tot/1200) -6.86*(1 -
lwt_preg1/lwt_lact1);
          }
       milk_yld = rtemp1/rtemp2;
       rtemp1 = log(milk_yld);
       rtemp2 = en_dig*en_dig/pi_tot;
       milk_en  = exp(1.4735 + 1.067*rtemp1-0.0119*rtemp2);
       milk_pro = exp(4.128 + 0.897*rtemp1+0.000112*pi_tot
- 0.01127*rtemp2);
       milk_dry = exp(5.1662 +1.0737*rtemp1-0.0017*en_dig);
       milk_ash = 0.09 * milk_yld;
```

```
    milk_fat = milk_dry - (milk_pro + milk_ash);
    itemp = day_lact[cur_dset];
    if (itemp > 5)
      itemp = 5;
    mamm_wt_p = mamm_wt;
    mamm_wt = 1107.3 + 3521*exp(0.118*itemp);
    ute_pro_p = ute_pro;
    ute_fat_p = ute_fat;
    ute_wt_p  = ute_wt;
    ute_wt    = 529.67 + 5041.2*exp(-0.2773*day_lact[cur_dset]);
    ute_pro   = 20.924 + 0.0993 * ute_wt;
    ute_water = 34.46 + 0.847 * ute_wt;
    ute_ash   = 0.01 *ute_wt;
    ute_fat   = ute_wt - (ute_pro + ute_water + ute_ash);
    if (ute_fat < 0.0)
      ute_fat = 0.0;
    pigl_gain = day_lact[cur_dset]*(74.237*exp(-0.1894*day_lact[cur_dset]) + 0.000973*milk_yld/drive[cur_dset][LS - DRIVE]);
    }

  /*
   --------------------------
   Mammary gland calculations for pregnant and lactating sow
   --------------------------
  */
  if ((cur_state == LACTAT) || (cur_state == PREGNANT && day_preg[cur_dset] > 59))
    {
     mamm_pro_p   = mamm_pro;
     mamm_fat_p   = mamm_fat;
     mamm_pro    = 117.15*pow(mamm_wt/1000.0,0.8915);
     mamm_water = 365.4*pow(mamm_wt/1000.0,1.2838);
     mamm_fat    = 460*pow(mamm_wt/1000.0,0.6955);
    }
  /*
   --------------------------
       Adjust available energy and nitrogen values for pregnant or lactating sow
   --------------------------
  */
  if (cur_state == PREGNANT)
    {
    if (day_preg[cur_dset] > 1)
      {
      rtempl = (ute_pro + fet_pro + memb_pro) - (ute_pro_p + fet_pro_p + memb_pro_p);
      rtemp2 = (ute_fat + fet_fat + memb_fat) - (ute_fat_p + fet_fat_p + memb_fat_p);
      en_av -= .0546*rtemp2+.0535*rtempl;
```

```
         ni_av -= rtempl/(0.9*6.25);
         hp += rtempl*0.02995 + rtemp2*0.0167;
         }
      if (day_preg[cur_dset] > 60)
         {
         rtempl = mamm_pro - mamm_pro_p;
         rtemp2 = mamm_fat - mamm_fat_p;
         en_av -= .0546*rtemp2+.0535*rtempl;
         ni_av -= rtempl/(0.9*6.25);
         hp += rtempl*0.02995 + rtemp2*0.0148;
         }
      }
   else if (cur_state == LACTAT)
      {
      en_av -= .0546*(mamm_fat -
mamm_fat_p)+.0535*(mamm_pro - mamm_pro_p);
      ni_av -= (mamm_pro - mamm_pro_p)/(0.9*6.25);
      ni_av -= milk_pro/(6.25*0.8);
      en_av -= milk_en/0.72;
      hp +=  0.28*milk_en;
      if (ni_av < 0)
         en_av -= ni_av*6.25*.0236;
      /*
        --------------------------------------
        energy increment for uterus degeneration
        --------------------------------------
      */
                en_av += (ute_pro_p - ute_pro)*0.011 +
(ute_fat_p - ute_fat)*0.037;
                ni_av += 0.8*(ute_pro_p - ute_pro)/6.25;
      }
   /*
     --------------------------------------
     Potential nitrogen retention in sow's body
     --------------------------------------
   */
     ni_ret_p = livewt * exp(-0.327 - 0.0136 * livewt);
   /*
     --------------------------------------
     Actual nitrogen retention in sow's body
     --------------------------------------
   */
   ni_ret = -2.7 - 0.092*livewt + 0.684*en_av +
ni_av*(0.395 + 0.0008*livewt -0.012*en_av);
   if (ni_ret > ni_ret_p)
      {
      ni_deam = ni_av - (ni_ret_p + 0.64*pro_bdy);
      ni_ret = ni_ret_p;
      }
   else
      ni_deam = 0.0;
   /*
```

```
      ----------------------------------------
      nitrogen from deamination
      ----------------------------------------
         */

    if (ni_deam < 0.0)
       ni_deam = 0.0;
    /*
      ----------------------------------------
      Protein retention
      ----------------------------------------
    */
    if (ni_ret < 0)
       pro_ret = ni_ret*5.68;
    else
       pro_ret = ni_ret * 6.25;

    /*
      ----------------------------------------
      Energy content and cost of protein retention MJ
      ----------------------------------------
    */
    if (pro_ret > 0)
       {
       en_pr = .0236*pro_ret;
       en_pr_c = .02995 * pro_ret;
       }
    else
       {
       en_pr = 0.0;
       en_pr_c = -0.007 * pro_ret;
       }
    hp += en_pr_c;
    /*
      ----------------------------------------
      Energy cost of background and machinery   MJ
      ----------------------------------------
    */
    en_bm = 1.1442 * pow(pro_bdy,0.8487) + 0.1354 *
(fabs(pro_ret)/livewt);
    hp += en_bm;
    /*
      ----------------------------------------
      Calculate energy left over after support costs
      ----------------------------------------
    */
    en_av -= en_bm;
    /*
      ----------------------------------------
      Calculate energy left over after prot retention
      ----------------------------------------
    */
```

```
   en_av -= en_pr + en_pr_c;
   /*
     ------------------------------------
     Calculate energy increment for protein deaminization
     ------------------------------------
   */
   if (ni_av > 0)
      en_av +=   0.07188*ni_deam;
   /*
     ------------------------------------
     Calculate energy costs in pregnancy
     ------------------------------------
   */
   if (cur_state == PREGNANT && day_preg[cur_dset] > 1)
      {
      en_av -= ((ute_pro + fet_pro + memb_pro) -
(ute_pro_p + fet_pro_p + memb_pro_p))*0.1354/livewt;
      }
   /*
     ------------------------------------
     Calculate energy costs in lactation
     ------------------------------------
   */
   else if (cur_state == LACTAT)
      {
      en_av -= 0.1354*milk_pro/livewt;
      }
   /*
     ------------------------------------
     Fat retention     1000/59.56 = 16.79
     ------------------------------------
   */
   if (en_av > 0)
      fat_ret = en_av/0.0546;
   else
      fat_ret = en_av/0.0433;
   /*
     ------------------------------------
    Fat retention  energy content and cost
     ------------------------------------
        */
   if (fat_ret > 0)
      {
      en_fat  = fat_ret * 0.0398;
      en_fat_c = fat_ret * 0.0148;
      }
   else
      {
      en_fat = 0.0;
      en_fat_c = -0.0035*fat_ret;
      }
   hp += en_fat_c;
```

```
/*
  ==================================================
  Live weight Gain  for sow
  ==================================================
*/
if (cur_state == DRY)
   lwg = 1.08*(1.1*fat_ret + 3.75*pro_ret);
else
   {
   lwg = 1.08*(1.1*fat_ret + 3.5*pro_ret);
   if (cur_state == PREGNANT && day_preg[cur_dset] > 1)
      {
      lwg += (ute_wt - ute_wt_p);
      lwg += (fet_wt - fet_wt_p);
      lwg += (memb_wt - memb_wt_p);
      if (day_preg[cur_dset] > 59)
         lwg += (mamm_wt - mamm_wt_p);
      }
   else if (cur_state == LACTAT)
      {
      lwg += (mamm_wt - mamm_wt_p);
      }
   }
/*
  ==================================================
  Update the stored values
  ==================================================
*/
   store[cur_dset][cur_day[cur_dset]][E_PTISS] =
en_pr_c;
   store[cur_dset][cur_day[cur_dset]][E_FTISS] =
en_fat;
   store[cur_dset][cur_day[cur_dset]][PR] =  pro_ret;
   store[cur_dset][cur_day[cur_dset]][FR] =  fat_ret;
   store[cur_dset][cur_day[cur_dset]][LIVEWT] = livewt;
   store[cur_dset][cur_day[cur_dset]][UTE_PRO] =
ute_pro;
   store[cur_dset][cur_day[cur_dset]][UTE_FAT] =
ute_fat;
   store[cur_dset][cur_day[cur_dset]][MILK_YIELD] =
milk_yld;
   store[cur_dset][cur_day[cur_dset]][MILK_EN] =
milk_en;
   store[cur_dset][cur_day[cur_dset]][MILK_PRO] =
milk_pro;
   store[cur_dset][cur_day[cur_dset]][HEATP] = hp;
/*
  ==================================================
  Set flags
  ==================================================
*/
   flags[cur_dset][cur_day[cur_dset]] = DATA_CALC +
```

```
DATA_INIT + cur_state + ( parity << 4) + (day_cyc << 8);

    /*
      ========================================
      Update the screen
      ========================================
    */
    numsupd();
    /*
      ========================================
      Increment day counter
      ========================================
    */
    if (cur_day[cur_dset] <= drive[cur_dset][RUN_DAYS -
DRIVE])
       {
    /*
      ========================================
      Update next day's livewt and body protein content
      ========================================
    */
       if (cur_state == DRY)
          {
          ++(day_dry[cur_dset]);
          if (day_dry[cur_dset] > drive[cur_dset][DRY_CYC -
DRIVE])
             {
             cur_state = PREGNANT;
             day_preg[cur_dset] = 1;
             }
          }
       else if (cur_state == PREGNANT)
          {
          ++(day_preg[cur_dset]);
          if (day_preg[cur_dset] > drive[cur_dset][PREG_CYC
- DRIVE])
             {
             cur_state = LACTAT;
             day_lact[cur_dset] = 1;
             lwg -= (fet_wt + memb_wt);
             }
          }
       else if (cur_state == LACTAT)
          {
          ++(day_lact[cur_dset]);
          if (day_lact[cur_dset] > drive[cur_dset][LACT_CYC
- DRIVE])
             {
             cur_state = DRY;
             day_dry[cur_dset] = 1;
             ++parity;
             }
```

```
         }
      ++(cur_day[cur_dset]);
      flags[cur_dset][cur_day[cur_dset]] = DATA_INIT +
cur_state;
      livewt += lwg/1000;
      store[cur_dset][cur_day[cur_dset]][LIVEWT] = livewt;
      pro_bdy += pro_ret/1000;
      store[cur_dset][cur_day[cur_dset]][PR] = pro_bdy;
      }
   else
      return(-1);
   }
return(0);
}
```