Dietary influences on nutrient partitioning and anatomical body composition of growing pigs; modelling and experimental approaches

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Forewords

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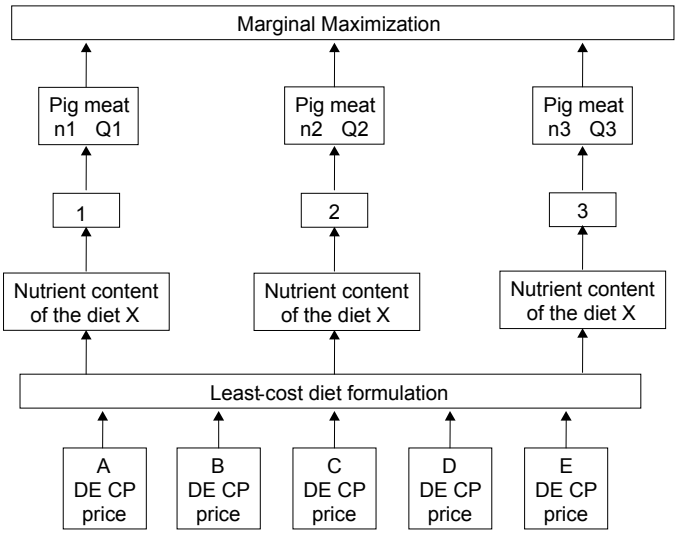
Contents

GENERAL INTRODUCTION

In many countries, pork is one of the most frequently eaten meats. According to USDA's statistics, 40 % of world meat consumption is pork, followed by 27 % of poultry, 26 % of beef and 4 % of others. In 2000, total pork production of the world was 91 million tonnes. There are three large pork production areas, being Europe, USA and South-East-Asia. Pork production represents about 40 % of the meat sector in the European Union, and the proportion of pork consumption of total meat consumption is also about 40 %. Several EU member states, such as Spain, Denmark, Germany, the Netherlands and France are among the top 30 of the world's pork consumers. The pork industry also predominates among the meat industries in Hungary. Both absolute, and relative, consumption of pork are similar to that in other EU countries (about 42 kg per person and 44 %). In general, the quantity and the quality of pork production are influenced by at least four factors being: i) genetics & reproduction, ii) feed industry – the volume and quality of pig feeding, iii) technology, and iv) management. At the farm level, production is influenced by these same factors. The genetic population and the production technology are seldom changed on individual farms. Unlike those factors, nutrition can be changed quickly. Production can be rapidly enhanced, but also hampered by nutrition. Thus, the quality of pig feeding, and the role of the feed industry, is significant. The main producers of pig feed in the EU are Spain with 7.7 million tonnes followed by The Netherlands, France and Germany with nearly 6.9 million tonnes in 1999 (Best, 2000), corresponding to the main pork consumer's countries. The size of the pig production sector in nearly all European Union member countries, and in the US, means that pig farms have to be highly organised, with knowledge being the key to success. The application of science, through the technology of pig production, is dependent upon two principles: quality assurance and integrated management control. Both of these require full and quantitative understanding of the whole process, and completion of all links in the chain of knowledge (Whittemore, 1999). Whittemore (1987) summarised successful management practise as: "Broadly, responses to changes in management practice are predicted by one of two means. The first is on the basis of historical precedence – previous experience has led to the conclusion that a certain action will result in a certain response. Unfortunately, in pig production, this is not a particularly useful means of response prediction, as both production and financial circumstances change so rapidly. A method must therefore be sought that is independent of historical data. This second approach requires an understanding of the causal forces of responses. If the nature of driving mechanisms for a response are understood, then responses may be predicted. It is this last approach that has led to the building of simulation models". In order to describe physiological processes of growth or production, the biology has to be simplified. Nutritional simulation models transform the knowledge and concepts of growth or production into mathematical equations by developing algorithms to describe the biology of the system. By integrating these equations, models predict production from nutrient intake. Thus with animal level models, the effects of desirable and undesirable changes can be simulated. Nutritional models, therefore, can be an effective tool for optimising production and carcass quality (Hartog and Peet-Schwering, 1995).

Farm management programmes usually include economic and nutritional models. These kinds of software calculate optimal production with a certain feeding strategy and housing management, and take into account market requirements. Profitability can be improved by using models. The process of a production system analysis is in Figure 1. With the help of feed optimisation, different diets can be formulated from available feedstuffs. Production is determined by dietary nutrients, by diet intake, and by genetic potential. The goal of margin maximisation is to achieve the highest income possible by manipulating production in accordance with the market. Meat production can be controlled at four points of intervention, namely diet formulation, feed allowance control, genetic control and product quality control (Whittemore, 1987). Nutritional models can be integrated into that system between least-cost diet formulation and economic analysis. This stepwise modelling approach guides the manager towards taking the correct production decisions at each of the control points, namely to decide upon nutrient specification, feed allowances, pig types to be used, weight of pig at sale, fatness of pigs at sale, and the meat packer selected (Whittemore, 1987). For realisation of an optimal quantity and quality of production, and hence optimal profit, the production has to be anticipated accurately. For that purpose, nutritional models are a useful tool in making the link between available feedstocks and possible production.

Figure 1
Production system analysis to achieve margin maximisation by several routes (Whittemore, 1987)



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LITERATURE OVERVIEW

Chapter 1

Modelling of performance and protein and fat deposition in pigs: a review

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Modelling of performance and protein and fat deposition in pigs: a review

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Abstract

The aim of this paper is review of modelling in growing and fattening pigs and the results of studies that have been conducted in this field. The authors present the types of models, the history of growth modelling, the basic principles underlying their development, the factors effecting modelling accuracy, and the areas where such models can be applied. It is concluded, on the basis of available data, that mathematical models enable a safer, more predictable, and less erratic, production as a result of which the economics of meat production can be substantially improved. Models make possible a determination of the nutrient requirements of the animals and predicting of the performance of fattening pigs. It is very important to further improve modelling accuracy, for which it is necessary to obtain a more thorough knowledge of the physiological and biochemical processes taking place in the animal body. Another possible challenge in modelling may be to provide an accurate estimate of the quality and quantity of meat at slaughter time.

Key words: pig, growth model, nutrient requirement, protein deposition, fat deposition

Introduction

Predictability of production is one of the prerequisites for achieving good production economics and high quality animal products (meat). With the progress in data processing, and a better knowledge of biological science, assessment of animal growth and nutrient requirements aided by mathematical modelling has become, during the last two decades, a dynamically developing field of nutrition research. Mathematical modelling of biological processes can be defined as one of the most efficient means for determining the nutrient requirements of animals, and predicting the impact of feed intake on growth at a given point of time, or in a given time interval. In a model, the biological processes of the animal are described with a system of mathematical equations which are based on the knowledge of the genetic, biochemical, and physiological processes as well as the environmental impact (Halas and Babinszky, 2000). There are several types of growth models that are presently applied in pig nutrition, both in the field of scientific research and commercial productions. No uniform position exists as to which of these models is the most suitable.

This review is aimed at providing an overview of mathematical modelling of the performance of growing and fattening pigs, presenting the various types of models, and also the basic principles to be relied on when developing such models. A further objective of this paper is to summarise the factors which have a major impact on the accuracy of models, and their scope of application, as well as to shed light on the problems which still await solutions in this field.

Types of models

Models can be described broadly as either *static* or *dynamic*, as either *deterministic* or *stochastic*, and as either *empirical* or *mechanistic* (Black, 1995b).

Static and dynamic models

Dynamic models describe time explicitly as opposed to static models that represent the requirements and the performance for only one instant of time. The first animal models were statistic ones calculating, for example, the lysine requirement of a pig weighing 60 kg. Computer simulation models are by their nature dynamic, and the state of the system is continually predicted over time (Black, 1995b).

Deterministic and stochastic models

Deterministic models have only one output representing the average of the population. These kind of models predict only one animal. Stochastic models, however, contain not only the mean but also the variation of the population. A distinction is made between genetic and environmental variation. By describing the genetic variance, estimates are obtained of the magnitude of total variation. Environmental variation can be modelled by varying, for example, the level of energy demand or supplying parameters which often cause major differences in growth values over the growth trajectory (Knap, 1995).

It is necessary to note, however, that no sufficiently accurate stochastic models have been developed, even with the aid of today's sophisticated computer data processes. Thus the present solution is offered by expansion of deterministic models with stochastic elements. For this purpose there are two options available. If we increase the number of inputs of the model, the individual animals of a given group will be described by a broader scope of the observed input variables, the results of which one gets an estimate of the population. In case the number of outputs of the model is increased, we can present the mean and variation for variables which substantially effect the economics (e.g. backfat thickness) (Black *et al*. 1986). A significant shortcoming of models so modified, however, is that in the course of calculations the so-called intermediate equations of the model are not expanded by the stochastic elements.

Empirical and mechanistic models

An empirical model describes the response of an animal to a given set of circumstances. It is usually attempts to develop predictive equations from experimental data sets using biometric procedures. The other type of model might be termed as mechanistic. Mechanistic models focus more on metabolic processes within the animal. They may operate at the tissue, cellular or molecular level. Such models are more flexible, and may be expected to predict responses and requirements over a wide range of condition (Close, 1996).

Evolution of models

The first models developed between 1940 and 1960 were factorial representations of energy and protein utilisation, and were used primarily to calculate nutrient requirements for animals at specific body weights. The calculations were based on empirical equations and, as a result, a static-empirical model was developed by Blaxter (1962). Baldwin (1970), and later Baldwin and Smith (1971), developed the first computer simulation model based primarily on representation of biochemical mechanisms as known at that time. The first pig growth model was developed by Whittemore and Fawcet (1974; 1976), which largely influenced models developed later. It was based mainly on empirical equations, but protein utilisation was represented mechanistically (Black, 1995b). As a result of the progress of computer data processes, the more thorough knowledge of the biological processes existing in the animal, and the ever more accurate determination of its requirements, the mathematical models developed since then can predict animal performance with increased accuracy.

The models of today were developed on the basis of metabolic processes occurring within the animal. Burlacu *et al*. (1989) have developed a model eliminating many of the imperfections of earlier ones. A valuable trait of the model is that it follows partitioning of nutrients in the body. Furthermore it takes into account the biological value of the protein in the utilisation of crude protein. Nevertheless, model prediction error is wide ranged and the accuracy is not high enough (Burlacu *et al*., 1989).

The modelling process

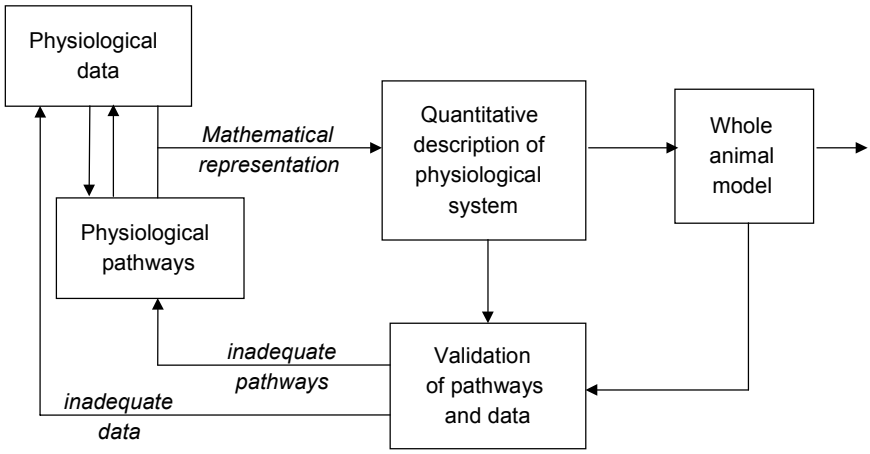
The philosophy behind the use of computer models to simulate animal systems has been described by Baldwin and Koong (1980), France and Thornley (1984) and Whittemore (1986). Despite the fact that the physiological processes existing within the animal are known to at least some degree, it has become clear that the combined impact of several factors can change these processes and can thus influence model performance (Black, 1995a).

The major steps of modelling are in Figure 1. The animal is a physiological system with measurable features (physiological data) and biological processes (physiological pathways). The first step in modelling is to complete an investigation to collect basic data, such as weekly body weights, daily protein and fat deposition or daily feed intake. The physiological process, and the control of the system, are then developed from this information. Traditionally in science, these two steps are repeated many times until the system can be described at some uniform level of detail (Black, 1995a). The concepts and data are transformed into mathematical equations by algorithms that can be solved rapidly by computer programs in a quantitative and dynamic approach.

The next step is to check the validity of the model with regard to pathways and data, by comparing predictions with the actual results. Whenever there is a considerable difference between the model predictions

and experimental observations, new approaches of pathway and equation parameters can be devised and tested within the model. The modelling process begins again in that case. When model outcome and experience agree over a wide range of different circumstances, some confidence in the understanding of the system is obtained (Black, 1995a), that this could be the final model.

Figure 1
A modelling process (adapted from Black, 1995a)



Principles of models

There are four main principles to determine growth models (Close, 1996):

Characterisation of the animal

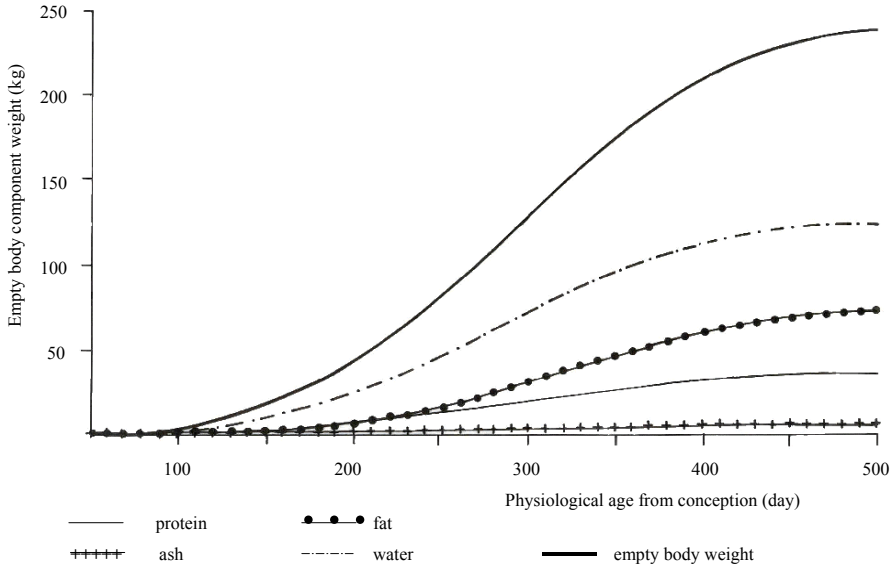
For models to operate satisfactorily and accurately, it is important to characterise the animal as well as possible. To achieve this, we have to know which features are the main determinants of animal production. Studies conducted show that production parameters are determined primarily by the following characteristics:

a) Relationship between the age and the body weight of the pig

The growth of an animal is often measured in terms of change in size (either dimensions or weight) over time. Historically, S-shaped or sigmoid curves have been used to describe this phenomenon in mathematical terms (Figure 2). The equation parameters are animal-specific and should be

determined for each group within any species being described (Bridges *et al*., 1986). Moreover, change in body weight can be estimated by adding body protein, ash, water and fat content. Increases in body components as a function of physiological age was approached curvilinearly by Bridges *et al*. (1986). Empty body weight is the sum of the component growth curves.

Figure 2
Empty body weight and the weight of chemical body components as a function of age (Bridges *et al*., 1986)



b) The effect of sex and genotype on the animal performance

Genotype is one of the most defining factors influencing the amounts of body tissues deposited during growth. In investigations performed by Quiniou and Noblet (1995), six groups were used to represent differences between types and sexes: lean pigs, obese pigs, and conventional genotype within boar, gilts and barrows. The above authors demonstrated that the difference between the amounts of adipose tissue deposited in obese pigs and in lean pigs at the same empty body weight, was mainly due to differences between amounts of external adipose tissue. The latter was found to be more important than differences in amounts of intermuscular adipose tissue. The lipid content of empty body weight was observed to differ widely among genotypes, whereas protein content was more constant.

Consequently, water content was lower in the obese pigs, than in the lean or conventional pigs, while ash content was similar in all groups (Quiniou and Noblet, 1995).

The amount of adipose tissue was higher in gilts by 5% and in barrows by nearly 15 % compared to boars. The amounts of bone and skin were higher for entire males than for barrows and gilts of the same live weight, and also boars had the highest amount of offal. Quiniou and Noblet (1995) found that sex had no effect on total body protein content. In contrast, Yen *et al*. (1986) and Batterham *et al*. (1990) showed strong sex effects in relation to protein deposition. Females and barrows contain more lipid, and less water, than boars, and approximately the same amount of ash (Quiniou and Noblet, 1995).

c) Appetite potential of the animal

The appetite potential is usually defined as energy intake capacity and it is related to body weight. Close (1994) in a review of the literature, has suggested that for modern genotypes the relationship between DE intake and body weight (BW) was best described as:

$$DE\ (MJ/d) = 3.44\ BW\ (kg)^{0.54}$$

NRC (1998) uses another third degree equation:

$$DE\ (Kcal/d) = 1{,}250 + 188\ BW - 1.4\ BW^2 + 0.0044\ BW^3$$

d) Effect of health status on the animal performance

Health status has a major influence on both feed intake of the animal and rate of lean tissue growth (Close, 1996). At a lower level of health, animals cannot realise their genetic growth potential.

Characterisation of the diet

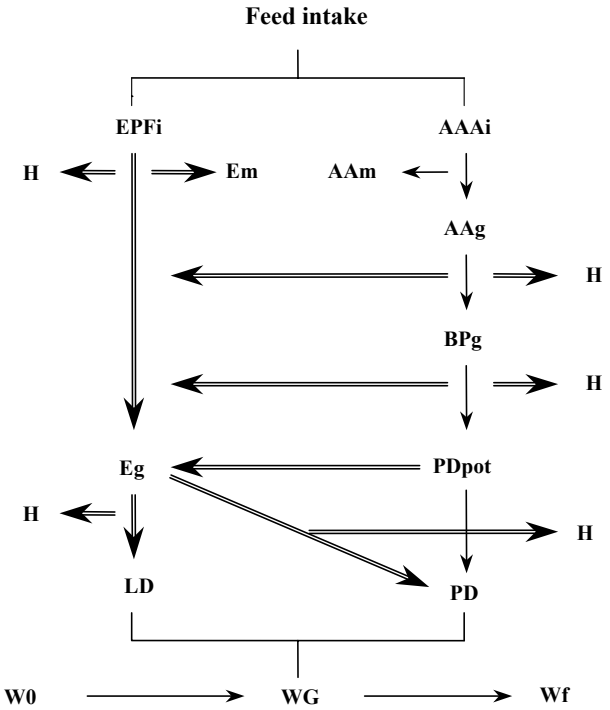
The most important parameters of feed are its energy content (DE or ME) and the amino acid profile. The amino acid content of feed can be expressed as either total or digestible (faecal or ileal digestible) amino acids. In diet formulation, the concept of "ideal protein" should also be used. Thus, depending upon whether the objective is to determine the response, or the requirements of the animal, either the nutrient intake of the animal is calculated from feed intake and nutrient composition of feed, or the energy and lysine requirements are calculated, from which the quantity and type of diet may be determined (Close, 1996).

Partitioning of nutrients

The principles of nutrient partitioning and growth as included in a simple model were described by Whittemore and Fawcet (1976); ARC (1981); Whittemore (1983); Moughan and Smith (1984); Moughan *et al*. (1987); Moughan and Verstegen (1988); Stanks *et al*. (1988). It is known that nutrient requirements at maintenance always have priority, and may represent up to 40 % of the energy and 10 % of the amino acid intake in cases of adequate nutrient supply (Close, 1996). As it can be seen in Figure

3, two main categories can be described for the nutrients in feed being: protein free energy and protein (de Lange, 1995). The balance remaining, after satisfying the energy and amino acid requirement for maintenance, is utilised for protein and fat deposition. At each stage of the transformation process, heat loss is expected. Body protein deposition occurs from the available amino acids via balanced protein, but using a part of the energy for gain. Weight gain can be calculated as the sum of fat deposition and protein deposition, and equals the difference between the final and initial body weight.

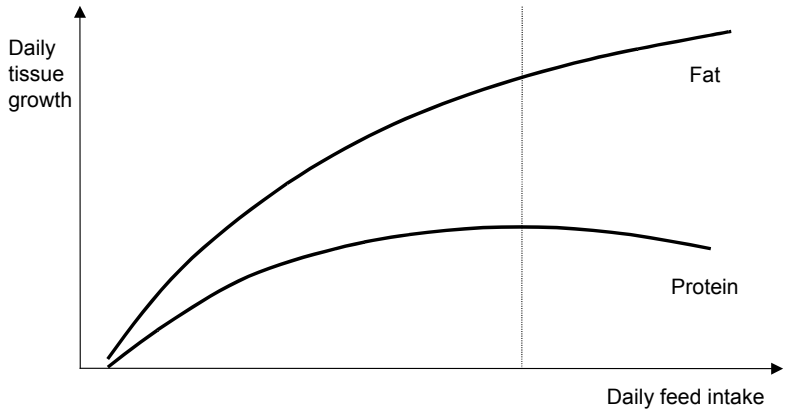
Figure 3
Partitioning of the nutrients (de Lange, 1995)
Meaning of symbols: EPFi - protein free digestible energy intake; H - heat loss; Em - energy required for maintenance; Eg - energy available for gain; LD - body lipid deposition rate; AAAi - available amino acid intake; AAm - amino acid requirements for maintenance; AAg - amino acids available for gain; BPg - balanced protein that can be utilised for body protein deposition; PDpot - potential body protein deposition rate; PD - actual body protein deposition rate; W_0 - initial body weight; WG - body weight gain; Wf - final body weight;
→ flow of material; ⟹ flow of energy.



Describing the impact of dietary nutrients on animal performance

In general increased feed intake increases the tissue growth. This does not mean, however, that the deposition of the two predominant components of growth, protein and fat, are continuous during the entire fattening period. Lean tissue deposition increases until it reaches peak genetic capacity, but fat deposition does not have this kind of linear-plateau response (Figure 4). The key issue is to define optimal feed intake, the value beyond which protein deposition does not increase. Thus, an important factor in model development is the nutrient content of diet consumed.

Figure 4
Relationship between daily feed intake and protein and fat deposition (Close, 1996)



The rate of protein deposition is determined both by the level of energy and amino acid supply, and in case of pigs especially by the first limiting amino acid, lysine. Protein and fat deposition increases linearly with dietary DE intake (Campbell *et al*., 1983; Campbell *et al*., 1985; Campbell and Traverner; 1988). The limiting factors to protein deposition, in cases of adequate energy supply, are the amount of available amino acids, and the peak level of genetically determined protein deposition.

The relationship between daily protein or lysine intake and protein deposition was described linearly by Zhang *et al*. (1984), as a two-phase-linear function by Batterham *et al*. (1990), curvilinearly by the Agricultural Research Council (ARC, 1981) and by Fuller and Garthwaite (1993), and as a linear-plateau response by Campbell *et al*. (1984, 1985), de Greef (1992) and Bikker (1994). The limiting factors to protein deposition - in case of an adequate energy supply - are the amount of available amino acids, and the peak rate of genetically determined protein deposition. Thus relationships of the model should be adjusted for the specifies of the herd, that is the factors

in the various equations should be replaced by the values characteristics of the given population.

Several studies (Bikker, 1994; Halas, 2000) have shown that there is a close correlation between ileal digestible (ID) lysine intake and average daily gain, as well as daily protein deposition and feed conversion ratio (Table 1). Halas (2000) found that increased ID lysine intake up to 12.6 g/d and 17.6 g/d at pig live weights of 30-60 and 60-105 kg, respectively, a linear lysine response was shown in respect to the foregoing three performance traits (Table 2). Batterham *et al*. (1990a) found similar results when studying a broader range of intake (1.53 g/kg - 12.27 g total lysine/kg diet and 15.3 MJ/kg diet), namely weight gain and that protein deposition can be safely increased, and the quantity of feed used for 1 kg of weight gain, and the daily fat deposition can be reduced by increasing lysine intake. The authors suggest a strong quadratic effect of the lysine intake on the daily gain and the feed conversion ratio. Extremes of the curves exist at the end of the current range. Among others, these relationships should be applied in the models to estimate the animal response to a given diet.

Table 1
Correlation between dietary ileal digestible lysine intake (g/d) and average daily gain (ADG) protein deposition (PD) and feed conversion ratio (FCR) (Halas, 2000)

	CORRELATION		
	ADG (g/day)	PD (g/day)	FCR (kg/kg)
30-60 kg	r = 0.94	r = 0.78	r = -0.94
	P = 0.0001	P = 0.0010	P = 0.0001
60-105 kg	r = 0.89	r = 0.77	r = -0.87
	P = 0.0001	P = 0.0013	P = 0.0001

Table 2
The effect of dietary ileal digestible lysine intake (LysInt)g/d) on average daily gain (ADG) protein deposition (PD) and feed conversion ratio (FCR) (Halas, 2000)

		Y = a * LysInt + b		
		a	b	r
30-60 kg	ADG (g/kg)	25.3	186.5	0.94
	PD (g/kg)	5.06	25.4	0.78
	FCR (kg/kg)	-0.18	5.36	0.94
60-105 kg	ADG (g/kg)	24.0	248.2	0.89
	PD (g/kg)	4.86	-0.25	0.77
	FCR (kg/kg)	-0.13	6.27	0.87

Practical applications of the models

Models offer a means to develop alternatives over a range of management, husbandry, environmental and dietary conditions. Using them, it is possible to predict the growth rate and performance of animals, even within a broad range of body weight. Furthermore, quality can also be predicted in case the body fat content, or the protein/fat ratio, is taken into account in calculations as a quality trait.

An accurate prediction of the profitable traits of animal production is a key issue for pig producers (de Lange and Schreurs, 1995). Models establish nutrient requirements, diets and feeding strategies at all stages of growth, and allow an economic analysis of current and alternative feeding strategies.

Table 3 shows the nutrient requirements of pigs at different stages of fattening (Close, 1996). The following example illustrates that, with the aid of the model, the nutrient supply of the animals required to achieve a given performance can be predicted. The prediction demonstrates how growth rates, and the protein and fat gains, change with increase in body weight and as a consequence, how energy and lysine requirements, and hence the lysine/energy ratio in diets, vary. The problem can also be reversed, i.e. in case of an adequate nutrient supply, animal performance can be predicted by models. Predictable production is the basis of profitable production.

Table 3
Predicted nutrient requirement and feed efficiency (Close, 1996)

	30-50 kg	50-70 kg	70-95 kg	Overall
Time taken to slaughter (d)	29	24	28	81
Growth rate (g/d)	100	825	900	800
Protein gain (g/d)	130	154	161	143
Fat gain (g/d)	95	117	170	138
Energy (MJ DE/d)	20.4	24.9	30.2	26.4
Lysine (g/d)	18.7	21.8	22.8	21.7
Feed efficiency (kg/kg)	2.26	2.40	2.92	2.57

Table 4 (Close, 1996) shows a comparison of economics among farms with different conditions. It appears from the figures that genotypes with a lower growth rate could reach a lower lean percentage. All genotypes need optimal nutrient supplies to realise their maximal level of genetic determined performance. As a consequence, in case of suboptimal nutrient intake the production costs are higher and the profitability of pig production decreases as shown by Table 4.

Models aid in comparison of performance actually achieved on farm, with animal genetic potential. Any shortfall will be an indication that external factors should be modified in order to improve production.

Finally, models can help feed manufacturers in development and testing of new diets, products and feeding regimes with which animal requirements can be better satisfied.

Table 4
Predicted nutrient requirements of pigs growing at different rates between 30-90 kg body weight (Close, 1996)

Growth rate (g/d)	650		700		750		800			850		
Lean %	54	56	54	56	56	58	56	58	60	56	58	60
Carcass len (g/d)	275	290	296	312	334	352	356	375	394	379	399	419
DE (MJ/d)	25.4	24.2	26.5	25.1	26.1	24.7	27.1	25.6	24.1	28.1	26.5	25.0
Lysine (g/d)	17.4	18.4	18.4	19.1	20.2	21.0	21.2	22.2	23.0.	22.2	23.2	24.0
Feed intake (kg/d)	1.93	2.01	2.01	1.91	1.99	1.88	2.06	1.95	1.93	2.14	2.02	1.90
Feed conversion (kg/kg)	2.97	2.83	2.87	2.73	2.65	2.51	2.58	2.44	2.30	2.52	2.38	2.25
Relative cost (%)	100	95	97	92	89	85	87	82	77	85	80	76

To conclude, the growth of animals can be accurately estimated by taking into account the animal and environmental factors affecting growth in metabolic model. There is limited information available for predicting protein and fat deposition with accuracy and their content in growing and fattening pigs is one of the key characteristics features of carcass quality. It is important to develop a mathematical model capable of more accurately predicting the protein and fat deposition in growing and fattening pigs, as this could contribute substantially to a more cost-effective, and better quality, pig production.

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Chapter 2

Conceptual paper for modelling protein and lipid accretion in different body parts of growing and fattening pigs: a review

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Abstract

The objective of this review is to outline those parts of modelling approaches in pig production which are not highly developed; these are the partitioning of protein and lipid accretion in different anatomical body parts. The authors introduce the present models with a critical evaluation and drown some conclusions for the further developments. Based on present knowledge this paper demonstrates the process of protein and fat accretion in different body compartments in pigs and influencing factors. A further aim is to assist in the conceptual development of a new pig model, which is more detailed, precise and accurate than currently available models. Existing models are generally deficient with regard to the translation of lipid and protein gain into lean and fatty tissue. Only assumed values for this translation have been used so far and the concepts underlying these values are not well understood. Therefore, it may be appropriate to develop a compartmental model to predict protein and fat deposition in growing and fattening pigs. With this new approach the model can supply sufficiently the changing consumer demands regarding to the possibility of meat quality prediction.

Key words: pig model, fat deposition, protein deposition, tissue composition, metabolism, slaughter quality

Introduction

Modelling the deposition rates and predict the chemical composition in growing and fattening pigs have become important issues in pig nutrition and in its applications. The complexity of the growth process and its interactions with the environment makes it virtually impossible for the human mind to assess accurately the consequences of any change in the output. In a model, concepts and knowledge are transformed into mathematical equations and integrated by using simulation modelling techniques. Computer programs are used for the direct application of information for the improvement of management. Models are also valuable for defining research priorities. Mathematical models are occasionally formulated to assist in optimising production (Halas and Babinszky, 2000)

Present models are quite sufficient to predict the time taken to slaughter, the average daily gain (ADG), the feed conversation ratio (FCR) or even the lean percentage and the backfat thickness (Close, 1996). However, there is no existing model for pigs to estimate the deposition of chemical components in different tissues like muscle or viscera. Changing human nutrition criteria, the quality of animal products and quality assurance are becoming central issues. Another challenge is the mathematical prediction of meat quality: qualitative parameters of meat need to be quantified as well as quantitative characteristics. Slaughter quality is defined as lean and fatty tissue and it can also be referred as the ratio of protein and fat in the carcass. One of the most important meat quality traits is the ratio of protein and fat in the lean meat. A new generation of mathematical models enable a safer, more predictable and less erratic production resulting substantially improved economy of meat production (Halas and Babinszky, 2000).

The aim of this review is to present the actual models with a critical evaluation and to draw some conclusions for their further development. Based on the present basic knowledge this paper summarises the accretion process of protein and fat in different body components and moreover, factors influencing them. A further aim is to assist in the conceptual development of a new pig model, which is more detailed, precise and accurate than current available models.

Presentation and evaluation of pig models

Modelling the growth and prediction of the performance has become a relevant issue. In pig production this demand forced the development of growth models. The first pig model was published by Whittemore and Fawcet (1974). The equations of the model were set up based on trial experience, but the protein utilisation was approached by conceptual equations. Latter on at the 80's and 90's among others Black at al. (1986), Burlacu at al. (1989), Pomar at al. (1991) and de Lange (1995) established pig models. Most of them represented the energy and protein metabolism with a factorial approach.

Kyriazakis (1999) concluded that the process of model development should be a concerted effort of the inventors and users and that the theories and hence models need to be tested, critized and eventually replaced. Several models have been developed but until now only a few publications have been reviewed the literature of modelling. However, during the last two decades mathematical modelling has become a dynamic field of nutrition research (Halas and Babinszky, 2000). It is intended to summarise the present models by demonstrating some basic knowledge of them and also the principle concepts of the mechanism of existing models.

Types and evaluation of present models

There are two types of models. The first type is the empirical model, which is applicable only to the experimental conditions for the "whole animal". An empirical model describes the response of an animal to a given set of circumstances. Usually attempts to develop predictive equations from experimental data sets using biometric procedures (Close, 1996). The other type of model might be termed as mechanistic as it represents the underlying mechanisms. It is based on the laws of physics and chemistry within the animal. It may operate at tissue, cellular or molecular level (Black, 1995a). Nevertheless, as Kyriazakis (1999) supposed, the complexity of the metabolic processes neither should nor could imply generality. There is a view that the modelling process has a greater chance of success if underlying biological processes are reduced to that of chemical or physical descriptions (Black, 1995a). The so called mechanistic models are flexible and may be expected to predict responses and requirements over a wide range of conditions.

There have been several models with different aims like to discover energy expenditure (Black, 1995b; van Milgen and Noblet, 2000), feed evaluation (Danfær, 2000) or pig performance (TMV- Technical Model for pig Nutrition, 1994). The inputs and outputs of these models are specific. However there are some standard variables

which can be sorted in following. (1) Characteristics of the diet, such as dry matter content, chemical composition of the dry matter, energy content of the dry matter, digestibilities and fermentabilities of individual chemical fractions, (2) characteristics of the pigs such as age at beginning of the simulation period, sex and genetic capacities for protein and lipid retention, and (3) characteristics of the environment, such as temperature in the pig house. The model specified to determinate feed evaluation and pig performance gives information on rates and composition of growth. Model outputs are the simulated numerical values of all state and rate variables at any time point during the simulation. From these data, the model calculates the predicted animal performance: feed intake, retention of protein, lipid, ash and water, heat and methane production, as well as energy and dry matter in faces and urine, carbon dioxide production (Black, 1995b; van Milgen and Noblet, 2000; Danfær, 2000).

Recent pig models predicting the further performance are mostly empirical and even semi-mechanistic. It means, with regard to empirical equations there are some conceptual equations to highlight some quantitative relations behind the growth process. These equations usually imply different factors to approach the efficiency of the utilisation of a certain nutrient (Burlacu *et al*, 1989; Lange, 1995). As it was mentioned previously, empirical models are not flexible, even if they has some conceptual equations. These kind of models are the result of statistical curve-fitting exercise. According to Kyriasakis (1999) empirical relationships can only be euphemistically called 'theories'.

In classical modelling only protein and energy inputs are used to simulate growth in pig. The non-protein energy part of the feed contains different macronutrients like fat, starch, sugar and cell wall components (Bastianelli *et al*, 1996). The gut epithelium can absorb the digested nutrients and also the fermented products of microflora in the hindgut. The micronutriens like fatty acids, glycerol, glucose, short chain fatty acids have different metabolic pathways contributing to growth processes. These different pathways are the reason for differences in efficiency of utilisation of nutrients. Therefore, models on the basis of the DE or ME content of the diet cannot give a reasonable result to predict the effect of different energy sources on energy metabolism and on performance of pigs.

Until now protein deposition could be predicted fairly accurately from nutritional input and certain animal traits. However, models are generally deficient with regard to the translation of lipid and protein gain into lean tissue and fatty tissue. They mostly predict protein and lipid deposition in the whole body (Burlacu *et al.*, 1989; Pomar *et al.*, 1991; TMV, 1994; de Lange, 1995). From the literature it can be concluded that there are only a few models based on these compartmental approaches and there is a lack of information for mechanistic models for growing and fattening pigs. Pettigrew *et al.* (1992) considered protein accretion in the two main parts of body, which are the lean body and viscera. Additionally milk production was considered in model of lactating sows. Gerrits (1996) has successfully developed a compartmental model for preruminant calves. This modelling approach is sufficient to predict the distribution of chemical components in different body parts. However, it is much more detailed for protein pools than for different fat stores. It can be concluded from the published data discussed above that in order to have a more mechanistic approach to predict meat production and meat quality at slaughter time it is necessary to develop a

compartimental model for growing and fattening pigs. A new approach is required to ensure the changing consumer demands regarding to the meat quality prediction.

Consequences for further developments in modelling

Available data show that the concepts underlying the accretion of lean and fatty tissue are not well described in recent pig models. It is necessary to represent the growth process on biological basis and to imply the biochemical and physiological principles into the model equations. The growth is the result of the deposition of chemical components, whereas the chemical composition of the body is determined genetically and by dietary nutrients. Growth rates of a certain chemical component are different in the various body compartments like muscle, organs, hide and bone. Considering that water and ash content is determined by protein content (de Lange, 1995) the authors aimed to demonstrate the accretion process of the two main influencing chemical components like protein and fat. This compartimental approach may improve the estimation of lean meat predicting the quantity and quality of meat.

Conceptual basis to develop a mechanistic model

The emphasis in meat production has shifted from maximising production volume to the efficient production of lean meat. Body composition can be manipulated to a large extent by nutritional means. It does, however, require integrated knowledge of protein and energy metabolism. Protein and fat metabolism result in protein and fat deposition and these are expected to be comprehended in the model. Otherwise equations describing relationships between body weight and pig performance, and anatomical and chemical composition of the body differed by sex and genotype are used in empirical models. A nutrient partitioning model is essentially constructed at some level bellow that comparing of the level of the required accurate prediction (Black, 1995a). The physiological processes behind these equations are described by mechanistic models, due to the conception of biochemical reactions at the tissue level is simulated by establishing mathematical equations.

The increase of body weight follows an S-shape as a function of age (Bridges *et al.*, 1986). Walsta (1980) found allometric relationships between carcass weight and carcass composition like the weight of bone, muscle, fat upon different feeding regime and sexes. The net growth of each body compartments is a result of the deposition of chemical components. Due to the fact that water and ash content related to protein content in the body, protein and fat can be consider determining variables to describe the growth process. In the following sections the authors intend to present the protein and fat metabolism and accretion.

Protein metabolism and protein accretion in body parts

Protein metabolism

All protein present in the body are in a dynamic state (Simon, 1989). To maintain homeostasis, body protein is continually being degraded and resynthesised. The aggregate catabolic and anabolic process involved in a certain amino acid flow is referred to as “protein turnover” (Knap, 2000). Accordingly the definition of protein turnover is described by three parameters: the fractional rate of synthesis (FRS) is the rate of daily (re)synthetised body protein from free amino acids; the fractional rate of

catabolism (FRC) is the rate of protein degradation resulting in free amino acids and the rate of turnover (TR) is the fraction of total body protein that daily degraded and resynthetisesed (Knap, 2000). The deposition or the loss of protein are the result of differences between FRS and FRC.

In growing animals fractional rate of protein synthesis is dominant but not necessarily correlated with protein deposition. The total protein deposition is the result of the different deposition rates in various body parts. Some tissues have high synthesis rate but low deposition due to the high fractional protein degradation rate. The ratio of protein deposition to protein synthesis is sensitive to several factors such as age and genetic constitution of the pig or nutritional stage. Protein synthesis and protein deposition rates decline with age even if the rate of protein catabolism does not fall as quickly as in the early postnatal period (Riis, 1983). The main factor responsible for these changes is the fall in capacity for protein synthesis (Simon, 1989). Table 1 shows the FRS values of different tissues according to various age and live weight of pigs. Genotype determines the level of daily maximal protein deposition which strongly correlates with deposited protein (r = -0.985) in model of Knap (1995). Based on trials carried out with rats, Simon (1989) suggested that protein turnover rate in muscle differs among the different genetic strains of a species. At comparable ages both synthesis and degradation rates are lower in animals with a high genetic potential. Physiological processes of rats and swine are similar and the rat is considered in some cases as a good model of the pig (Forsberg *et al.*, 1987; Jakobs and Metzler, 1999; Pearson *et al.*, 1999). Indeed since this number of pig trials are small it could be necessary to use data of rats for the pig modelling purpose.

Table 1
Published data on fractional rate of protein synthesis [% per day] in different body parts in pigs

Body part	Seve *et al.* (1986)[1]	Edmunds and Buttery (1978)[2]	Riis (1983)[2]	Simon (1989)[2]	Knap (2000)[2]	Garlic *et al.* (1976)[3]
Muscle	12.7-17.4	5.8	10.0	2.4-5.9	5.0	4.8
Liver	59.4-69.7	36.9	60.0	12.0-28.7	40.0	23.3
Pancreas				75.3-88.0		
Heart		9.4		4.3-7.4		6.8
Intestine	66.8-79.4	23.1-38.5	60.0	16.2-56.3	40.0	
Other organs		17.7-47.5		12.7-22.2	20.0	8.3-24.5
Blood plasma			150.0		150.0	
Bone	64.8		5.0		5.0	
Skin			5.0	3.7-8.6	5.0	

1 = 17-day old weaned piglets; 2 = 50 kg live weight; 3 = 75 kg live weight.

The literature shows that both protein synthesis and protein degradation are involved in mechanisms controlling protein accretion and are affected by nutritional factors. It is assumed that the major nutritional factors determining the diurnal rhythms of the body in protein and amino acid turnover are feed intake, energy, protein and amino acid supply. Results of Reeds *et al.* (1980) and Krawielitzki (1984) indicate that with increasing energy supply, the protein synthesis in pigs is increased. In the experiment of Reeds *et al.* (1981), a high protein diet resulted in an increase in the protein synthesis rate of 36 % and the breakdown rate of 28% in growing pigs. It means that the addition of protein and providing a similar energy intake was most effective in stimulating whole body protein synthesis but the effect need is associated with an increase in the rate of protein degradation (Reeds *et al.*, 1981). Simon (1989) suggested that at sub-optimal feeding levels all the protein turnover parameters of rats are reduced such as synthesis, breakdown, and the deposition of protein in skeletal muscle. Contradictory to that in a trial carried out with pigs fed at sub-optimal protein level (4% vs. 16 % crude protein) the FRS of protein hardly changed at 40 to 50 kg body weight (Simon, 1989).

The recent knowledge on protein evaluation suggests to consider not only the protein but also the amino acid supply of the pig. Stimulatory effects of some individual amino acids on protein deposition have been observed. This effect was caused both by increased protein synthesis rates and decreased degradation rates in muscle (Li and Jefferson, 1978). *In vitro* studies indicate that increased amino acid supply to the liver stimulates the synthesis of liver protein as well as that of export (plasma) proteins as reviewed by Riis (1983).

According to the experimental results protein synthesis rates of the whole body and of individual tissues correlate generally positively with the feeding level and with the protein and amino acid intake at any given feeding level. Extra synthesis with extra feed does not always occur especially also high levels of protein retention occurs simultaneously with increased levels in the degradation rates of proteins. It seems evident that the response of protein deposition to different protein and/or energy supply is the result of changes in turnover rates of the large protein pools, especially of the muscle (Simon, 1989).

Protein accretion in different body parts

The protein metabolism at the tissue level was discussed in the previous section. The protein synthesis and degradation results in protein deposition, which differs in various tissues like muscle, connective tissue or in viscera. According to the individual rate of protein turnover of each tissue it is necessary to prove the difference in protein accretion upon different body parts.

Muscle

The proportion of body protein present in the muscle (%) is described by Susenbeth and Keitel (1988) in the range of 17-116 kg with a hyperbolic curve function $Y = a + b \cdot X^{-1}$, whereas there is a linear response of protein content (kg) in lean to empty body weight (kg). Knap (2000) suggested an allometric equation to relate muscle protein in % of body protein (Y) as a function of total body protein in kg (X) in which the intercept is 39.652 and the regression coefficient is 7.314 (% per ln[kg]).

The data from the literature are contradictory in case of the effect of energy and protein intake on protein deposition. Susenbeth and Keitel (1988) did not find any significant difference in the percentages of lean protein in the whole-body protein at different daily energy intake. They suggested that the protein content of lean depends on its fat content and when related to fat-free mass the protein content is nearly constant (Susenbeth and Keitel, 1988). Contrary to the above, Jørgensen *et al.* (1985) found a negative effect of feeding intensity (MJ ME/day) and energy density (MJ ME/kg dry matter) in relation to total body protein in the muscle on partial coefficients of –1,44 and –0,88 of muscle protein (as %). On the other hand, Bikker (1994) observed a linear increase in protein deposition in lean tissue with an increase in feeding level (from 1.7 times maintenance requirement to *ad libitum* feeding level) in pigs of 45-85 kg body weight.

Wünsche *et al.* (1983) found no difference in N-content of the muscle of pig after feeding different protein levels. Bikker (1994) suggested a linear-plateau response for whole body protein deposition to an increasing daily ileal digestible protein intake. Halas and Babinszky (2001) found correlation coefficients of 0.78 (P = 0.001) and 0.77 (P = 0.0013) for the relationships between dietary ileal lysine intake and daily protein deposition in pigs in the range of 30-60 and 60-105 kg body weight, respectively. It can also be concluded from the literature that protein synthesis is chiefly a function of the age of the pigs, while the magnitude of fat synthesis at any time is a function of the feeding intensity (Nielsen, 1973). The protein and fat content in lean and fat may not necessarily be constant.

Organs

After studying the literature data it can be concluded that chemical composition in organs changes with body composition. Barrows have more fat and less protein in dry matter in their entrails than gilts (Jørgensen *et al.*, 1985). The protein content in organs followed a hyperbolic curve during the growth of animal (Susenbeth and Keitel, 1988). An allometric equation ($\ln y = 0.17123 - 0.02581 \cdot \ln x$ for entrails and $\ln y = 0.03751 - 0.00188 \cdot \ln x$ for blood) has been established by Knap (2000) to describe the percent of body protein in organ fraction as a function of total body protein (kg). Seve *et al.* (1986) on the other hand observed a linear relation between the protein contents of the digestive tract (r^2=0.94), liver (r^2=0.73) and other viscera plus blood (r^2=0.44) with body weight in weaned piglets.

Bone and hide

Nielsen (1973) suggested that there is 37.4-38.0 % of protein in dry matter of bones and the total amount of protein in bones is about 16.0-16.3 % of total body protein. It may be derived that genotype affects the bone protein content because higher maximal daily protein deposition also increased the protein deposition in connective tissue. Boars have approximately 2.4 % higher fat and 1.3 % lower protein (P<0.001) in bone than gilts (Jørgensen *et al.*, 1985). The percentage of body protein of the bone fraction can be described in a hyperbolic curve as a function of body weight (Susenbeth and Keitel, 1988). Jørgensen *et al.* (1985) obtained results which showed that increasing energy density and feeding intensity decreases protein in

bone, whereas increasing digestive protein per ME increases the bone protein % in dry matter.

The hide fraction, including skin and bristles, is independent of nutritional factors. It contains 59.7-61.4 % protein in dry matter which is equivalent to 9.0-9.3 % of total protein in pigs of 90 kg body weight (Nielsen, 1973). In agreement with this Just and Petersen (1976) found that proportions of hide protein in the body is about 10%. Nielsen (1973) however did not find any statistical difference in the chemical composition of skin between sexes.

Conclusion of protein metabolism for modelling

According to experimental studies some concepts can be recommended for pig modelling. As a conclusion from the previous section the protein metabolism is influenced by several factors. The characteristics of the animal like age, sex and genotype and also the nutrition has an impact on it. At tissue level the protein metabolism can be realised as the synthesis and catabolism and results in protein deposition. By nutrient supply the protein metabolism can be changed. The energy and protein or amino acid levels have the most pronounced effect on protein deposition, since protein synthesis is obligatory derived from amino acids and requires relatively high energy supply.

Lipid metabolism and accretion

Lipid metabolism

In adipose tissue the amount of trigliceride is rather constant. However there is a dynamic equilibrium between esterification, hydrolisis, and subsequent re-esterification. It is suggested in the literature that adipose tissue contains at least two components (Leat, 1983). A small component is situated in the cytoplasma and this has a fast turnover rate. The other component is very large and is presented in the main lipid stores. This is only slowly modified by dietary changes (Leat, 1983). Modelling is therefore focused on this latter larger part which contains the major depot in body fat pools. Fat deposition can be characterised chemically by a continuos accretion of lipids, primarily in the form of triacilglicerols, and morphologically by adipocyte differentiation and hypertrophy (Nürnberg *et al.*, 1998).

The three main fat storages of the body are (1) the external adipose tissue (backfat and abdomen fat), (2) the liver and (3) the muscle. The lipid accretion of tissues are however different. Bee *et al.* (1999) observed 10 times higher lipogenic enzyme activity in the adipose tissue than in the liver.

Lipid metabolism is strongly affected by age, sex and genotype of the animal. It is known that *de novo* fatty acid synthezis is increased with age (Enser, 1991). In metabolic processes it is mainly saturated fatty acids that are produced. The accumulation of saturated acids in adipose tissue increases also with age and growth of pigs. The relative percentage of unsaturated fatty acids decrease up to 180 days of age where after there are no changes in fatty acid composition (Nürnberg *et al.*, 1998).

The difference in fat metabolism among the genotypes and also three sexes has been observed in several studies. The fat content of the body decreases significantly ($P<0.05$) in order of males < females < castrates (Quiniou and Noblet, 1995; Kouba

et al., 1999). The lipogenic capacity of porcine inrtamuscular adipose tissue was studied by Mourot and Kouba (1998) in Large White and Meishan pigs to represent the difference between lean and obese genotype. The results of their study indicates that intramuscular fat could be synthesised *in situ* and the degree of the synthesis depends on two enzymes activity (acetyl-CoA-carboxylase and malic enzyme), which differ with genotype. This is in agreement with the results of Hauser *et al.* (1997). They showed that the adipocyte diameter of backfat, inter- and intramuscular fat in Pietrain pigs was lower than in obese phenotypes.

From the literature it can be concluded that there are not sufficient data to describe the fat turnover in different body fractions such as muscle, viscera, hide and bone. These pools should therefore focus mainly on meat and organs. Regarding fat metabolism, it is shown that age, sex, genotype and nutritional level all influence fat deposition, but there is no data for the rate of synthesis or degradation of lipids for different animal traits and nutritional conditions. These parameters are estimated from empirical equations.

Body fat is derived from two sources, by synthesis from endogenous sources and exogenously from the dietary fat. The fatty acid composition of deposited fat will reflect the relative contribution from these two sources (Leat, 1983). *De novo* fatty acid synthesis occurs from carbohydrate, volatile fatty acid (VFA) and deaminated amino acids. The result of the synthesis is mainly palmitic and stearic acid (Nürnberg *et al.*, 1998). The energy efficiency of the transformation of glucose into body fat is estimated of 74 % (Black, 1995b) and in the case of glucose conversion to glycogen there is also a 5 % loss (Leat, 1983). Conversion of acetate into fat has an efficiency of about 80 % (Milligan, 1971). The energetic conversion of amino acid into body lipid is estimated of 53 % efficiency (Black, 1995b). During growth both the proportion of energy available for fat deposition in pigs increases as well as the rate of *de novo* fatty acid synthesis (Enser, 1991).

Exogenous fatty acids are predominantly from dietary origin but they also include fatty acids, which are modified and synthesised by microorganisms in the lumen of the gut. In the non-ruminant animals dietary fatty acids are absorbed virtually unchanged (Leat, 1983). The process of the conversion of dietary fatty acid into deposited fat is the most efficient 90% (Black, 1995b). Dietary fat consumption depresses the lipogenesis in adipose tissue. In animals fed 12.5 g lipid/100 g diet (2.5 g endogenous lipid/100 g diet plus 10 g/100 g added fatty acids) the lipogenesis in adipose tissue was lower ($P<0.05$) than with the cornstarch diet (2.5 g lipid/100g) (Smith *et al.*, 1996).

Data on the effect of fatty acid source on lipogenesis from the literature seems inconsistent. In several studies it was observed that dietary fatty acid composition had pronounced effects on lipogenesis. Eighter the carbon-chain length (Smith *et al.*,1996) or the saturation of the fatty acids influenced the lipid synthesis in adipose tissue (Bee *et al.*, 1999; Kouba and Mourot, 1999). Kouba and Mourot (1999), however, found that the lipid source like corn oil or tallow supplemented 4 % had no effect on muscle lipogenezis. Contradictory to above Allee *et al.* (1971) demonstrated that 13% dietary corn oil and 13% dietary beef tallow were equally effective in depressing lipogenesis from glucose in porcine adipose tissue. This would suggest that unsaturated and saturated fatty acids were similar in their effect on *de novo* fatty acid biosynthesis.

Pigs fed diets containing 15.4 MJ DE/kg exhibited higher lipogenic activity in backfat comparing to pigs fed 9.5 MJ DE/kg (Bee *et al.*, 1999). Increase in dietary protein and lysine intake at isocaloric energy supply did not significantly affect the lipid metabolism in growing and finishing pigs (Lien *et al.*, 1998). Rosebrough and McMurtry (1993) carried out an *in vitro* and *in vivo* study and observed lipogenesis when both protein and lysine contents of the diet were increased. Although dietary crude protein levels noticeably changed the rates of *in vitro* lipogenesis in broiler chickens, changing either the level of a single limiting amino acid or the levels of several limiting amino acids did not result in a large change of lipogenesis (Rosebrough and McMurtry, 1993).

Lipid accretion in different body parts

Muscle

The fat content of the muscle or lean fraction can be mathematically described by the allometric equation $\ln Y = \ln a + b \cdot \ln X$, where Y is the fat content (kg) in muscle or lean and X is the empty body weight in kg (Susenbeth and Keitel, 1988; Kouba *et al.*, 1999). Kouba *et al.* (1999) also established an allometric equation for intramuscular fat content (kg) as a function of muscle mass (kg).

The energy supply of the animal and the protein/MJ ME ratio of the diet determines the amount of fat in the lean fraction (Nielsen, 1973; Jørgensen *et al.*, 1985). As shown by Jørgensen *et al.* (1985), the fat percentage per unit dry matter in the muscle increases with increasing dietary energy concentration (b=0.65) and daily energy intake (b = 1.53) and decreases with increasing digestible protein/MJ ME ratio (b=-0.74) in pigs of 90 kg body weight.

Organs

A linear response was observed between fat % in the empty body minus carcass and fat % of empty body and also between fat % in organs and body fat (Jørgensen *et al.*, 1985). Knap (2000) found an allometric equation for the relation between body fat % in entrails and blood and total body fat in kg. The fat proportion of the organ fraction increased linearly with increasing energy intake (Bikker, 1994).

Bone and hide

In bone fraction the chemical composition is determined by nutrition supply. Jørgensen *et al.* (1985) found that bone fat % in dry matter increased with increasing energy density of the diet and feeding intensity and decreased with increasing digestive protein per ME. The chemical composition of hide is considered constant. Nielsen (1973) measured 40.5-41.9 % of fat in dry matter of hide in pigs at 90 kg body weight. Although the content of chemical components do not changed upon various nutrition supply, the subcutaneous fat differs with energy intake and energy source. *Ad libitum* feed consumption results in higher average backfat thickness (Godfrey *et al.*, 1991). The energy source seems to have a considerable effect on subcutaneous fat as well. Feeding high dietary fat content the backfat area was higher compared to pigs fed low fat diet when the main energy source was starch (Mersmann *et al.*, 1984). The backfat area was defined by backfat depth over the vertebral column. The shoulder and the midback area were statistically different at the 14^{th} week. Short chain fatty acids derived from the microbial fermentation of the hind gut are also available

for pigs as an energy source. Scipioni *et al.* (1991) studied the effect of maize silage (0.5 of dry matter) and pressed sugar beat pulp silage (0.5 of dry matter) on the subcutaneous fat. A large part of the energy comes from short chain fatty acids upon feeding silage. They found that compared to a common diet pigs consumed silage deposited less fat at subcutaneous region (Scipioni *et al.*, 1991).

Conclusion of lipid metabolism

The following conclusions can be drawn from the lipid metabolism. Similarly to the protein, lipid metabolism is also influenced by age, sex and genotype of the pig. The lipid turnover is much lower in main lipid droplets comparing to protein turnover. It can be influenced by nutrition similar to protein. The energy supply strongly determines the lipid deposition due to increasing energy consumption increases the lipogenesis. The energy may originate from different sources like long chain fatty acids, short chain fatty acids or glucose equivalents. Considering that metabolic pathways for these are different the rate of the lipid synthesis can change with different energy sources. In some cases it may be influenced in fat deposition and fat distribution in growing and fattening pigs.

Recommendation for modelling

It can be concluded from the literature that a comprehensive model, which predicts the performance of growing and fattening pigs in different “pools”, is not available. Developing a model on biological bases the following principles are to be considered; both the protein and fat deposition are the result of synthesis and catabolism in the body. The fractional rate of protein synthesis and degradation decreases with age in each fraction. The rate change of anabolic and catabolic process are pronounced at the beginning of the animal life and later on after the maturity when the rate of catabolism exceeds the rate of synthesis. At the weight range of growing and fattening pigs the rate of FRS and FRD of protein and fat can be considered as constant values. For muscle protein the average FRS and FRD are about 2.4-5.9 % per day (Simon, 1989) and 2.0-2.3 % per day (van den Hemel-Grooten, 1996), respectively.

By consuming different nutrient composition the chemical composition of the body can be changed. In skeletal muscle energy, protein and amino acid intake have a considerable effect on FRS and FRD. Increasing energy, protein or amino acid supply the protein synthesis increases more dynamic than the protein degradation and result a higher accretion. In the model equation for protein synthesis is supposed to depend both on energy and protein or amino acid supply.

The lipid turnover in adipose tissue is slow and it is influenced by the energy level and the source of energy. With increase in energy consumption the fat accretion increases linearly. The source of energy also has a considerable effect on lipid metabolism. In case of dietary fat supply the lipogenesis is depressed compared to the situation when the main energy source is carbohydrate. The protein or amino acid supply does not appear to influence lipid turnover directly.

Consequently the process of synthesis and degradation of protein and fat storage from different nutrients require the representation of the main stages of the metabolism. Different nutrients follow different metabolic pathways after ingestion and

results in accretion of protein, fat, water and ash. Describing those conversions can be done with a model reasonably well.

The ratio of the body parts is changing during the growth of pigs. The relation between the chemical components in a certain body compartment usually described by allometric or hyperbolic equations. The accretion of chemical components results the historical S-shape curve. Both the amount and the chemical composition of the muscle fraction are affected by age, sex, genotype and nutritional factors. There have been equation established to describe the relationship between nutrient intake and change in body parts. Energy supply seems to influence the protein content of muscle, organs and bone in a 'linear-plateau' manner whereas the fat content is influenced in a linear manner. Protein and amino acid pattern determine the protein deposition while the energy supply is sufficient. Although protein or amino acid intake does not affect the lipogenic enzymes activity, supplying protein above the requirement for maximal protein deposition dietary protein is available for fat synthesis according to linear-plateau concept.

According to the published data a mechanistic model which predicts the performance of growing and fattening pigs in term of lean, fatty tissue and organs in the whole body does not exist. There is only limited information for the prediction of protein and fat deposition and these content in the different body parts such as muscle, organs, hide and bone fraction. Based on previous discussed biological principles it is suggested to develop a compartimental model to predict protein and fat deposition in growing and fattening pigs which is consequently appropriate to estimate the meat quality as well.

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Conclusions from the literature and scope of the thesis

Conclusions from the literature

Reviewing the literature, in Chapter 1 and 2, shows that nutritional models can be classified by type, however in practice they usually exist in combinations, such as empirical-static, empirical-dynamic or mechanistic-dynamic. It has been shown that in either type of model the modelling process is similar. Thus, model development requires animal trial, data analysis, equation definition and model evaluation with independent data. An experiment to be useful in modelling the following information needs to be obtained: characteristics of the animal and the diet, distribution of the nutrients within the body for maintenance and production (as protein and fat deposition), and quantification of animal response to nutrient intake. It was also confirmed from the literature, that the practical applications of nutritional models are diverse. Different types of models are used in practice, however models enable more profitable, and less erratic, production systems to be defined.

It can be also concluded from the literature that growth models should be developed on a biological basis. According to that principle, a flexible model would predict pig production, although there is currently no model for growing and fattening pigs that predicts body composition in terms of chemical composition in the various body compartments such as muscle, bone, hide and organs. However, a compartmental modelling approach allows both a quantitative and a qualitative prediction. The demand for a quality production approach has appeared due to changes in consumers' requirements in the last few years.

It was also confirmed from the literature that there is only limited information on the dynamics of protein and fat deposition in the different body parts. There are three principles that are the proposed entities of a new pig model. Firstly, a mechanistic approach should be chosen in order to represent the biological bases of the partitioning of ingested nutrients to growth (e.g. protein and fat turnover are described explicitly, including their limitations). Secondly, intermediary metabolism of different energy sources should be presented, including interactions among various metabolites. Pig growth models usually fail to distinguish the origin of non-protein energy intake. However, there is only limited information on the effects of energy sources on fat deposition. Thirdly, the anatomical body composition should be related to chemical composition. Since the chemical composition in different parts of the body can be described by mathematical equations with relatively high accuracy, the distribution of protein and fat deposition can also be accurately estimated.

The scope of the present thesis

1. To develop a mechanistic-dynamic model for growing and fattening pigs predicting the anatomical and chemical body composition at slaughter time.

2. To show which model parameters are sensitive to changes in the model.

3. To discuss model accuracy by quantitative and qualitative prediction of the model tested with independent data.

4. To define fat production potential of various energy sources at low and high feeding levels.

5. To study the effect of different energy sources at two energy intakes on distribution of fat deposition during the fattening period.

MODEL DEVELOPMENT

Chapter 3

General set up of the thesis

The aim of the present chapter is to introduce the work done in the thesis. It clarifies the lay out of the project and explains the data process of model development. This chapter also summarises the methodologies of different parts of the thesis and presents the logical sequence of chapters. However, the detailed methodology is given in each chapter.

Review of the literature on growth modelling confirmed the existence of various approaches. The classification of different types of models and the benefits of their use is presented in Chapter 1. It is clearly shown that the following principles should be considered in modelling: 1) description of the animal, 2) description of the diet, 3) distribution of nutrients within the body and 4) quantification of the impact of dietary nutrients on animal performance. The general modelling process is the same in all types of models as far as data collection and analysis, model development and testing are concerned. After a general overview of modelling (Chapter 1) a critical evaluation is given on existing models (Chapter 2). It is concluded that the mechanistic approach should be used. A conceptual basis of a mechanistic model is outlined regarding the elementary properties of protein and lipid metabolism. A review of the literature reveals that protein metabolism had been studied from several aspects unlike energy and lipid metabolism. It was concluded from the literature, that a comprehensive model for predicting the anatomical body composition in terms of muscle, bone, hide and organs did not exist. Finally, the elements needed to be considered in the development of a compartimental mechanistic-dynamic pig growth model were selected.

The scope of the present thesis is to develop a model for growing and fattening pigs in order to predict their body composition in terms of protein and fat deposition and distribution of protein and fat among body parts. The compartimental approach serves as a tool for predicting the amount of meat and the fat to protein ratio in the meat. The general design of the PhD project is presented in Figure 1. The work was conducted within a sandwich program at two research sites: University of Kaposvár (Hungary) and Wageningen University and Research Centre (The Netherlands) (Figure 1). The basic data set for the growth model was available, the mathematical procedure, the model development and the evaluation started in Wageningen and continued in Kaposvár. The model was developed based on a data set comprising chemical body composition of different body parts of approximately 200 individually housed pigs fed by different feeding strategies and nutrient content and also on data from the literature (Chapter 4). The basic data set contained two experiments, both had been carried out with VOC, Nieuw-Dalland gilts (Table 1). In the first experiment the pigs received different treatments with increasing lysine intake at 2.5 and 3.0 times maintenance energy requirements at the growing period (20-45 kg). In the second experiment the pigs were fed with the same nutrient content in the feed, but the diet proportion was different in 6 treatments. The daily feed intake was adjusted to 1.7 maintenance energy requirements in the first treatment and it was increased by 0.5 increments up to 4.2 times maintenance energy requirement considered *ad libitum* feed intake. The whole growing and fattening period was studied as it is shown in Table 1. The experimental method was a comparative slaughter technique in both experiments.

The bodies were dissected and the chemical composition of different body parts was determined (Chapter 4). The growth model predicts the partitioning of nutrients within the body. Estimation of chemical and anatomical body composition is given from nutrient intake between 20-105 kg body weight. The model also predicts technical parameters such as growth rate, feed conversion, carcass mass, etc. Some qualitative parameters can be also predicted like meat percentage, fat content and fat to protein ratio in the muscle fraction at slaughter time. The model was developed on principles set forth in Chapter 2. The evaluation of the model included a sensitivity analysis and a model testing (Chapter 5). The sensitivity analysis was carried out by changing the model parameters and the maintenance energy requirement and varying the stochasticity. The model was also tested by independent data sets taken from published studies (Table 2). The aim of the evaluation with independent data sets was to highlight the strong and weak points of the model. For that purpose different types of treatments were tested such as increasing protein intake, different protein to lysine ratio, different lysine to DE ratio and different energy sources such as starch and lipid. The experimental method was a comparative slaughter technique with chemical body analysis in all trials used in the evaluation (Chapter 5). The predicted variables in each study are presented in Table 2.

It was concluded from both the model evaluation with independent data sets (Chapter 5) and the review of literature on energy metabolism (Chapter 2), that the effect of energy source on lipid metabolism should be further studied. A fattening trial was carried out in Kaposvár to study the effect of energy source at two feeding levels on distribution and deposition of fat in fattening gilts and barrows (Figure 1, Table 1). A total of 58 pigs (29 barrows and 29 gilts) with an initial live weight of 48 kg were used. The pigs were housed individually and assigned to one of 8 dietary treatments: control as a normal diet and isocaloric proportions of rapidly fermentable NSP, starch and digestible fat were added to the control at two feeding levels. The pigs were fed until 106 kg live weight. The effect of dietary treatments was investigated by comparative slaughter technique. After slaughtering the bodies were dissected and the chemical composition of the body parts was determined. The results of the trial are presented in Chapter 6. The consequences of the experimental results in a modelling context are considered in the General Discussion. A further evaluation of the model is carried out with the fattening trial (Figure 1). The energetic efficiency of fermentable NSP, digestible starch and digestible fat found in the trial and simulated by the model is discussed. Some practical issues are also presented in connection with the present model. Furthermore, factors other than nutrition (disease, environment) are examined in the modelling context. Finally, some practical implications are discussed and the main conclusions are summarised. A separate section at the end of the thesis contains the new scientific results.

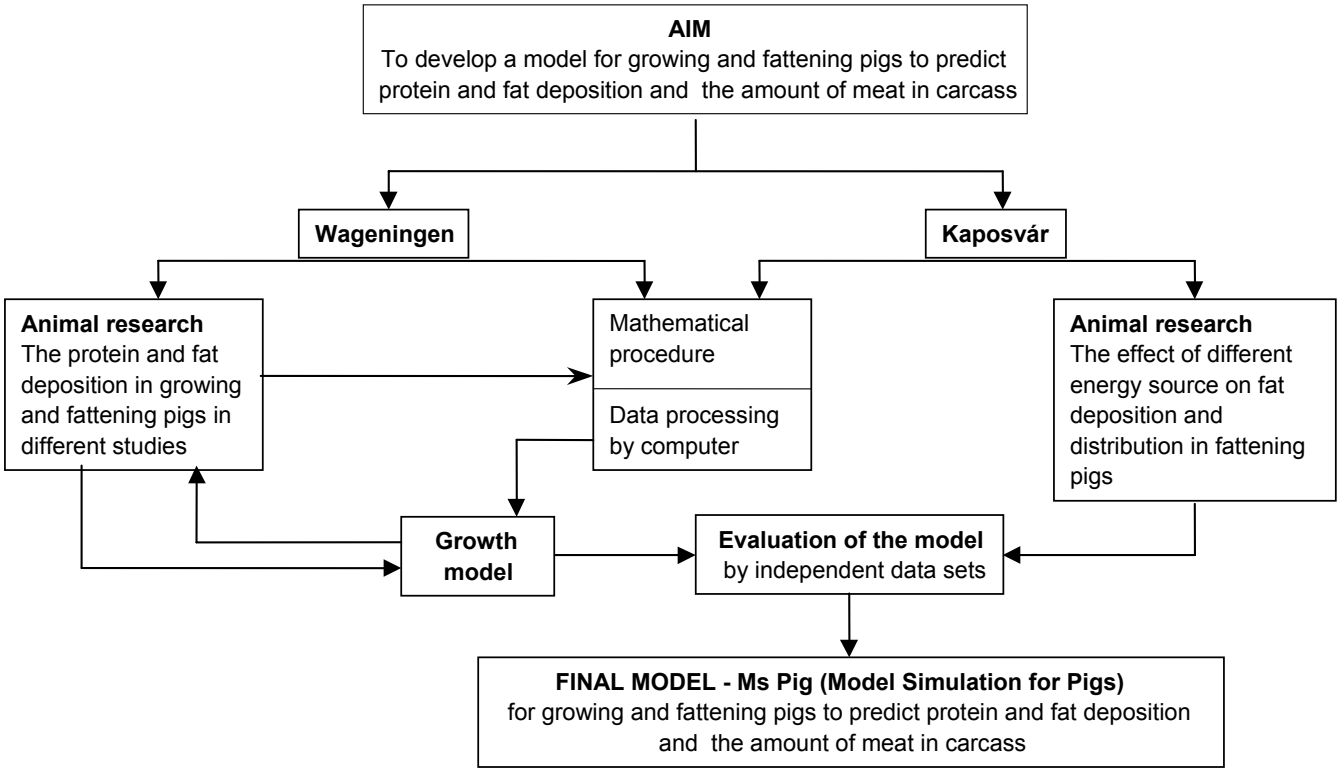
Table 1
Experimental conditions in different studies for model development in the thesis (Chapters 4 and 6)

	Wageningen University and Research Centre		University of Kaposvár
	Experiment 1	Experiment 2	
Number of pigs	95	100	58
Genotype	VOC, Nieuw-Dalland	VOC, Nieuw-Dalland	KA-HYB
Sex	gilt	gilt	gilt, barrow
Weight range	20-45 kg	20-45 kg 45-85 kg 45-105 kg	45-105 kg
Treatments	Increasing lysine intake at two energy levels	Increasing energy intake from 1.7 times maintenance to *ad libitum* feed intake	Feeding different energy sources at two energy levels
Housing	Individually	Individually	Individually
Experimental method	Comparative slaughter with chemical body analysis	Comparative slaughter with chemical body analysis	Comparative slaughter with chemical body analysis

Table 2
Experimental conditions in independent published studies used for model evaluation (Chapter 5)

	Noblet *et al*. (1987)	Beach *et al*. (1991)	van Lunen and Cole (1996)	Chen *et al*. (1999)
Genotype, sex	Large White female	Large White male	High lean genotype female	High lean genotype female
Weight range	20-50 kg	20-50 kg	20-95 kg	51-115 kg
Number of pigs per treatments	8	10	4	5
Number of treatments	3	2	6	5
Treatments	Different protein and lysine intake	Different energy source	Different lysine/DE ratio	Increasing protein intake
Housing	individually	individually	individually	individually
Experimental method	Comparative slaughter with chemical body analysis	Comparative slaughter with chemical body analysis	Comparative slaughter with chemical body analysis	Comparative slaughter with chemical body analysis
Predicted parameters	Average daily gain Carcass weight gain Carcass protein gain Carcass fat gain	Average daily gain Empty body gain Carcass gain Muscle gain Organ gain Adipose tissue gain Muscle protein dep. Carcass protein dep. Body protein dep. Body fat dep. Protein dep. in EBG Fat dep. in EBG Protein dep. in carc.gain Fat dep. in carc.gain	Average daily gain Feed conversion ratio Protein deposition Fat deposition	Average daily gain Carcass gain Protein deposition Fat deposition Carcass protein content Carcass fat content

Figure 1
General design of the PhD project



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Chapter 4

Modelling of nutrient partitioning in growing pigs to predict their anatomical body composition: 1. Model description

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Abstract

A dynamic mechanistic model was developed for growing and fattening pigs. The aim of the model is to predict growth rate and both the chemical and anatomical body compositions of gilts of 20-105 kg live weight from digestible nutrient intake. The model represents the partitioning of digestible nutrients from intake through intermediary metabolism to body protein and body fat. State variables of the model are lysine, acetyl-CoA equivalents, glucose, VFA, and fatty acids as metabolite pools, and protein in muscle, hide, bone and viscera and body fat as body constituent pools. It is assumed that fluxes of metabolites follow saturation kinetics depending on metabolite concentrations. The anatomical body composition is predicted from the chemical body composition and accretion using allometric relationships. Partitioning of protein, fat, water and ash in muscle, organs, hide and bone fractions are described by empirical allometric equations, driven by the rates of muscle protein and body fat deposition. Model parameters were adjusted to obtain a good fit of the experimental data from literature. Differential equations were solved numerically for a given set of initial conditions and parameter values. In the present paper, the model is presented, including its parameterization. The evaluation of the model is described in a companion paper.

Keywords: pig, modelling, anatomical body composition, chemical body composition

Introduction

Since the introduction of pig growth models, applicable both in a scientific and a practical environment in the seventies and eighties (see e.g. Whittemore and Fawcett, 1976; Black *et al*. 1988; Moughan *et al*. 1987), interest in prediction of pig growth has increased over the years. Since then, new models have been introduced, each serving their own objective: some models focused on nutrient digestion processes (Bastianelli *et al*. 1996) or especially on protein digestion in the small intestine (Rivest *et al*. 2000); or estimating amino acid requirements (Moughan, 1989); others aimed to model growth rate and its composition in terms of protein and lipid (Burlacu *et al*. 1989; Pomar *et al*.1991; Danfaer, 2000; Birkett and de Lange 2001*a*), or especially fatty acid composition of the body fat (Lizardo *et al.* 2002) or improving understanding of different processes like protein turnover and ion pumping (Gill *et al*. 1989*a*) or growth process (Lovatto and Sauvant, 2003). In addition, pig growth modelling efforts have been reviewed and various approaches have been discussed extensively (Black, 1995; Halas and Babinszky, 2000; Gerrits and Dijkstra, 2000; Birkett and de Lange, 2001*b*). Most pig growth simulation models until the 90's were considering protein and energy as separate entities (de Lange, 1995). As acknowledged in more recently developed models, this ignored the effects of differences in the composition of the dietary energy (Danfaer, 2000; Birkett and de Lange, 2001*b*). In addition to models predicting chemical body composition, prediction of anatomical body composition is of great interest, relating chemical body composition to slaughter and meat quality. Anatomical body composition in this respect is defined as the proportion of muscle, bone, hide and organs in the body. Some research groups have developed models for the prediction of anatomical body composition, depending on feed intake and

composition. These models are almost exclusively based on empirical relationships (e.g. TMV, 1991). Since nutrients are almost exclusively absorbed in hydrolysed form and used in different ways, it is obvious to track these pathways in the representation of the animal metabolism. Thus, simulation of use of nutrients for growth, should, at least to some extend, make use of biochemical pathways (Gill *et al*., 1989*b*). Therefore, a biologically based approach to simulation of anatomical body composition, follows nutrients from ingestion through intermediary metabolism to the deposition of chemical body fat and protein, preferably in distinct tissues or tissue groups. Prediction of anatomical body composition therefore has to be based on deposition of chemical entities. The preferred level of aggregation chosen for the representation of (bio)chemical constituents, depends on both model objectives and available data.

In this paper, a mechanistic, dynamic model is described in which this approach is followed to predict the anatomical body composition of gilts between 20 and 105 kg live weight. The model is driven by nutrient intake, and predicts both chemical and anatomical body compositions. In the present paper, the model is presented, including its parameterisation. In a companion paper, an evaluation of the model is presented, including behavioural analysis, sensitivity analysis and comparison with independent data (Halas *et al*. 2004).

Model description

The growth process is affected by genetics and environment particularly by nutrition. The present model focuses on the partitioning of nutrients in growing pigs. Representation of sexes and genotypes is not part of this model, but the consequences for the approach taken are discussed on page 98. In the literature, there is no direct link from ingested nutrients to anatomical body composition on a biological basis. Macro nutrients like protein, lipids and carbohydrates are degraded to metabolites such as amino acids, long chain fatty acids and glucose. Through different pathways these metabolites are oxidised or deposited as body protein and body fat. Therefore, in the current model the prediction of anatomical body composition from nutrient intake involves two steps which are referred to as `metabolic` and `anatomical` parts of the model. The approach used in the model is schematically presented in Figure 1. In the metabolic part, absorbed nutrients enter the intermediary metabolism. The results of the intermediary metabolism in the model are the daily muscle protein and body fat deposition and the daily heat production. The equations established in this part of the model are commonly applied in enzyme kinetics (Gill *et al*. 1989*b*). In the anatomical part of the model it is presumed that the muscle protein deposition rate determines the deposition rate of hide, organ and bone protein and that the body fat deposition rate determines the fat deposition rate in hide, muscle and organs. Deposition of water and ash are related to protein deposition. All of these relationships are described by allometric equations. Anatomical body composition is defined as the proportion of muscle, bone (including head, feet and tail), hide (skin and subcutaneous fat) and organs (blood and viscera) in the body. The complete listing of the model equations is given in Appendix 1.

Representation of the metabolic part of the model

The growth model is driven by digestible nutrient inputs; it describes the partitioning of nutrients from ingestion through intermediary metabolism into body stores. A diagrammatic representation of the metabolic part of the model is presented in Figure 2. In empirical models, only protein and energy inputs are used to simulate growth of pigs (Halas *et al.* 2003). The present model uses nutrients derived from the digestion of protein, fat, starch and sugar and from fermentation of cell wall components. Under practical circumstances, lysine usually is the limiting amino acid for protein deposition (ARC, 1981). Therefore, lysine availability was assumed to be the amino acid, potentially limiting the rate of protein synthesis. Body metabolite pools are lysine, acetyl-CoA, glucose, long chain fatty acids and volatile fatty acids (VFA). The body storage pools comprise protein and lipid in bone, hide, organs and muscle.

Figure 1
Schematic representation of the model approach

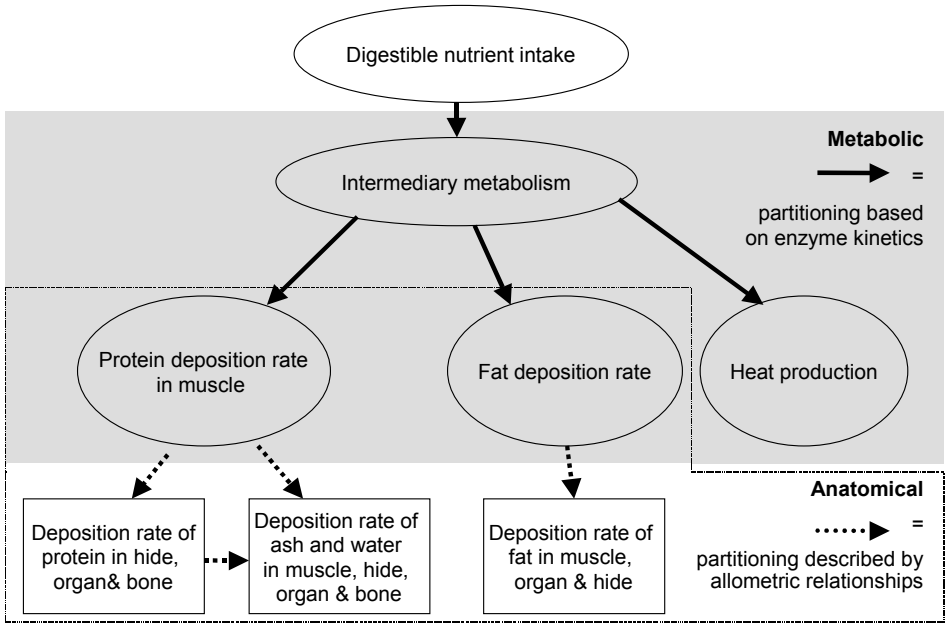
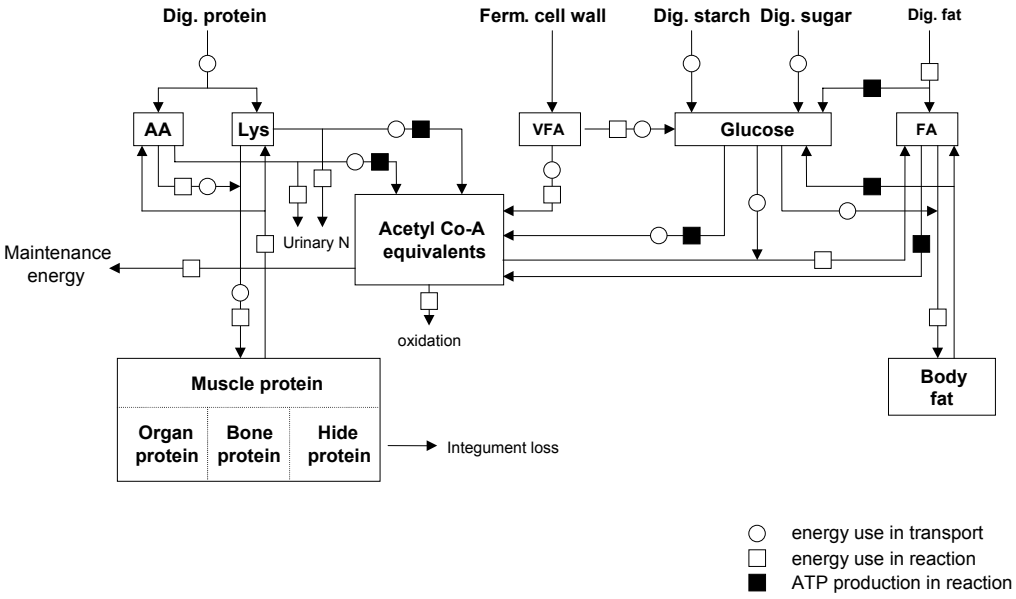


Figure 2
Diagrammatic representation of the growth model



In line with other mechanistic growth models in beef cattle (France *et al*. 1987), sows (Pettigrew *et al*. 1992) and pre-ruminant calves (Gerrits *et al*. 1997) the majority of the flux equations are described using standard expressions from enzyme kinetics. The principle of the model is that net growth results from the balance between synthesis and degradation processes. It is assumed that synthesis depends on the concentration of substrates available and that the utilisation of metabolites follows saturation kinetics.

The rate of change of a pool in time is defined by the sum of all fluxes into and out of that pool. Actual pool sizes are the quantities of the metabolite (mol) or body store (kg) calculated by integration of pool changes over time. Metabolite concentrations are calculated based on empty body weight. Indeed, in many reactions it is the metabolites present in the intracellular pool that act as substrates (Pettigrew *et al*. 1992). Metabolite concentrations, expressed per kg body weight are, however, difficult to find in literature. Therefore normal concentrations in blood plasma were adopted to calculate initial metabolite pool sizes for lysine, glucose and fatty acids.

Stoichiometry and model parameterisation

The abbreviations used in the model are given in Table 1a and b; stochiometric yield and requirement factors for protein and energy metabolism are shown in Table 2 and 3, respectively. These factors include transport costs; absorption costs of the nutrients are considered explicitly. The yield factors of protein synthesis (Y*i*,ly*i)* and proteolysis (Yly,*i*ly; Yaa,*i*ly) and the amino acid requirements of protein synthesis (Raa,ly*i*) were calculated based on tissue amino acid composition data presented by Wünsche *et al*. (1983). In accordance with Gill *et al*. (1989a) and Gerrits *et al*. (1997) we presumed that the energy requirement is 4 mol ATP per peptide bond in protein synthesis. In previous models (Gill *et al*. 1984; Baldwin *et al*. 1987; Pettigrew *et al*. 1992) no energy cost were assumed for protein breakdown. However, utilisation of energy in hydrolysis of phosphate bounds appears essential to proteolysis. Rapoport *et al*. (1985) suggested 1 mol ATP per peptide bond cleaved in reticulocytes. Gerrits *et al*. (1997) concluded from the literature that the ATP cost of proteolysis varies, depending on the mechanism involved. As an average 1 mol ATP/ peptide bond cleaved was assumed.

The yield factors of the energy metabolism and the energy and glucose requirements in the model are presented in Table 3. Some transactions, like body fat synthesis have different stoichiometric parameters, such as yield of body fat from fatty acids (Ytf,fatf; kg/mol), glucose requirement of fat synthesis (Rgl,fatf; mol/mol) and acetyl-CoA requirement of fat synthesis (Ray,fatf; mol/mol). All data in the table were calculated based on molecular weight, energy yield per mol substrate, average N content and transport cost (0.33 mol ATP/ mol substrate). The absorption costs were taken from previous models (Gill *et al*. 1989*a*; Pettigrew *et al*. 1992; Gerrits *et al*. 1997). It was assumed that each mol of glucose or amino acid absorbed from the gut requires 0.33 mol ATP. It was also assumed that dietary fat is absorbed as monoacylglycerol and two fatty acids. Subsequent re-esterification to make a triacylglycerol costs 1.33 mol ATP/fatty acid equivalent (Gerrits *et al*. 1997). Re-esterification maintains an inward diffusion gradient, so no extra absorption costs are assumed.

Associated energy costs of bone mineralization are assumed small because ash deposition is low compared with deposition of the other chemical components. In the present model, the energy costs of bone mineralization were assumed to be proportional with Ca and P deposition in bone tissue. The average Ca and P contents are 37.6 % and 18.4 % of ash fraction in pig bone, adopted from Larsen *et al*. (2000). As suggested by Gerrits *et al*. (1997), 2 mol ATP/ mol Ca and P incorporated in bone ash was assumed.

Parameters to be quantified in the fluxes are the maximum velocity of the reaction (Vmax), the affinity (Mijk) and inhibition constants (Jiji) and the steepness parameters (Sij) (Table 4). Since there are no existing models for growing and fattening pigs with our approach, we calibrated these parameters on experimental data (Bikker *et al*. 1994, 1995, 1996*a*,*b* and unpublished), as described later. For the calculation of Vmax values, it was assumed that the maximal velocity of a certain transaction are proportional with the tissue mass where the transaction is taking place. The Vmax values were mainly calculated from experimental data. These data, however, are most certainly an underestimate of the theoretical Vmax,

because in *in vivo* experiments, conditions will never be optimal (Gill *et al*, 1989*b*). In order to approach realistic Vmax, each value obtained were arbitrarily increased by 25%. Subsequently, affinity and inhibition constants and steepness parameters were adjusted to obtain a good fit of the experimental data regarding to the measured average muscle protein and body fat deposition rates as discussed later.

Table 1a
Abbreviation of names for entities of the model

Symbol	Entity	Unit
aa	Amino acids others than lysine	mol
at	ATP	mol
ay	Acetyl-CoA	mol
bf	Bone fat mass	kg
bp	Bone protein mass	kg
cw	Cell wall components	kg
da	Dietary minerals	kg
df	Dietary fat	kg
dp	Dietary protein	kg
ew	Empty body weight	kg
ex	Exogenous protein loss (skin&hair)	kg
fa	Fatty acid	mol
gl	Glucose	mol
gr	Additional cost for growth	mol Ay/d
hf	Hide fat mass (backfat)	kg
hp	Hide protein mass	kg
li	Liver mass	kg
lw	Live weight	kg
ly	Lysine	mol
ma	Maintenance requirement	mol Ay/d
mf	Muscle fat mass	kg
mp	Muscle protein mass	kg
of	Organ and abdominal fat mass	kg
op	Organ protein mass	kg
ox	Oxidation of Ay	mol
st	Starch	kg
su	Sugar	kg
ta	Total body ash	kg
tf	Total fat mass	kg
un	Urinary N	mol
vf	VFA	mol

Table1b
Notation of the model

Notation	Translation	Units
Ai	Absorption cost for *i*	mol Ay/kg *i* or mol Ay/mol *i*
Ci*	Concentration of *i*	mol *i*/kg ew or g *i*/kg diet
Di	Digestibility of nutrients	-
FDRi	Fractional degradation rate of *i*	d^{-1}
Ji,jk	Michaelis-Menten inhibition constant for *j-k* transaction with respect to *i*	mol/kg
Mi,jk	Michaelis-Menten affinity constant for *j-k* transaction with respect to *i*	mol/kg
Pi,jk	Rate of production of *i* by *j-k* transaction	mol/d or kg/d
Qi	Quantity of *i*	mol or kg
Ri,jk	Requirement of *i* in *j-k* transaction	mol *i*/mol or kg *j*
Sjk	Steepness parameter for *j-k* transaction	-
Ui,jk	Rate of utilization of *i* by *j-k* transaction	mol/d or kg/d
Vjk	Maximum rate of velocity for *j-k* transaction	$mol/kg^{0.75}$ /day**
Yi,jk	Yield of *i* in *j-k* transaction	(mol or kg *i*)/(mol or kg *j*)

* lysine and amino acid concentration in the diet are Cdply and Cdpaa
** in body fat synthesis the unit is mol/kg/day, in additional energy cost for growth the unit is $mol/kg^{0,67}$/day

Table 2
Stoichiometry of protein turnover

Synthesis	Y*i*,ly*i** (kg *i*/mol ly)	Ray,ly*i** (mol ay/mol ly)	Raa,ly*i** (mol aa/mol ly)	Ray,aa*i** (mol ay/mol aa)
Muscle protein	1.6497	0.361	10.8965	0.361
Organ protein	1.6404	0.361	10.9886	0.361
Hide protein	3.1739	0.361	26.8519	0.361
Bone protein	3.1064	0.361	25.3024	0.361
Degradation	**Yly,*i*ly*** **(mol ly/kg *i*)**	**Ray,*i*ly*** **(mol ay/kg *i*)**	**Yaa,*i*ly*** **(mol aa/kg *i*)**	**Ray,*i*aa*** **(mol ay/kg *i*)**
Muscle protein	0.6062	0.051	6.6051	0.550
Organ protein	0.6096	0.051	6.6985	0.558
Hide protein	0.3151	0.026	8.4602	0.705
Bone protein	0.3219	0.027	8.1453	0.679

* *i* is muscle, organ, hide or bone protein, respectively

Table 3
Stoichiometry of the energy metabolism not related to protein turnover (mol/mol)*

Transaction**	Yi,jk	Yat,jk	Rgl,jk	Ray,jk
Ay,lyay	1.973	12.00		
Ay,lyun				0.0046
Ay,aaay	0.780	14.07		
Ay,aaun				0.0046
Un,lyay	2.000			
Un,aaay	1.456			
Ay,faay	9.000	36.00		
Ay,glay	1.973	14.00		
Ay,vfay	1.000			
Fa,dffa	3.394			
Fa,tffa	3.394			
Fa,ayfa	0.102		0.157	
Tf,fatf	0.295		0.167	0.282
Gl,stgl	6.173			
Gl,sugl	5.55			
Gl,vfgl	0.500			
Gl,dffa	0.566	2.26		
Gl,tffa	0.566	2.26		
Vf,stvf	8.642			
Vf,cwvf	7.778			
Aly				0.0275
Aaa				0.0275
Agl				0.0275
Afa				0.1108
Ta,data				2.555

* the unit is mol/kg in cases of yield of fatty acid in body fat (Yfa,tffa) and dietary fat degradation (Yfa,dffa), yield of glucose in dietary fat (Ygl,dffa) and in body fat degradation (Ygl,tffa), yield of VFA from dietary starch (Yvf,stvf) and cell wall (vf,cwvf) and mineral incorporation (Yta,data), the unit is kg/mol in case of yield of body fat synthesized from fatty acids (Ytf,fatf)
** Notations and abbreviations are found in Tables 1a and b.

Table 4
Maximal velocity (Vjk, mol/kg$^{0.75}$/d*), steepness parameter (Sjk), affinity (Mijk, mol/kg) and inhibition constant (Jkjk, mol/kg) of transactions

Transaction**	Vjk	Sjk	Mijk	May,jk	Jkjk
Ly,lymp	0.0423	1.5	0.00001	0.00025	
Ly,lyay	0.4932	2	0.00015		
Fa,fatf	0.2882		0.0009		
Fa,faay	0.1207		0.005		0.0003
Ay,ayfa	2.5266		0.004		0.1
Ly,aygr	1.1885		0.0001	0.006	
Gl,glay	0.5532		0.005		
Vf,vfay	0.1551		0.0005		

* the unit of Vaygr is mol/kg$^{0.67}$/d, the unit of Vfatf is mol/kg/d
** notation of the metabolites involved in the transaction is given in Table 1a and b

Protein metabolism

Lysine pool (Qly). The inputs to the lysine pool are from the apparent absorption of dietary ileal digestible lysine (eq. 1.2) and from body protein degradation (eq. 1.3-1.6). The outputs from the pool are to protein synthesis (eq. 1.7-1.10) and to acetyl-CoA production (eq. 1.11). Initial pool concentration is 0.1 mmol/kg adopted from Defa *et al*. (1999). The utilisation of lysine to protein synthesis is driven by lysine and acetyl-CoA concentrations (eq. 1.7). The reason for the acetyl-CoA dependency of the transaction is that protein synthesis may be limited by energy supply according to the linear-plateau concept (Campbell *et al*. 1984; 1985; Bikker *et al*. 1994). The site of the muscle protein synthesis is located in muscle protein. Maximal velocity of the transaction is therefore scaled with muscle protein mass (Qmp) as Qmp$^{0.75}$ (eq. 1.7). The Vmax for muscle protein synthesis was set as follows: the maximum rate of protein deposition in the experiment of Bikker *et al*. (1996*b*; *ad libitum* feed intake, averaged over 45-85 kg) of 190 g/d was assumed to correspond to a maximum of 150 g/d at 50 kg body weight. According to Simon (1989) half of the body protein deposition rate was considered to be muscle protein (75 g/d). The fractional degradation rate of muscle protein was set as 2.23 %/d (see later), which results in daily 111.5 g muscle protein degradation. Utilisation of lysine in muscle protein synthesis is computed as the daily rate of muscle protein synthesis (summing up the daily deposition and degradation) divided by the yield factor of muscle protein produced from 1 mol lysine (Yly,mply, see eq. 3.1). Subsequently 0.0338 mol/Qmp$^{0.75}$/d was obtained for Vmax, and that value was increased by 25% as discussed previously.

The same approach was adopted for lysine oxidation assuming that the concentration of lysine influences its oxidative metabolism (eq. 1.11). The size of the reaction site was scaled with liver weight (Qli$^{0.75}$) considering that catabolism of lysine is mainly located in the liver (Nelson and Cox, 1982). The liver mass was obtained from organ protein mass (eq. 13.2) By oxidation, lysine yields acetyl-CoA (eq. 1.11), some ATP (eq. 7.13) and urinary N (eq. 7.19). The maximal velocity of

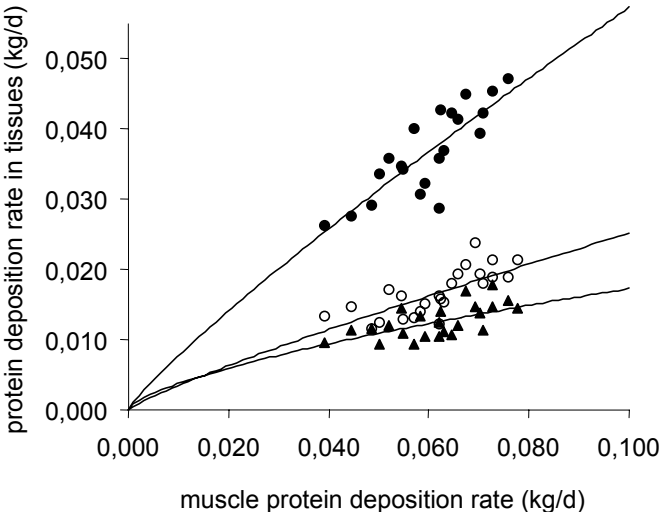
the lysine oxidation was assumed to equal the whole body lysine flux, i.e. the sum of lysine from degraded body proteins and ileal digestible lysine intake. In the case of a pig of 50 kg body weight, body protein mass is approximately 10 kg. It is split among muscle, organs, hide and bone as some 50, 15, 25 and 10 %, respectively (Simon, 1989). the daily amount of lysine released from degradation of muscle, hide, organ and bone protein was 0.2636 mol. It was presumed that 2.5 kg feed intake with 160 g/kg digestible protein content and 0.6075 mol lysine per kg protein yields 0.2430 mol lysine per day. Therefore, the Vmax for lysine oxidation was set to 0.3946 mol lysine/$Qli^{0.75}$/d (see eq. 13.2 for Qli) and the obtained Vmax was increased by 25% as mentioned previously.

Amino acid pool (Qaa). The inputs to the amino acid pool are from apparent absorption of dietary ileal digestible protein (eq. 2.1) and from body protein degradation (eq. 2.2-2.5). The average mol weight (MW) of the amino acids other than lysine in dietary, muscle, organ, bone and hide protein are assumed to be 130, 138, 136, 117, 113 g/mol, respectively (Wünsche *et al*. 1983). Outputs are to protein synthesis (eq. 2.6-2.9) and acetyl-CoA (eq. 2.10). The utilisation of amino acids for protein synthesis depends on utilisation of lysine to protein synthesis. For reasons of simplicity, all amino acids not used for protein synthesis are assumed to be catabolized to yield acetyl-CoA (eq. 2.10), ATP (eq. 7.14) and urinary N (eq. 7.20). Consequently the change of amino acid pool size in time is zero (eq. 2.11) and is a zero-pool (Baldwin *et al*. 1987).

Muscle protein pool (Qmp). The muscle protein pool represents approximately half of the body protein (Simon, 1989). The synthesis of muscle protein is dependent on lysine and acetyl-CoA concentrations. The turnover of the muscle protein can be manipulated by nutrition. Both synthesis and degradation increase with increasing nutrient supply as reviewed by Halas *et al*. (2003). A high protein turnover due to the excess nutrient supply results in a high protein deposition rate. For reasons of simplicity, the fractional degradation rate (FDR) is considered to be constant for each protein pool in the model (eq 3.2, 4.2, 5.2, 6.2). The FDR of muscle protein was assumed 2.23 % per day (van den Hemel-Grooten, 1996). Values in the literature vary between 2 and 4 %/day depending on nutrient supply and experimental method used (Mulvaney *et al.* 1985; Bergen *et al*. 1989; Simon, 1989; Rathmacher *et al*. 1996). The maximal velocity for muscle protein synthesis was calculated as follows. The lysine needed for maximum muscle protein deposition at 50 kg live weight (75 g/d) and the lysine yielded from daily muscle protein degradation (112 g/d) was added up and divided by $Qmp^{0.75}$. As discussed above the value was increased by 25% to approach a realistic Vmax.

In the model, the deposition rate of protein in organs, hide and bone are related to the deposition rate of muscle protein (Figure 3). These relationships were estimated from a serial slaughter experiment of pigs from 20 to 105 kg bodyweight (after Bikker, unpublished - see later in section *Prediction of tissue accretion*).

Figure 3
Partitioning of protein deposition rates in hide (●), organs (○) and bone (▲) as a function of muscle protein deposition rate. The relationships were estimated from data of Bikker (unpublished)



Organ protein pool (Qop) Literature data shows that the organ protein pool is characterised by a very high turnover rate, with fractional synthesis and degradation rates close to each other. The fractional protein synthesis rate is reported to vary between 12-60 % per day in 50 kg pigs depending on the organ and on the method used (Riis, 1983; Simon, 1989). In the model, an average value of 17.8 % per day for fractional degradation rate in organ fraction was adopted. The rate of organ protein synthesis (eq. 4.1; kg/d) is calculated as the sum of net accretion (Figure 3) and degradation rates. The organ protein breakdown rate is calculated from the pool size and FDR (eq. 4.2).

Hide protein pool (Qhp). The hide protein pool has a relatively low turnover rate, even lower than that of muscle protein. The fractional synthesis rate is some 5% per day (Riis, 1983; Simon, 1989). According to that value, the FDR of hide protein was calculated from the experiments as a corresponding FDR of 2 % per day. Outputs from this pool are from degradation of hide protein (eq. 5.2), and through losses of protein by skin and hair (eq. 5.3). Protein losses by skin and hair are related to metabolic body weight and adopted from Moughan (1989) as $0.094 g/kg^{0.75}$/day (eq. 5.3). The rate of hide protein synthesis was calculated by summation of the rate of hide protein deposition (depending on muscle protein deposition rate, Figure 3), hide protein degradation and hair and skin protein losses (eq. 5.1).

Bone protein pool (Qbp). According to the literature data, the fractional degradation rate of bone protein between 20 and 120 kg body weight was

estimated at 5%/d based on Riis (1983) and Simon (1989). Similar to the other protein pools, the rate of protein synthesis is calculated from rate of bone protein accretion (depending on muscle protein accretion rate, Figure 3) and rate of protein degradation (eq. 6.1).

Energy metabolism

The energy metabolism covers all of the transactions that are involved in the energy production and protein and fat accretion. For reasons of simplicity and as discussed by Gerrits *et al*. (1997), energy is supplied by oxidation of acetyl-CoA. In some energy yielding transactions, direct production of ATP is also indicated (see Table 3). Following standard biochemistry, 1 mol acetyl-CoA is equivalent to 12 mol ATP (Stryer, 1981).

Acetyl-CoA pool (Qay). The inputs to the acetyl-CoA pool are from the oxidation of lysine (eq. 7.2), amino acids (eq. 7.3), fatty acids (eq. 7.4) and glucose (eq. 7.5). The acetic and butyric acid absorbed from the gut is considered to appear as acetyl-CoA (eq. 7.6). The rate of production of acetyl-CoA is determined by the rate of utilization of the metabolites. The outputs of the pool are utilization for fatty acid synthesis (eq. 7.7), and to provide energy for all energy requiring transactions (eq. 7.9, 7.10), including maintenance energy (eq. 7.12). The initial pool concentration was set arbitrarily to 3 mmol/kg.

In *de novo* fatty acid synthesis, non-lipid nutrients are converted to fatty acids via acetyl-CoA. Similar to the model of Gerrits *et al*. (1997), it is assumed that fatty acid synthesis follows saturation kinetics and is inhibited by the end-product formed. Fatty acid synthesis takes place in adipose tissue (Nürnberg and Wegner, 1990). Therefore, the maximal velocity of fatty acid synthesis is scaled by body fat mass ($Qtf^{0.75}$) (eq. 7.7). The maximal velocity of the transaction was arbitrarily set to enable a *de novo* rate of fatty acid synthesis of 680 g/d for a pig of 100 kg body weight comprising 25 kg of body fat, sufficient to provide 80% of the total fat synthesis rate of 850 g/d (derived from unpublished data of Bikker). The obtained value was increased by 25 % to approach the realistic Vmax.

In several models, it has been shown that the approach chosen for representation of maintenance energy requirements has a significant impact on the simulation results (e.g. Gerrits *et al*. 1997). Baldwin *et al*. (1987) and Gerrits *et al*. (1997) used empirical relationships derived originally by Smith (1970) to estimate basal energy expenditure of lean body mass, body fat and viscera. By that approach, the difference in maintenance requirements among genotypes and sexes can be explained better than by the use of fixed energy requirements per unit metabolic weight in current energy systems (e.g. ARC 1981) as discussed by Noblet *et al*. (1999) and Schinckel and de Lange (1996). Pettigrew *et al*. (1992) modified the equation of Baldwin *et al*. (1987), and related the maintenance energy to protein in lean body and in viscera and to body fat mass, rather than tissues. In the present model the latter approach was adopted (eq. 7.12). The tissue maintenance energy costs include the cost of membrane transport and of substrate cycling like protein and fat turnover. The energy costs of these transactions are explicitly represented in the present model. Reeds *et al*. (1987) suggested that protein turnover represented 15 to 25 % of total basal energy expenditure.

Similarly, Gill *et al*. (1989*a*) assumed 20.6 % of total ATP expenditure to be associated with muscle protein turnover in their model (taken from Reeds *et al*. 1985). Since in the present model maintenance expenditure includes tissue turnover, part of the maintenance energy is double counted. Therefore, arbitrarily, the maintenance requirement was reduced by 20%. It should be emphasized, however, that this was done prior to fitting the model to the experimental data of Bikker *et al*. (1994, 1995, 1996*a,b* and unpublished). It is important that all energy costs are quantitatively accounted for, albeit difficult to accurately assign them to the biological process represented in the model or to a lump-sum, like maintenance energy or additional energy costs of growth (described later).

Some transactions yield ATP as oxidation of lysine, amino acid, glucose and fatty acids (eq. 7.13, 7.14, 7.16 and 7.18), and glucose production from dietary or body fat (eq. 7.15 and 7.17). However, ATP was not represented as a state variable. Because ATP cannot be used as a substrate, the inevitable ATP production from equations mentioned above was used to satisfy maintenance energy requirements. In test simulations, it was confirmed that the sum of ATP yielding transactions is always lower than the maintenance energy requirements (eq. 7.8). The remaining maintenance energy requirements was satisfied by oxidation of acetyl-CoA.

An additional energy requiring transaction was introduced and referred to as additional energy costs for growth (eq. 7.10). This flux represents the energy costs of tissue deposition, not represented by the biological processes explicitly represented in the model. For example, the energy requirements for ion pumping, synthesis of endogenous protein and some other substrate cycling costs, are not represented by the model. The rate of acetyl-CoA oxidation satisfying these additional costs for growth depends on both acetyl-CoA and lysine concentration (eq. 7.11). The Vmax and the affinity parameters of the flux were set to cover the discrepancy between the energy utilization accounted for in the model and the observed energetic efficiency in the trials used to calibrate the model. The maximal reaction velocity is assumed to be related to empty body weight ($Qew^{0.67}$), being the site of the biological processes represented by this flux.

Volatile fatty acid pool (Qvf). The input to this pool is from VFA that arise from fermentation of cell wall components, mainly in the hindgut (eq. 8.2). The outputs from the VFA pool are to the acetyl-CoA pool (in the form of acetate and butyrate, eq. 8.3) and to glucose (in the form of propionate, eq. 8.4). The default VFA ratio in the model is 70% acetic plus butyric acid (PRayvf =0.7) and 30% propionic acid (Kennelly *et al*. 1981; Michael and Rerat, 1998). The utilisation of VFA depends on the VFA concentration and is scaled with empty body weight ($Qew^{0.75}$). The Vmax was set to account for complete clearance of VFA on a high fibre diet corresponding to 300g daily intake of fermentable cell wall components. The obtained maximal velocity was increased by 25%. The initial VFA concentration was set to 0.1 mmol/kg. The VFA concentration was assumed to be lower than in sows. Hence initial acetic acid concentration of 0.3 mmol/kg in sow model of Pettigrew *et al*. (1992) was reduced.

Glucose pool (Qgl). The glucose pool has a high turnover rate. Glucose is produced from dietary starch (eq. 9.2) and sugars (eq. 9.3) directly, from VFA pool

(propionate only, eq. 9.5) and from glycerol released from degraded dietary (eq. 9.4) and body fat (eq. 9.6). It is assumed that the MW of sugars is 180 and that of starch is 162 g/mol. The outputs of the glucose pool are used directly for oxidization (eq. 9.7) and indirectly for fatty acid (through NADPH, eq. 9.8) and fat synthesis (as glycerol, eq. 9.9). Glucose is used as a source of glycerol in the esterification of fatty acids during fat synthesis (eq. 9.8) and as the major source of reduced NADPH in fatty acid synthesis (eq. 9.9) (Wijayasinghe *et al*. 1986). It is assumed that in non-ruminants, with usually sufficient quantities of glucose, all the required NADPH is produced by metabolism of glucose through the pentose phosphate pathway (Pettigrew *et al*. 1992). The Vmax of the glucose oxidation was calculated for a pig of 50 kg body weight, assuming all of the glucose inflow can be oxidized after supplying the glucose requirement of 400 g/d fat synthesis. Assuming a maximal absorption of 750 g of glucose per kg diet, this yields 8.278 mol glucose daily. The Vmax of glycolysis is scaled with $Qew^{0.75}$ (eq. 9.7) and increased by 25%. The initial glucose concentration was set at 4 mmol/kg (Stangl *et al*., 1999). Glucose synthesis from glucogenic metabolites other than propionate are not included in the model. In line with the sow model of Pettigrew et al. (1992), it was presumed that non-ruminants absorb most of their energy as glucose, and therefore no need for significant gluconeogenesis occurs from amino acids. On the other hand glucogenic amino acids degraded are passing through the glucose pool just to be oxidised later in the acetyl-CoA pool, therefore there is no real point to include it. Subsequently we considered no gluconeogenesis from amino acids in the model.

Fatty acid pool (Qfa). The inputs to the fatty acid pool are from dietary and body lipid hydrolysis (eq. 10.2 and 10.3, respectively) and *de novo* synthesis (eq. 10.4). In the interest of simplicity, the degraded dietary and body lipid are considered to produce 3 mol fatty acids and 0.5 mol glucose per mol lipid. Outputs are to body fat synthesis (eq. 10.5) and fatty acid oxidation (eq. 10.6). The mol weight of fatty acids are set as 282 g, initial pool concentration is 0.7 mmol/kg adopted from Stangl *et al*. (1999). Fatty acid oxidation increases with increasing fatty acid concentration and is inhibited by acetyl-CoA concentration (eq. 10.6). The maximal velocity of that energy yielding process is scaled with $Qew^{0.75}$. The Vmax for fatty acid oxidation was set to enable quantitative oxidation of all fatty acids absorbed from a high fat diet and those released during lipolysis, assuming no re-utilization of fatty acid to body fat. For this calculation, the dietary fat content and rate of lipolysis were assumed to be 160 g/kg and 260 g/d, respectively. Body fat synthesis depends on fatty acid concentration, and Vmax is scaled with body fat mass (Qtf) (eq. 10.5). The maximum velocity of body fat synthesis was set to 600 g fat/d for a pig of 100 kg derived from unpublished data of Bikker, assuming a fixed fractional degradation rate of 1% (see below). The maximal velocities of fatty acid oxidation and body fat synthesis were increased by 25% to approach the realistic Vmax.

Body fat pool (Qtf). The body fat pool has one input, viz. synthesis of fat from fatty acids (Eq. 11.1), and one output, viz. degradation of fat (eq. 11.2). The body fat pool represents chemically determined fats, assumed to comprise only triacylglycerol with a molar weight of 884 g. Danfaer (1999) reported 0.9 %/day

fractional degradation rate of lipolysis in adipose tissue. According to that a fixed fractional degradation rate of 1 % per day was used in the model for the body fat.

Representation of the anatomical part of the model

Prediction of tissue accretion

Nutrient intake affects whole body protein and lipid gain but also the partitioning into body compartments. Variation in nutrient intake results in different accretion rates of tissues and organs and consequently in differences in anatomical body composition during the animal life (Walstra, 1980). In certain conditions increasing energy intake increases both the protein and the fat deposition (de Greef *et al*. 1994; Bikker *et al*. 1994). In addition to the amount of nutrients, the nutrient balance also has an influence on fat deposition. By increasing dietary lysine and protein content, Bikker *et al*. (1994) found an increase in protein and a decrease in fat deposition in pigs fed at 2.5 and 3.0 times the energy requirements for maintenance. The distribution of protein and fat deposition is also affected by nutrient intake and nutrient balance. Jørgensen *et al*. (1985) found that subcutaneous fat was more sensitive to increasing energy intake and/or increasing protein intake than muscle fat. Therefore, the partitioning of fat deposition must have a certain degree of priority among tissues.

In the model development, these principles were considered. In the metabolic part of the model, deposition rates of muscle protein and total body fat are predicted. In the anatomical part, these are regarded as the driving force for distribution of deposited fat over muscle, hide, organs and bone, as well as the protein deposition rate in hide, bone and organs (see Figure 1), as described below.

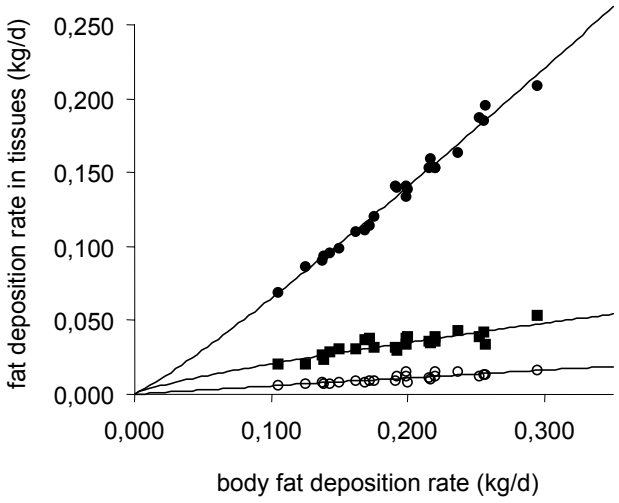
For establishing the equations in the anatomical part of the model, data of Bikker (unpublished) were used. The chemical body composition of 24 pigs fed in a whole fattening period from 20 to 105 kg body weight was determined. Those animals received 2.2 or 3.7 times maintenance energy intake at a body weight range of 20-45 kg, and 2.2, 2.7 or 3.7 times maintenance energy intake thereafter until 105 kg body weight. The daily muscle protein and body fat depositions were in a range of 39-78 g/d and 105-295 g/d, respectively. The relationships between various deposition rates were described by allometry (see Figures 3 and 4). Analogous to the approach of Gerrits *et al*. (1997) and as discussed by them, rates of protein deposition of organs, bone and hide were related to rate of muscle protein deposition (see section *Protein metabolism*, Figure 3 and eq. 4.1, 5.1, 6.1). Figure 3 illustrates that protein deposition rates in hide, organs and bone increase with the increasing muscle protein deposition rate, but not in a similar way. It is assumed that at zero muscle protein deposition the total protein mass does not change. At low rates of muscle protein deposition, bone protein deposition has some priority over organ protein (Figure 3).

According to Kotarbinska (1971) and de Greef (1992), water and ash contents are strongly related to body protein. From the available experimental data, water and ash deposition rates were estimated as a function of protein deposition rate in each fraction (eq. 12.2, 12.3).

Whereas the bone protein:fat ratio was considered to be constant, the partitioning of fat deposition over muscle, hide (including backfat), and organs (for a large part mesenteric fat depots) was considered to be dependent on the rate of fat deposition. As illustrated by Jørgensen *et al.* (1985) and also by the unpublished data of Bikker, fat distribution across these tissues varies with nutrient intake. In the model, it was decided to make this distribution dependent on the rate of fat deposition, knowing the strong relationship between fat deposition rate and energy (nutrient) intake and assuming that the excess nutrients can be stored as fat, but that the partitioning between tissues depends on the excess to be deposited. The unpublished data of Bikker, used to estimate this relationship, confirm this dependency (see Figure 4). Furthermore, the chemical composition of bone tissue was assumed constant (Field *et al*. 1974), and therefore not sensitive to changes in the rate of body fat deposition. Therefore, the rate of bone fat deposition was made dependent on the rate of bone protein deposition (eq. 13.6). It has to be mentioned that bone fat content increases with increasing energy intake (Jørgensen *et al*. 1985), but quantitatively it is not substantial. A pig of 100 kg body weight has about 8.5 kg bone (Gu *et al*. 1992) in which 13-14% is the fat content (Just Nielsen, 1973; Jørgensen *et al*. 1985).

The empty body weight was calculated by summation of protein deposition in muscle, organs, bone and hide and the deposition rate of fat, water and ash in the total body (eq. 12.1). From experimental data of Bikker (1994, 1995, 1996*a,b*) the relationship between empty body weight and live weight was obtained (eq. 13.1). Liver weight was assumed to be related to the organ protein mass (eq. 13.2). The anatomical body composition is calculated by summation of protein, fat, water and ash mass in muscle (eq. 14.1), organs (eq. 14.2), hide (eq. 14.3) and bone (eq. 14.4). Lean mass can be calculated by adding up muscle and bone mass (eq. 14.5), and carcass is the lean and the hide together (eq. 14.6). The protein and fat mass in lean and carcass can be obtained in a similar way (eq. 14.7, 14.8, 14.9 and 14.10).

Figure 4
Partitioning of fat deposition rates in hide (●), organs (○) and muscle (■) as a function of body fat deposition rate. The relationships were estimated from data of Bikker (unpublished)



Model calibration

For calibration purposes, two complete experiments were selected. The advantages of the experiments for modelling were the followings. 1) These trials were carried out upon a large variation in protein and energy intake. 2) The measurements were done over large body weight ranges. 3) Measurements of both chemical and anatomical composition were included.

Experimental data

The present pig growth model was calibrated on experimental data of 195 individually housed gilts of a commercial strain (VOC, Nieuw-Dalland, Venray, The Netherlands) (Bikker *et al*. 1994, 1995, 1996*a*,*b* and unpublished). These animals had been used in two experiments with the aims: 1) to determine the optimal ratio of ileal digestible lysine to digestible energy for growing pigs (Bikker *et al*. 1994) and 2) to study the effect of energy intake on tissue deposition and body composition in growing and fattening pigs (Bikker *et al*. 1995, 1996*a*,*b*). The experimental diets were based on corn and soybean meal. In the first experiment, 95 gilts from 20 to 45 kg body weight were used and pigs were fed at either 2.5 or 3.0 times the energy requirements for maintenance (ARC, 1981). At each of the two digestible energy intakes, lysine intake was increased from 6.4 to 18.2 g/d ileal digestible lysine in 15 steps. For calibration purposes, dietary contents and nutrient digestibility were adopted from Bikker *et al*. (1994). The gilts were slaughtered at 20 (initial slaughter group) or 45 kg bodyweight and dissected into organ and carcass fraction. The slaughter procedures and the carcass analysis are given by

Bikker *et al*. (1994). The equations to obtain the partitioning of protein, fat, water and ash among muscle, hide and bone in the carcass were adopted from the second experiment.

The second experiment included two feeding periods with a total number of pigs of 100. Twenty-eight gilts of 20 kg body weight were assigned to a reference group and to one of 6 dietary treatments. The pigs were fed a diet, constant in composition, at intakes increasing from 1.7 to 4.2 (*ad libitum*) times the energy requirements for maintenance. All gilts of dietary treatments were slaughtered at the end of the grower period (45 kg body weight). Further 72 gilts were used to represent the growing and fattening period with initial body weight of 20 kg. These animals were fed either 2.2 or 3.7 times maintenance energy requirements up to 45 kg body weight. From 45 kg live weight the pigs received one of 6 dietary treatments from 1.7 to 4.2 (*ad libitum*) times the energy requirements for maintenance. In this way, pigs above 45 kg body weight had one of two different feeding histories. Data on digestible nutrient contents and daily feed intake of these animals were available. Gilts were slaughtered at 20 (reference initial slaughter group) or at 45, 85 or 105 kg body weight. Pigs were dissected into organ and blood, fat (hide and subcutan fat) and lean (including bone) fractions as described by Bikker *et al*. (1995, 1996*a*,*b*).

Numerical solution

The growth model was developed in SMART (Kramer and Scholten, 2003). A complete listing of the equations that constitute the model is given in Appendix 1. The differential equations for the lysine, acetyl-CoA, glucose, fatty acids, VFA, muscle protein and body fat state variables are solved numerically for a given set of initial conditions and parameter values. The integration interval used was 0.01 day, with the fourth-order fixed-step-length Runge-Kutta algorithm. All the steepness parameters, affinity and inhibition constants were adjusted step by step to obtain a good fit of the experimental data. The response of muscle protein and body fat deposition rates on different nutrient intakes were considered in different weight ranges and in the whole fattening period. The results presented are not sensitive to small changes in initial conditions and smaller integration step sizes.

Results and discussion

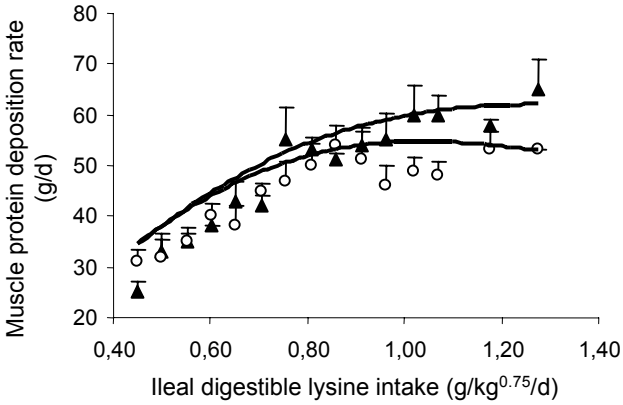
The general model behavior shows that the metabolite pool sizes are small and comparable with metabolite pool sizes in plasma and body fluids chosen for initial values. There are two storage pools among the state variables: muscle protein and body fat mass. These two parameters are the link between the metabolic and anatomical part of the model. The equations in anatomical part determine the body composition and subsequently the body weight. Consequently, muscle protein and body fat deposition rates were focused in the model calibration. The simulated daily muscle protein and body fat deposition in a certain body weight range has to correspond to experimental data. The growth model was calibrated simultaneously on different data sets, originating from different experiments as described above. Therefore the variation due to differences in nutrient intake and age from other inter-experimental variations have to be separated. The main aim

is to predict differences in performance due to variation in nutrient intake and age accurately, and that achieving a good prediction of absolute levels of fat and muscle protein deposition rates is of secondary importance.

The observed and simulated responses to increasing ileal digestible lysine intake of the calibration data set of Bikker *et al*. (1994) are presented in Figure 5. Overall, the increase in muscle protein deposition rate and decrease in total fat deposition rate with increasing ileal digestible lysine or energy intake are simulated satisfactorily. As a result of the saturation kinetics in protein synthesis the protein deposition pretend a maximal curve. The increment of protein deposition rate in the muscle decreases with increasing ileal digestible lysine intake and the reduction is different at low and high energy intake. The muscle protein deposition rate at low lysine intakes is slightly overestimated, whereas at intakes above 0.8 g/kg$^{0.75}$/d, the muscle protein deposition rate fits the observed data. In addition, the contrast in muscle protein deposition rate with increasing energy intake is well predicted. Fat deposition rate was consistently overestimated by the model (30 g/d). However, the contrast in fat deposition rate between energy intake levels, as well as the decrease in fat deposition rate with increasing lysine intake were well predicted by the model.

The experimental and simulated effect of energy intake on the muscle protein and body fat deposition in different body weight ranges is given in Figures 6, 7, 8 and 9. In general the model responses are satisfactory regarding to the simulated effect of increasing energy intake on muscle protein and body fat deposition rates. The predicted muscle protein deposition rate was slightly underestimated (5 g/d) between 20-45 kg (Figure 6) and overestimated by 10 g/d between 45-85 kg of body weight (Figure 7). The predicted body fat deposition rate was overestimated (22 g/d) between 20-45 kg (Figure 6) and underestimated by 15 g/d between 45-85 kg of body weight (Figure 7). Bikker *et al*. (1995, 1996*a*,*b*) suggested that the protein deposition increases linearly with energy intake (with a constant composition) in both weight ranges between 20-45 kg and 45-85 kg body weight (Figures 6 and 7). In contrast, the model predicts a curvilinear response of protein deposition to energy intake, since at high energy intake the muscle protein deposition rate is close to its maximum. Within the theory it is possible, especially in the second period (45-85 kg) when the feed intake capacity is high and hence the energy supply allows achievement of the potential protein accretion rate. In agreement with that assumption, Dunshea *et al*. (1998) found a quadratic response of protein deposition to DE intake in 60-90 kg pigs. The underestimation of muscle protein deposition rates at 3.7 and 4.2 times maintenance energy intake results in an overestimation in body fat deposition between 20-45 kg body weight (Figure 6). The predictions of the body fat deposition in the later period is in line with the observed values (Figure 7).

Figure 5
Simulated (lines) and observed (symbols) response of muscle protein and body fat deposition rates of gilts from 20 to 45 kg body weight to increasing intakes of ileal digestible lysine at each of energy intake levels; energy intakes are 3.0 (▲) and 2.5 (○) times the energy requirements for maintenance, and are constant on a DE basis



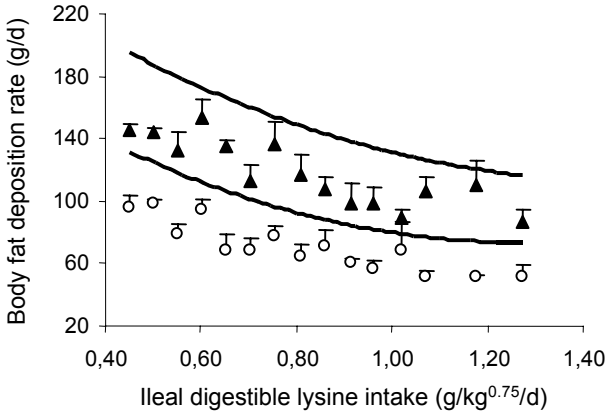
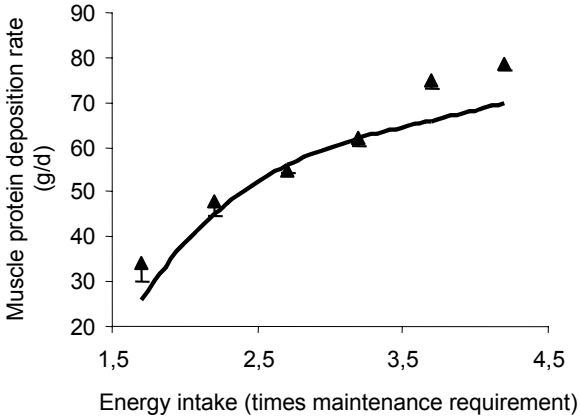


Figure 6
Simulated (lines) and observed (symbols) response of muscle protein and body fat deposition rates of gilts from 20 to 45 kg body weight to increasing energy intake



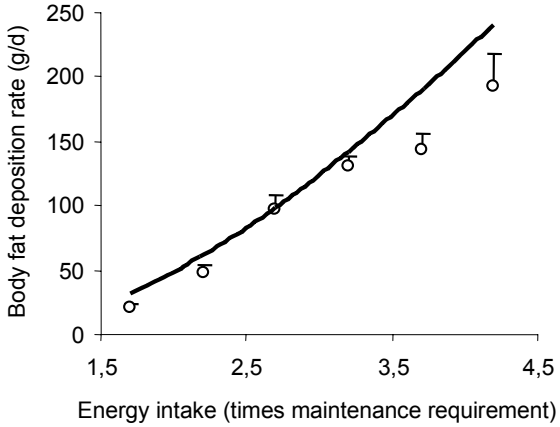
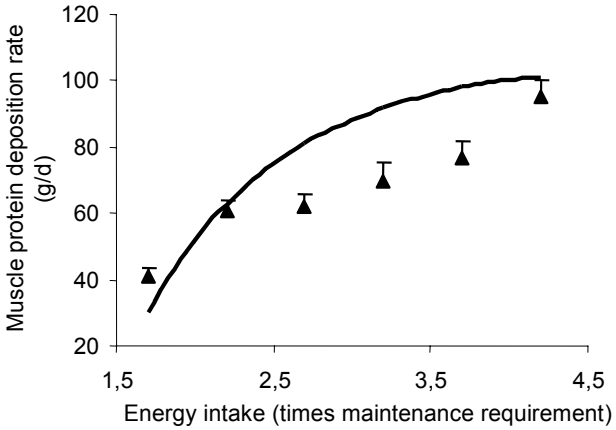
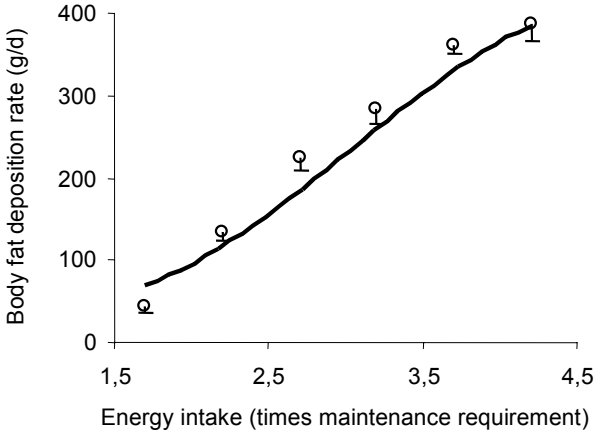


Figure 7
Simulated (lines) and observed (symbols) response of muscle protein and body fat deposition rates of gilts from 45 to 85 kg body weight to increasing energy intake

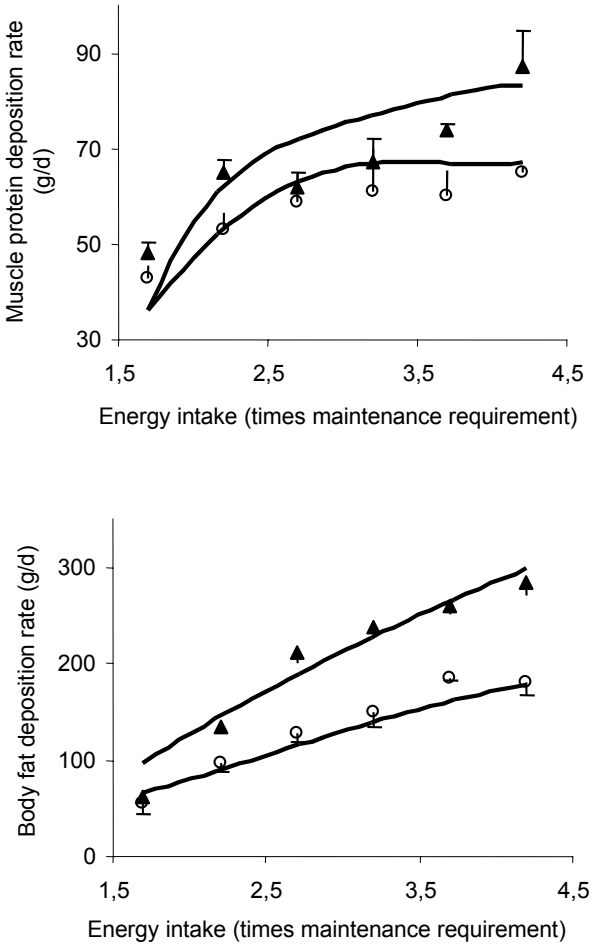




The effect of energy intake between 20-85 kg body weight is presented in Figure 8. During the 20-45 kg period, the high energy groups were fed 3.7 times maintenance and the low energy groups were fed 2.2 times maintenance. From 45 kg of body weight the energy supply varied from 1.7 times maintenance to *ad libitum* feed intake. The overall prediction is perfect in this weight range. The mean deviation of predictions from observations is 2 and 1 g/d for muscle protein and body fat deposition rates, respectively. The observed data for muscle protein deposition at 20-85 kg body weight suggest a plateau, and the simulations also

clearly indicate that plateau. The model predicts the fat deposition accurately as can be seen in Figure 8.

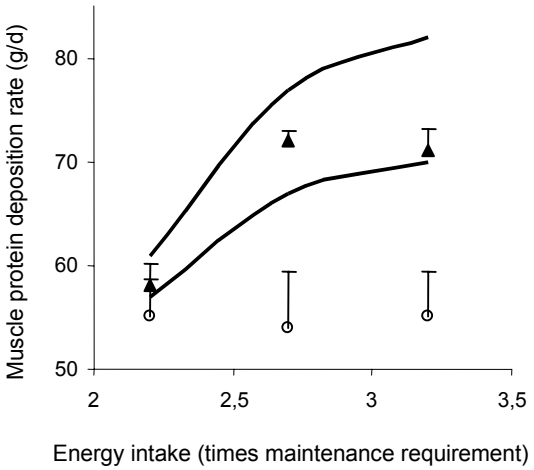
Figure 8
Simulated (lines) and observed (symbols) response of muscle protein and body fat deposition rates of gilts from 20 to 85 kg body weight to increasing energy intake; feeding levels between 20-45 kg are 2.2 M (○) and 3.7M (▲)

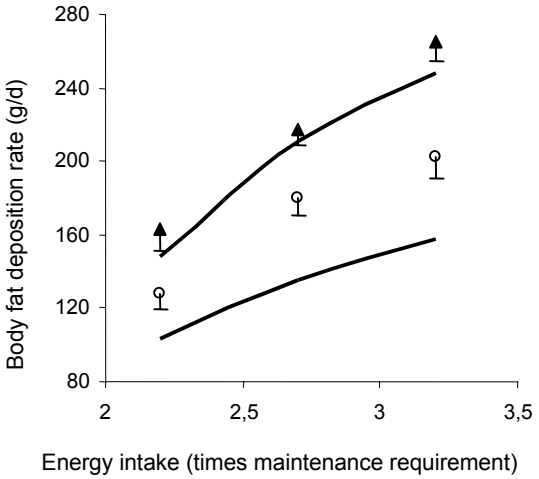


For the entire fattening period (20-105 kg), the number of treatments was limited. Only three energy intake levels with two feeding histories were studied (Bikker, unpublished). The prediction of muscle protein and body fat deposition are less well related than in the weight range of 20-85 kg (Figure 9). In general the

daily muscle protein deposition was slightly overestimated (8 g/d) while the daily body fat deposition was underestimated by 25 g/d. The reason for the deviation was that the observed muscle protein deposition rate was not increased as a result of an increase in energy intake level at the pigs received low feeding level between 20-45 kg body weight. The model predicted an increase in deposition rate at both energy intake levels. Consequently, total fat deposition was underestimated in pigs with a low feeding level at growing period. The high feeding level at the growing period resulted in a higher deposition rate in muscle protein and body fat as well.

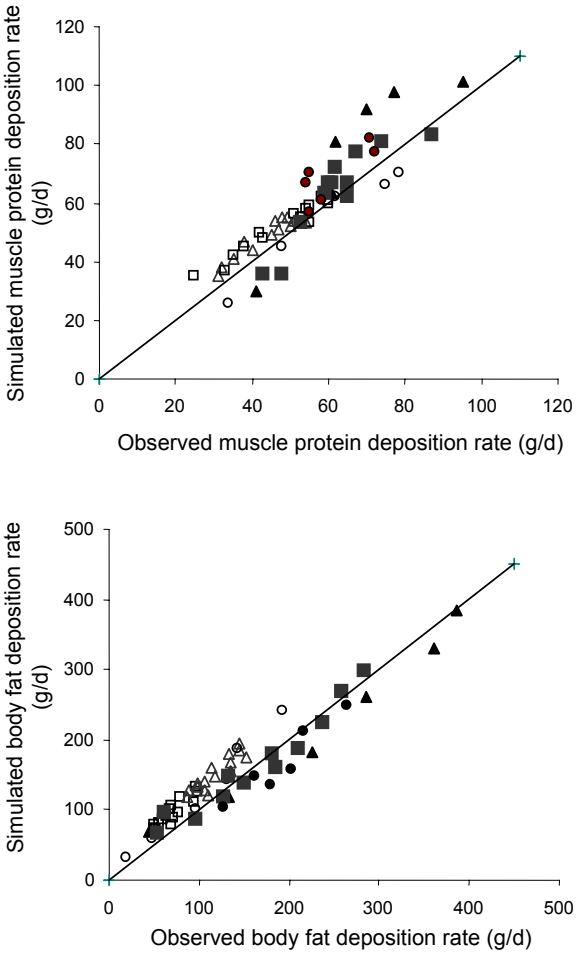
Figure 9
Simulated (lines) and observed (symbols) response of muscle protein and body fat deposition rates of gilts from 20 to 105 kg body weight to increasing energy intake; feeding levels between 20-45 kg are 2.2 M (○) and 3.7M (▲)





A summary of observed and predicted values of all experiments is presented in Figure 10. The results show that the model gives a good prediction in general. The line of regression of simulated on observed data for muscle protein deposition rate is y=1.025x + 2.32 (R^2 = 0.815) and for total body fat deposition rate is

Figure 10
Agreement of the observations and model simulation in different studies regarding to muscle protein and body fat deposition.



Different ileal digestible lysine intake at 2.5 M feeding level between 20-45 kg (∆), different ileal digestible lysine intake at 3.0 M feeding level between 20-45 kg (□), different energy intake between 20-45 kg (○), different energy intake between 45-85 kg (▲), different energy intake between 20-85 kg (■), different energy intake between 20-105 kg (●)

y=0.829x + 35.6 (R^2=0.902). The deviation of body fat deposition rate from the regression being 1 increased according to the consistently overestimated fat deposition rates in the first study (see Figure 5). However, in the same weight range (20-45 kg) the daily fat deposition was well estimated in the second experiment (see Figure 6). It can be concluded that the general response to changes in nutrient intake and age are normal and prediction of contrasts is quantitatively satisfactory. The difference in the accuracy of the model prediction is supposed to be derived from the inter-experimental variation.

Practical application

There are some restrictions for application of the present model. The growth model was developed on the data basis of gilts from 20-105 kg. Subsequently the model is valid for growing and fattening female pigs but not for heavy pigs. Considering that lysine is the driving variable in protein synthesis, the model is valid only in feeding situation when lysine is the limiting amino acid. The present model may operate crudely at extremely low feeding level (some above maintenance energy intake). The predictions of responses were developed on a daily basis, so it cannot predict the within-day variation in metabolic responses. The model needs separate calibration on other genotypes and sexes (castrates, entire males). The growth model was developed on the data basis of pigs kept under optimal environmental conditions and therefore may not respond appropriately to changes in nutrient inputs under poor environmental conditions and/or low health status.

For effective application of pig growth models, it should be taken into account that there are different sexes and genotypes. Representation of sexes and genotypes in our approach is in kinetic parameters, particularly Vmax-es. Manipulation of maximal velocity of protein and fat synthesis and amino acid oxidation results in changed protein and fat deposition and different chemical body composition at slaughter. The fractional degradation rate of muscle protein also candidates as a tool to change the daily protein deposition rates. In rats (Bates and Milward, 1981) and in chicks (Maruyama *et al*., 1978; Jones *et al*., 1986) the fractional degradation rate of muscle protein was lower in fast-growing *vs*. slow growing animals. Therefore, the growth model needs re-calibration on these - genotype sensitive - parameters for each genotype. In addition, ratio of muscle to bone may be different as confirmed by Quiniou and Noblet (1995). Also, the location of the fat - therefore the allometric equations used - may well be different. As reported in the literature, maintenance energy requirement of different strains and sexes are different (Whittemore, 1983; ARC, 1981; Noblet *et al*., 1999) Maintenance energy, as far as caused by differences in body composition (metabolically active tissues) is already represented by the model. It has to be noted, however, that re-calibration of the growth model needs good data sets.

In summary, the present paper describes a mechanistic-dynamic pig model. The model was calibrated to predict growth rate and body composition of gilts to a wide range of digestible nutrient supply over the entire growing-fattening period. Generally, model predictions of protein and fat deposition rates to changes in digestible nutrient intake at various weight ranges compared well with these complex experimental data. General model behaviour, sensitivity of model predictions to changing parameters and a comparison with independent experimental data are the topic of the companion paper (Halas *et al*. 2004).

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Appendix 1
Mathematical statement of the pig growth model

Protein metabolism

Lysine pool, Qly (mol)

Concentration:	$Cly = Qly/Qew$	(1.1)
Input:	$Ply,dply = Dly*Cdply*FI/MWly$	(1.2)
	$Ply,mply = Yly,mply*Ump,mply$	(1.3)
	$Ply,oply = Yly,oply*Uop,oply$	(1.4)
	$Ply,bply = Yly,bply*Ub,pbply$	(1.5)
	$Ply,hply = Yly,hply*Uhp,hply$	(1.6)
Output:	$Uly,lymp = Vlymp* Qmp^{0.75}/(1 + (Mly,lymp/Cly)^{Slymp} + May,lymp/Cay)$	(1.7)
	$Uly,lyop = Yly,oply*Pop,lyop$	(1.8)
	$Uly,lybp = Yly,bply*Pbp,lybp$	(1.9)
	$Uly,lyhp = Yly,hply*Php,lyhp$	(1.10)
	$Uly,lyay = Vlyay* Qli^{0.75}/(1 + (Mly,lymp/Cly)^{Slyay})$	(1.11)
Differential equation:	$dQly/dt = Ply,dply + Ply,mply + Ply,oply + Ply,bply + Ply,hply – Uly,lymp – Uly,lyop – Uly,lybp – Uly,lyhp – Ulylyay$	(1.12)

Amino acid pool, Qaa (mol)

Input:	$Paa,dpaa = Ddp*Cdpaa*FI/MWaa$	(2.1)
	$Paa,mply = Yaa,mply*Ump,mply$	(2.2)
	$Paa,oply = Yaa,oply*Uop,oply$	(2.3)
	$Paa,bply = Yaa,bply*Ubp,bply$	(2.4)
	$Paa,hply = Yaa,hply*Uhp,hply$	(2.5)
Output:	$Uaa,lymp = Raa,lymp*Uly,lymp$	(2.6)
	$Uaa,lyop = Raa,lyop*Uly,lyop$	(2.7)
	$Uaa,lybp = Raa,lybp*Uly,lybp$	(2.8)
	$Uaa,lyhp = Raa,lyhp*Uly,lyhp$	(2.9)
	$Uaa,aaay = Paa,dpaa + Paa,mply + Paa,oply + Paa,bply + Paa,hply – Uaa,lymp – Uaa,lyop – Uaa,lybp – Uaa,lyhp$	(2.10)
Differential equation:	$dQaa/dt = 0$	(2.11)

Muscle protein pool, Qmp (kg)

Input:	$Pmp,lymp = Ymp,lymp*Uly,lymp$	(3.1)
Output:	$Ump,mply = Qmp*FDRmp$	(3.2)
Differential equation:	$dQmp/dt = Pmp,lymp – Ump,mply$	(3.3)

Organ protein pool, Qop (kg)

Input:	$Pop,lyop = 0.1822*dQmpdt^{0.8599} + Uop,oply$	(4.1)
Output:	$Uop,oply = Qop*FDRop$	(4.2)
Differential equation:	$dQop/dt = Poplyop – Uopoply$	(4.3)

Hide protein pool, Qhp (kg)

Input:	$Php,lyhp = 0.4269*dQmpdt^{0.8716} + Uhp,hply + Uhp,hpex$	(5.1)
Output:	$Uhp,hply = Qhp*FDRhp$	(5.2)
	$Uhp,hpex = 0.094*Qew^{0.75}/1000$	(5.3)
Differential equation:	$dQhp/dt = Php,lyhp – Uhp,hply – Uhp,hpex$	(5.4)

Bone protein pool, Qbp (kg)

Input:	$Pbp,lybp = 0.0793*dQmpdt^{0.6621} + Ubp,bply$	(6.1)
Output:	$Ubp,bply = Qbp*FDRbp$	(6.2)
Differential equation:	$dQbp/dt = Pbp,lybp – Ubp,bply$	(6.3)

Energy metabolism

Acetyl-CoA pool, Qay (mol)

Concentration:	$Cay = Qay/Qew$	(7.1)
Input:	$Pay,lyay = Yay,lyay*Uly,lyay$	(7.2)
	$Pay,aaay = Yay,aaay*Uaa,aaay$	(7.3)
	$Pay,faay = Yay,faay*Ufa,faay$	(7.4)
	$Pay,glay = Yay,glay*Ugl,glay$	(7.5)
	$Pay,vfay = Yay,vfay*Uvf,vfay$	(7.6)
Output:	$Uay,ayfa = Vayfa*\ Qtf^{0.75}/(1 + May,ayfa/Cay + Cfa/Jfa,ayfa)$	(7.7)
	$Uay,ayma^{\#} = Uay,ayma*0.80 - (Pat,lyay + Pat,aaay + Pat,dfgl + Pat,glay + Pat,tfgl + Pat,faay)/12)$	(7.8)
	$Uay,ayox = (Ray,lymp + Ray,aamp*Raa,lymp)*Uly,lymp + (Ray,lyop + Ray,aaop*Raa,lyop)*Uly,lyop + (Ray,lybp + Ray,aabp*Raa,lybp)*Uly,lybp + (Ray,lyhp + Ray,aahp*Raa,lyhp)*Uly,lyhp + Ray,fatf*Ufa,fatf + (Ray,mply + Ray,mpaa)*Ump,mply + (Ray,oply + Ray,opaa)*Uop,oply + (Ray,bply + Ray,bpaa)*Ubp,bply + (Ray,hply + Ray,hpaa)*Uhp,hply + Ply,dply*Aly + Paa,dpaa*Aaa + (Pgl,stgl + Pgl,sugl + Pgl,dffa)*Agl + Pfa,dffa*Afa + Ray,lyun*Uly,lyun + Ray,aaun*Uaa,aaun + Ray,data*0.0855*(dQmpdt + dQopdt + dQbpdt + dQhpdt)^{0.6215}$	(7.9)
	$Uay,aygr = Vaygr*\ Qew^{0.67}/(1 + May,aygr/Cay + Mly,aygr/Cly)$	(7.10)
Differential equation:	$dQay/dt = Pay,lyay + Pay,aaay + Pay,faay + Pay,glay + Pay,vfay – Uay,ayfa – Uay,ayma^{\#} - Uay,ayox – Uay,aygr$	(7.11)
Auxiliary equations:	$Uay,ayma = 0.836*(Qmp + Qbp + Qhp)^{0.75} + 4.231*Qop^{0.75} + 0.113*Qtf^{0.75}$	(7.12)
	$Pat,lyay = Yat,lyay*Uly,lyay$	(7.13)
	$Pat,aaay = Yat,aaay*Uaa,aaay$	(7.14)
	$Pat,dfgl = Yat,dfgl*Ddf*Cdf*Fl/1000$	(7.15)
	$Pat,glay = Yat,glay*Ugl,glay$	(7.16)
	$Pat,tfgl = Yat,tfgl*Utf,tffa$	(7.17)
	$Pat,faay = Yat,faay*Ufa,faay$	(7.18)
	$Uly,lyun = Yun,lyay*Uly,lyay$	(7.19)
	$Uaa,aaun = Yun,aaay*Uaa,aaay$	(7.20)

VFA pool, Qvf (mol)

Concentration:	$Cvf = Qvf/Qew$	(8.1)
Input:	$Pvf,cwvf = Dcw*Ccw*Fl*Yvf,cwvf/1000$	(8.2)
Output:	$Uvf,vfay = Vvfay*\ Qew^{0.75}*PRayvf/(1 + (Mvf,vfay/Cvf)$	(8.3)
	$Uvf,vfgl = Uv,fvfay * (1 - PRayvf)/Prayvf$	(8.4)
Differential equation:	$dQvf/dt = Pvf,cwvf – Uvf,vfay – Uvf,vfgl$	(8.5)

Glucose pool, Qgl (mol)

Concentration:	$Cgl = Qgl/Qew$	(9.1)
Input:	$Pgl,stgl = Dst*Cst*Fl*Ygl,stgl/1000$	(9.2)
	$Pgl,sugl = Dsu*Csu*Fl*Ygl,sugl/1000$	(9.3)
	$Pgl,dffa = Ddf*Cdf*Fl*Ygl,dffa /1000$	(9.4)
	$Pgl,vfgl = Ygl,vfgl*Uvf,vfgl$	(9.5)
	$Pgl,tffa = Ygl,tffa*Utf,tffa$	(9.6)

Output:	$Ugl,glay = Vglay * Qew^{0.75}/(1 + (Mgl,glay/Cgl)$	(9.7)
	$Ugl,ayfa = Rgl,ayfa * Uay,ayfa$	(9.8)
	$Ugl,fatf = Rgl,fatf * Ufa,fatf$	(9.9)
Differential equation:	$dQgl/dt = Pgl,stgl + Pgl,sugl + Pgl,dfgl + Pgl,tffa + Pgl,vfgl – Ugl,glay – Ugl,fatf – Ugl,ayfa$	(9.10)

Fatty acid pool, Qfa (mol)

Concentration:	$Cfa = Qfa/Qew$	(10.1)
Input:	$Pfa,dffa = Ddf * Cdf * FI * Yfa,dffa/1000$	(10.2)
	$Pfa,tffa = Yfa,tffa * Utf,tffa$	(10.3)
	$Pfa,ayfa = Yfa,ayfa * Uay,ayfa$	(10.4)
Output:	$Ufa,fatf = Vfatf * Qtf/(1 + (Mfa,fatf/Cfa)$	(10.5)
	$Ufa,faay = Vfaay * Qew^{0.75}/(1 + Mfa,faay/Cfa + Cay/Jay,faay)$	(10.6)
Differential equation:	$dQfa/dt = Pfa,dffa + Pfa,tffa + Pfa,ayfa – Ufa,fatf – Ufa,faay$	(10.7)

Body fat pool, Qtf (kg)

Input:	$Ptf,fatf = Ytf,fatf * Ufa,fatf$	(11.1)
Output:	$Utf,tffa = Qtf * FDRtf$	(11.2)
Differential equation:	$dQtf/dt = Ptf,fatf – Utf,tffa$	(11.3)

Summative equations

Empty body weight, Qew (kg)	$dQew/dt = dQmp/dt + dQop/dt + dQhp/dt + dQbp/dt + dQtf/dt + dQtw/dt + dQta/dt$	(12.1)
Body water mass, Qtw (kg)	$dQtw/dt = 4.6279*(dQmp/dt)^{1.109} + 5.1138*(dQop/dt)^{1.0407} + 1.3169*(dQhp/dt)^{0.7682} + 1.896*(dQbp/dt)^{1.0051}$	(12.2)
Body ash mass, Qta (kg)	$dQta/dt = 0.0534*(dQmp/dt)^{1.0355} + 0.0985*(dQop/dt)^{1.1359} + 0.0258*(dQhp/dt)^{0.7597} + 1.2503*(dQbp/dt)^{0.9963}$	(12.3)

Other equations

Live weight, Qlw (kg)	$Qlw = 1.287*Qew^{0.9531}$	(13.1)
Liver weight, Qli (kg)	$Qli = exp(1-1/Qop)$	(13.2)
Hide fat, Qhf (kg)	$dQhf/dt = 0.8449*(dQtf/dt)^{1.1144}$	(13.3)
Muscle fat, Qmf (kg)	$dQmf/dt = 0.1217*(dQtf/dt)^{0.7704}$	(13.4)
Organ fat, Qof (kg)	$dQof/dt = 0.0519*(dQtf/dt)^{0.9584}$	(13.5)
Bone fat, Qbf (kg)	$dQbf/dt = 0.9074*(dQbp/dt)^{1.0091}$	(13.6)

Anatomical composition

Muscle mass, Qmm (kg)	$dQmm/dt = dQmp/dt + dQmf/dt + 4.6279*(dQmp/dt)^{1.109} + 0.0534*(dQmp/dt)^{1.0355}$	(14.1)
Organ mass, Qom (kg)	$dQom/dt = dQop/dt + dQof/dt + 5.1138*(dQop/dt)^{1.0407} + 0.0985*(dQop/dt)^{1.1359}$	(14.2)
Hide mass, Qhm (kg)	$dQhm/dt = dQhp/dt + dQhf/dt + 1.3169*(dQhp/dt)^{0.7682} + 0.0258*(dQhp/dt)^{0.7597}$	(14.3)
Bone mass, Qbm (kg)	$dQbm/dt = dQbp/dt + dQbf/dt + 1.896*(dQbp/dt)^{1.0051} + 1.2503*(dQbp/dt)^{0.9963}$	(14.4)

Lean mass, Qlm (kg)	Qlm = Qmm + Qbm	(14.5)
Carcass mass, Qcm (kg)	Qcm = Qlm + Qhm	(14.6)
Lean protein, Qlp (kg)	Qlp = Qmp + Qbp	(14.7)
Lean fat, Qlf (kg)	Qlf = Qmf + Qbf	(14.8)
Carcass protein, Qcp (kg)	Qcp = Qlp + Qhp	(14.9)
Carcass fat, Qcf (kg)	Qcf = Qlf + Qhf	(14.10)

Chapter 5

Modelling of nutrient partitioning in growing pigs to predict their anatomical body composition: 2. Model evaluation

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Abstract

The objective of the present paper is to evaluate a mechanistic-dynamic model for growing and fattening pigs presented in a companion paper. The model predicts the rate of protein and fat deposition (chemical composition), rate of tissue deposition (anatomical composition) and performance of pigs depending on nutrient intake. In the model evaluation, the predicted response of the pig to changes in model parameters and to changes in nutrient intakes are presented. As a result of the sensitivity analysis, changes in the maintenance energy requirements and the fractional degradation rate of muscle protein have the largest impact on tissue deposition rates. The model is also highly sensitive to changes in the maximal velocity and steepness parameter of the lysine utilisation for muscle protein synthesis. The model was further tested by independent published data. The model successfully predicts the response of pigs to a wide range of variation in nutrient composition. Consequently, the model can be applied to develop feeding strategies to optimise pig production. It also gives a possibility to predict not only the slaughter performance but also the meat quality.

Keywords: pig model, evaluation, anatomical body composition, chemical body composition

Introduction

In a companion paper (Halas *et al*. 2004) a mechanistic-dynamic model for growing and fattening pigs was described. The aim of the model is to predict the rate of protein and fat deposition (chemical composition), rate of tissue deposition (anatomical composition) and performance of gilts of 20-105 kg live weight depending on nutrient intake. Model evaluation is concerned with establishing the appropriateness and accuracy of predictions over a wide range of simulated conditions. The wider the circumstances under which the model predictions are accurate, the more confidence is developed in the appropriateness of the concepts and accuracy of parameters upon which it is based and the more useful will its predictions be (Black, 1995).

The objective of the present paper is to evaluate the response of the pig as predicted by the growth model to changes in model parameters and to changes in nutrient intakes. Firstly, the sensitivity of predictions to changes in the main model parameters is evaluated. Secondly, a comparison of the model predictions with observations from independent published trials is presented.

Sensitivity analysis

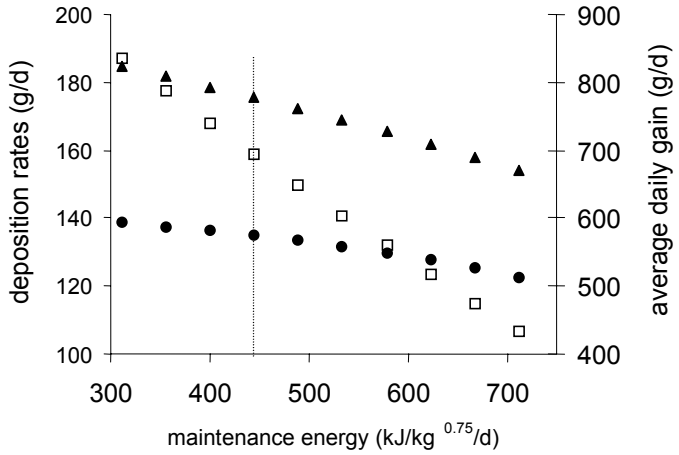
A reference simulation was chosen as a starting point for the sensitivity analyses. The initial live weight was 20 kg and the simulation was performed for 30 days. The pig response to a normal diet (DE = 15.1 MJ/kg, ileal digestible lysine 11.2 g/kg, ileal digestible amino acids 157.8 g/kg, digestible fat 53 g/kg, starch 404 g/kg, sugar 25 g/kg, fermentable cell wall components 67 g/kg) was predicted. The animals were fed at 3.2 times the maintenance energy requirements.

Sensitivity to changes in maintenance protein and maintenance energy requirements

As discussed in the companion paper, maintenance protein and energy requirements are accounted for (Halas *et al*. 2004). Obligatory nitrogen losses with urine and endogenous gut protein losses are implicitly considered in the model. The daily integument loss was assumed to be 0.094 g protein/metabolic body weight ($kg^{0.75}$). Multiplying the default value of skin and hair loss by either 0.4 or 2.0 gave a small change in protein and fat deposition rates and average body gain. Although these changes are negligible, the model predictions are reasonable. An increased value of integument loss increases the lysine and other amino acids utilisation to hide protein synthesis. A larger drain to protein synthesis reduces the lysine concentration and hence reduces the utilisation of lysine and other amino acids for body protein synthesis or for oxidation to acetyl-CoA.

The maintenance energy requirements are considered to be related to carcass protein mass, organ protein mass and body fat mass (Halas *et al*. 2004). In the reference simulation, the maintenance energy requirements corresponded to 443 kJ/ $kg^{0.75}$ per day. Maintenance energy requirements were varied between 0.7 to 1.6 times the default value, and results are presented in Figure 1. As expected, increasing maintenance energy requirements by 50 % decreases deposition rates of protein, fat and body gain by 7, 28 and 11 %, respectively. Maintenance energy in the model is provided by ATP yielding transactions and by acetyl-CoA oxidation. Increasing the maintenance energy expenditure increases acetyl-CoA oxidation and lowers its concentration. Subsequently, protein synthesis and *de novo* fat synthesis are reduced, resulting in lower deposition rates of protein and fat.

Figure 1
Sensitivity of predicted average daily gain (g/d, ▲), protein deposition rates (g/d, ●) and fat deposition rate (g/d, □) to changes in maintenance energy requirement (default value is indicated by the broken line)

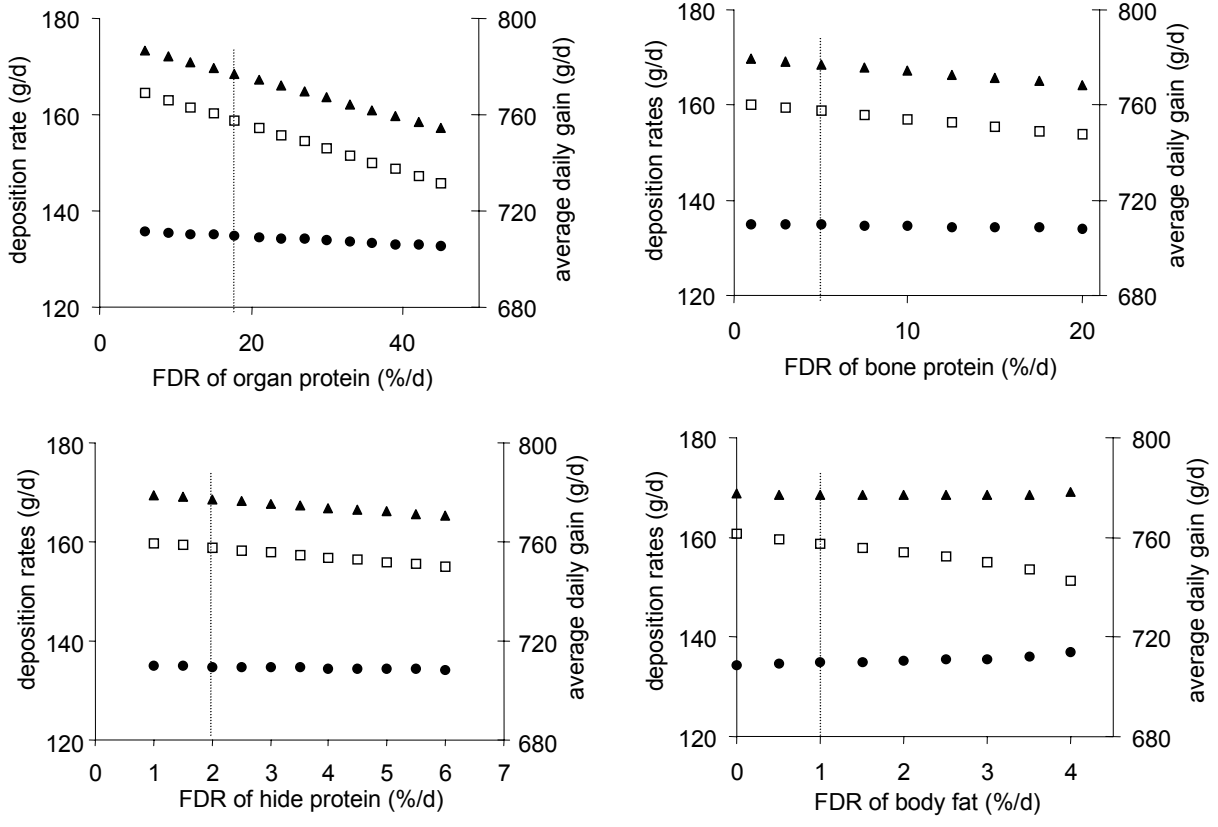


Sensitivity to changes in fractional degradation rates (FDR)

The accretion rate of muscle protein determines the organ, hide and bone protein accretion rates (Halas *et al*. 2004). Deposition is defined as the difference between synthesis and degradation, where fractional degradation rates are assumed constant for each tissue. By changing the fractional degradation rates of protein pools, protein turnover can be manipulated. As discussed by Gerrits *et al.* (1997), who used a similar approach, testing the sensitivity of model predictions to changes in the FDR of muscle protein is complicated by the relationships between muscle protein deposition and protein deposition in organs, bone and hide. Therefore, the results of testing model responses to changes in the FDR of muscle protein are similar to those of Gerrits *et al.* (1997). An increase in FDR of muscle protein from 0.01 to 0.03 d^{-1} (default is 0.0223 d^{-1}) decreases body protein deposition rate and average daily gain from 199 to 100 g/d and from 1056 to 626 g/d, respectively. Body fat deposition rate decreases slightly from 162 to 159 g/d. It can be concluded that the parameters are interrelated. Changes in FDR of muscle protein are logically accompanied by changes in transactions related to total body protein rather than only muscle protein metabolism.

Model responses to changes in the FDR of organ, hide and bone protein and body fat are given in Figure 2. Generally, the rate of body protein deposition is hardly influenced by the FDR of organ, hide and bone protein, because the deposition rates of these protein pools are related to the rate of muscle protein deposition (Halas *et al*. 2004). In contrast, fat deposition rates decrease because of an increased energy expenditure on protein turnover. Increasing the FDR of organ protein from 0.178 to 0.356 d^{-1} reduces the protein and fat deposition rates by 0.7 and 5.5%, respectively. Due to the decreasing protein and fat deposition rates, average daily gain also decreases with increasing FDR (Figure 2). The minor change in body protein deposition is caused by the slight change in amino acid oxidation with changing FDR as discussed by Gerrits *et al*. (1997). Increasing the FDR of hide protein from 0.02 to 0.04 d^{-1} decreases protein and fat deposition rates by 0.2 and 1.2 %, respectively. Increasing the FDR of bone protein from 0.05 to 0.10 d^{-1} decreases protein and fat deposition rates by 0.2 and 1.1 %, respectively. Model sensitivity to changes in the fractional degradation rate of body fat was examined in a range of 0 and 0.04 d^{-1} (default 0.01 d^{-1}). Protein deposition rate increased from 135 to 137 g/d and fat deposition rate decreased from 161 to 151 g/d (Figure 2). Unlike the results obtained in a veal calf model of Gerrits *et al*. (1997), changing the FDR of body fat has only a small impact on the acetyl-CoA concentration via the fatty acid pathway and results in a slightly changed protein and fat synthesis. In the measured period (20-46 kg body weight) the fat content of the body is small compared to a larger body weight. Increasing the FDR of the fat pool would not yield much extra fatty acid. On the other hand the increased fatty acid concentration also increases the body fat synthesis. Hence a large effect of a change in FDR of body fat was not expected.

Figure 2
Sensitivity of predicted average daily gain (▲), protein deposition rate (●) and fat deposition rate (□) to changes in fractional degradation rates of the organ protein pool, hide protein pool, bone protein pool and body fat pool (default values are indicated by broken lines)



Sensitivity to changes in kinetic parameters

The sensitivity of the model predictions to changes in kinetic parameters of protein and energy metabolism is given in Table 1. Default model values of all kinetic parameters (maximal velocity - Vij, affinity constants - Mijk, inhibition constants - Jkjk and steepness parameters - Sij) were used in the reference simulation and changed by –20 and +20 %. The response of the flux directly affected, as well as effects on body protein and fat deposition rates and the average daily gain were examined.

Changing the maximal velocity of lysine utilisation to muscle protein (Vlymp) has the largest influence on protein deposition (Table 1). A reduced maximum velocity of muscle protein synthesis rate obviously decreases the protein and increases the fat deposition rate. According to the decreased protein synthesis, more lysine and other amino acids are oxidised and yield acetyl-CoA for *de novo* fatty acid and body fat synthesis. The average daily gain was expected to reflect the protein deposition rate to a large extent since protein gain is accompanied by deposition of water and minerals. A 20 % increased Vlymp increases the simulated protein synthesis and slightly decreases the simulated fat synthesis. Therefore, a higher body weight at the 30^{th} day of simulation was obtained as compared with the reference situation. The nutrient intake increased proportionally with metabolic body weight. Hence, at higher body weight the pig received more feed per day, leading to an increased rate of fat deposition. This completely compensates the reduced energy available for fatty acid synthesis as a result of increased energy expenditure on protein deposition. Consequently, both the body protein and body fat deposition rate increases with increasing Vlymp due to a higher intake at higher body weight (Table 1).

Increasing the affinity constants for lysine or acetyl-CoA use in muscle protein synthesis (Mly,lymp and May,lymp) reduced protein synthesis and thereby protein deposition (Table 1). Changing the steepness parameter (Slymp) changes the steepness of the saturation curve. However, the effect of changing a steepness parameter generally depends on metabolite concentrations. Considering the rate of the flux is around half of its maximum (with substrate concentration close to the value of the affinity constant), the transaction is sensitive to changes in Sij. Changing Slymp by +/- 20% resulted in –11.0 and +7.8 g/d change in the rate of protein deposition. The affinity constants and the steepness parameter related to protein synthesis slightly influence the fat deposition as well.

As expected, the rate of lysine oxidation (Uly,lyay) is increased by either a higher maximal velocity, a lower affinity constant or a lower steepness parameter (Table 1). Increasing oxidation reduces protein synthesis and daily protein deposition and increases acetyl-CoA concentration. It thereby increases *de novo* fatty acid synthesis and results in an increased rate of fat deposition.

Generally, changing the maximal velocity of the reaction has the largest impact on the certain flux and on predicted protein and fat deposition rates (Table 1). Increasing Vij values of either the fatty acid or the fat synthesis decreases the protein deposition rate slightly while the fat deposition rate increases a bit more pronounced. By increasing Vayfa the acetyl-CoA pool decreases due to the larger drain on the fatty acid pool. The resulting increase in fatty acid pool size increases

the synthesis rate of body fat, while the lower acetyl-CoA concentration slightly reduces the rate of protein synthesis. Increasing Vfatf increases the rate of body fat synthesis and reduces the fatty acid pool size. Consequently, the rate of fatty acid oxidation is reduced as well as the acetyl-CoA pool size, which, in turn, reduces the rate of protein synthesis.

Table 1
Sensitivity of predicted body protein and fat deposition, average daily gain and the size of the transaction to changes in kinetic parameters

	Change in protein deposition g/d		Change in fat deposition g/d		Change in average daily gain g/d		Effect on the flux mmol/d	
	-20%	20%	-20%	20%	-20%	20%	-20%	20%
Vlymp	-48.9	46.7	1.1	0.3	-211	200	-29.5	30.4
Mly,lymp	5.8	-5.6	0.0	0.1	25	-24	3.5	-3.4
May,lymp	2.9	-2.6	-0.1	0.1	11	-11	1.9	-1.8
Slymp	-11.0	7.8	0.2	-0.1	-47	34	-6.7	4.8
Vlyay	3.0	-2.7	-2.6	2.2	10	-9	-1.3	1.2
Mly,lyay	-6.3	4.2	4.9	-3.7	-22	14	2.7	-1.8
Slyay	-7.6	4.3	5.8	-3.8	-27	15	3.0	-1.8
Vayfa	3.5	-3.3	-4.3	3.6	11	-11	-404.6	333.1
May,ayfa	-2.0	1.5	2.2	-1.8	-6	5	226.4	-178.3
Jfa,ayfa	0.0	0.0	0.0	0.0	0	0	-1.7	1.2
Vaygr	1.4	-1.5	9.7	-9.0	16	-16	-536.0	493.6
May,aygr	-0.5	0.4	-3.3	2.9	-6	5	217.7	-185.0
Mly,aygr	-0.7	0.6	-4.4	3.9	-8	7	216.2	-194.8
Vfaay	-0.7	0.6	1.8	-1.6	-1	1	-19.5	18.3
Mfa,faay	0.2	-0.2	-0.4	0.4	0	0	6.7	-6.1
Jay,faay	-0.5	0.4	1.3	-1.1	-1	1	-12.5	10.5
Vfatf	0.5	-0.4	-1.5	1.0	1	-1	-7.2	5.9
Mfa,fatf	-0.2	0.2	0.6	-0.4	0	0	3.9	-2.9

(Vij – maximal velocity of the transaction, Mijk – affinity constant of i in jk transaction, Jiji – inhibition constant of i in ji transaction, Sij – steepness parameter in ij transaction, ly – lysine, mp – muscle protein, ay - acetyl-CoA, fa – fatty acid, gr – extra energy for growth, tf – total body fat)

Changing kinetic parameters of fatty acid oxidation generally results in effects opposite to those resulting from changing kinetic parameters of fatty acid synthesis. Increasing Vfaay results in slightly higher protein and lower fat deposition rates.

In general, the mechanisms discussed above either in protein or in energy metabolism result in opposite changes of protein and fat deposition rates. An exception to this general observation is the response to a change in "additional energy for growth". Increasing the maximal velocity of this transaction (Vaygr) reduces both the protein and fat deposition rates by reducing acetyl-CoA pool size and subsequently acetyl-CoA concentration (Table 1).

Results of changes in Mijk values are in the opposite direction to those of changes in Vij because a higher affinity constant reduces the particular flux rate (Table 1). The flux of fatty acid oxidation is regulated by affinity and inhibition constants (Mfa,faay and Jay,faay). The purpose of the inhibition constant is to prevent acetyl-CoA to accumulate in the model. In changing Jay,faay by +/- 20%, the change in deposition rate is –0.5 vs. 0.4 g/d and that in fat deposition rate is 1.3 vs. –1.1 g/d. The effect of the inhibition constant in fatty acid synthesis is negligible. Changing kinetic parameters involved in glucose and VFA metabolism only marginally affected fluxes of related metabolites. This was expected as these parameters were set to prevent accumulation of these metabolites. Therefore, results of these sensitivity analyses are not presented.

Sensitivity to changes in energy requirements for tissue deposition

The effect of changing some of the main stoichiometric assumptions was tested, using the reference simulation as a starting point. The energy costs of protein synthesis, protein degradation, fat synthesis and Ca and P incorporation in bone were varied. Table 2 presents the changes in predicted deposition rates and heat production compared with the reference simulation. Increasing the ATP requirement for peptide bond formation (default is 4 ATP/ peptide bond) or hydrolysis (default is 1 ATP/ peptide bond cleavage) decreases protein and fat deposition rates and hence the average daily gain. Total heat production increases with increasing energy cost of the protein turnover. The ATP requirement of fat synthesis is 4 mol ATP for glycerolphosphate production and 2 mol ATP for fatty acid activation. An increase in the default energy cost of fat synthesis and bone mineralization (default is 2 ATP/ mol Ca and P incorporation) hardly changes the heat production (Table 2). In general, increasing the energy cost of the intermediary transactions will increase the drain of acetyl-CoA oxidation and the model responses are similar to increasing "additional energy cost for growth".

It has been suggested that the energy content of ATP is differed depending onto the metabolite (i.e., glucose, tripalmitin, amino acids) from which it was utilised (van Milgen, 2002). Thus, due to the uncoupling of ATP synthesis in the mitochondrion 1 mol of acetly-CoA may give some less ATP than assumed previously. Considering that assumption in model context, reduction of ATP production potential of acetyl-CoA results in less production of acetyl-CoA equivalents, since the transactions in which ATP is produce supply less acetyl-CoA. Decrease in acetyl-CoA concentration, such as in cases of increasing

maintenance energy requirement and “additional energy for growth”, the fat synthesis decreases with a slight reduction in protein synthesis as well.

Table 2
The effect of changing stoichiometric assumptions in the model simulating metabolism of growing and fattening pigs on the energy costs of protein synthesis, protein degradation, fat synthesis and mineralization (ATP requirements in italics denote the reference value)

	Change in protein deposition (g/d)	Change in fat deposition (g/d)	Change in average daily gain (g/d)	Change in heat production (%)
4 ATP		*Protein synthesis*		
3 ATP	0.7	4.4	7.5	-1.7
5 ATP	-0.7	-4.4	-7.6	1.6
1 ATP		*Protein degradation*		
0 ATP	0.4	2.9	4.9	-1.2
2 ATP	-0.5	-2.9	-4.9	1.2
6 ATP		*Fat synthesis*		
3 ATP	0.3	1.7	2.9	-0.7
9 ATP	-0.3	-1.6	-2.8	0.7
2 ATP		*Mineralization*		
0 ATP	0.2	1.1	1.9	-0.4
4 ATP	-0.2	-1.1	-1.9	0.4

Conclusion of the sensitivity analyses

In conclusion, the growth model for fattening pigs is sensitive to changes in a number of the examined model parameters. Changes in the maintenance energy requirements and the fractional degradation rate of muscle protein have the largest impact on tissue deposition rates. The model is highly sensitive to changes in the maximal velocity and steepness parameter of the lysine utilisation for muscle protein synthesis. Those parameters directly affecting the size of the lysine pool generally have a considerable influence on the model predictions. Furthermore, it should be noted that the results of this sensitivity analysis depend on the nutrient intakes of the reference simulation. The reason for the relative insensitivity of the model to the changes of parameters belonging to energy metabolism is probably that protein and/or lysine is more limiting within the simulated circumstances.

Comparison of model predictions with published trials

Independent data sets of published experiments were used to evaluate model performance. The literature studies were selected based on the following principles: 1) representing a large variation of nutrient intakes 2) a high genetic potential population was used in the trial and 3) the chemical composition of the body was determined by comparative slaughter techniques. The digestible nutrient compositions of the diets were recalculated based on Dutch table values (CVB, 1998). Data of different studies were simulated and the model predictions were compared with experimental observations. As an indicator for the error of predicted values relative to the observed values, the mean square prediction error (MSPE) was calculated:

$$MSPE = \Sigma (Oi - Pi)^2 / n$$

in which Oi and Pi are the observed and predicted values; i = 1, …, n, and n = number of experimental observations (Bibby & Toutenburg, 1977). The root MSPE is a measure in the same units as the output and is expressed as a percentage of the observed mean. The MSPE may be decomposed into three fractions. Firstly, errors attributed to overall bias (B%) represent the proportion of MSPE due to a consistent over- or underestimation of the experimental observations by the model predictions. Secondly, deviation of regression slope from one, being the line of perfect agreement (R%) represents the proportion of MSPE due to inadequate simulation of differences between experimental observations. Thirdly, disturbance proportion (E%) represents the proportion of MSPE unrelated to the errors of model prediction. The prediction is very good if the MSPE is small and if a small proportion of MSPE is explained by the regression error and the deviance in bias.

Model response to variation in dietary protein content

Chen *et al*. (1999) evaluated the effect of increasing protein intake on growth performance and carcass characteristics of finishing gilts. The animals received one of five dietary treatments comprising of 130, 160, 190, 220 and 250 g crude protein/kg of diet (n = 5 in each treatment). Pigs were allowed *ad libitum* access to the diets, which were formulated to be equal in ME content (13.74 MJ/kg), and dietary protein was exchanged for starch. Initial body weight was 51 kg and the trial was conducted on time constant basis of 75 days. The observed nutrient intakes were considered in the simulation.

The predictions of average daily gain, the carcass gain and carcass protein and fat deposition rates are shown in Figure 3. The MSPE and the decomposition of MSPE are presented in Table 3. The root MSPE of average daily gain, carcass weight gain, carcass protein and fat deposition rates varied between 39 and 71% of the observed mean (Table 3). For average daily gain, carcass weight gain and carcass protein gain, the vast majority (>90%) of this error was attributed to an overall bias, and these gains were overpredicted by 356, 405 and 72 g/d, respectively. For carcass fat deposition, a higher proportion of MSPE was attributed to deviation in slope, and less to overall bias (R% = 29%, B% = 68%) compared to the other parameters.

Experimental variations in average daily gain, carcass weight gain and carcass protein gain were well predicted by the model. The consistent

overestimation can be caused by erroneous model predictions, or alternatively reflects a real difference in experimental conditions between Chen *et al.* (1999) and our calibration datasets (Bikker *et al*. 1994, 1995, 1996a and b). At *ad libitum* feed intake the pigs gained in average 1307 g/d between 45-85 kg in the trial of Bikker *et al*. (1996a). However, the average daily gain was only between 817 and 926 g/d in 51-110 kg weight range in the trial of Chen *et al*. (1999). Experimental variation in the rate of carcass fat deposition was less well predicted. This is likely related to the low variation in the carcass fat deposition rate between the experimental treatments of Chen *et al*. (1999): 85 g/d. Considering that the experimental contrast was 13 vs 25 % crude protein in the diets one would expect a large variation in fat deposition rate within the trial. Furthermore, it illustrates the complexity of good predictions of fat deposition rates. Generally, fat deposition is considered a depot for nutrients remaining after meeting maintenance requirements and providing nutrients and fuel for protein deposition (Whittemore & Fawcett, 1976). Therefore, any difference in experimental condition between the experiment of Chen *et al*. (1999) and our calibration datasets would be expected to be reflected first in differences in fat deposition rates. The model overpredicted both the fat and protein deposition rates. The pigs in the trial of Bikker *et al* (1996a) were more efficient than those in the trial of Chen *et al.* (1999). The energetic efficiency of energy retention in the carcass from daily ME intake was in average 44.4% in Bikker's and in a range of 26.6-31.9 % in Chen's trial.

Figure 3
Comparison of experimental observations with model of average daily gain (kg/d, ■), carcass gain (kg/d, ∆), carcass protein deposition rate (g/d, ●) and carcass fat deposition rates (g/d, □) in the experiment of Chen *et al*. (1991)
(MSPE analysis performed for each parameter separately can be seen in Table 3)

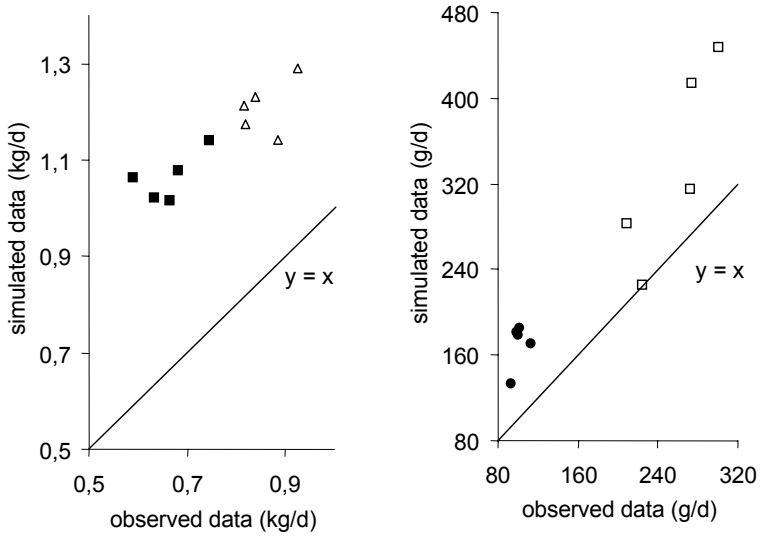


Table 3
Mean square prediction error (MSPE) and decomposition of the MSPE for observations from Chen *et al*. (1991) and van Lunen and Cole (1996)

	rootMPSE	relMPSE %	B%	R%	E%
Chen et al., 1999					
Average daily gain (kg/d)	0.356	41.6	98.0	0.8	1.2
Carcass weight gain (kg/d)	0.405	61.1	99.1	0.1	0.8
Carcass protein deposition (g/d)	71.7	71.1	94.4	5.0	0.6
Carcass fat deposition (g/d)	99.4	38.9	68.3	28.5	3.2
van Lunen and Cole, 1996					
Average daily gain (kg/d)	0.086	9.7	17.9	6.9	75.2
Feed conversion ratio (kg/kg)	0.219	10.3	10.7	2.3	87.0
Protein deposition (g/d)	16.2	11.3	2.7	1.7	95.6
Fat deposition (g/d)	22.6	12.6	0.5	22.6	76.9

rootMPSE is the root of mean square prediction error, relMSPE % is the root MSPE expressed as a percentage of the observed mean, B% is the error attributed to overall bias of prediction, R% is the error attributed to the deviation of the regression slope from one, E% is the error due to the data disturbance

Model response to variation in dietary lysine and protein level

Noblet *et al*. (1987) studied the effect of a reduction in protein level with or without lysine supplementation on energy and nitrogen balance. Thirty-two female Large White pigs with an initial body weight of 20 kg were used in the experiment. The pigs were assigned to 3 treatment groups (8 animals per treatment) and fed for 7 weeks. The dietary crude protein and lysine contents of the diets were 153 and 6.7 g/kg (diet 1), 153 and 8.0 g/kg (diet 2) or 178 and 8.1 g/kg (diet 3), respectively. The diets were based on corn and soybean meal. The composition of diets 1 and 2 were similar, except that diet 2 was supplemented with lysine. A small proportion of corn was replaced by soybean meal in Diet 3. Diets were iso-energetic on a gross energy basis. The pigs received 120 g diet/$kg^{0.75}$ daily. A digestibility study was also performed to define the digestible protein, lysine and energy contents of the diets. The DE contents of the diets were 14.2, 14.2 and 14.4 MJ/kg as-fed basis in diet 1, 2 and 3, respectively. The higher digestible energy content of diet 3 was caused by the higher protein content and its associated higher digestibility. At the end of the fattening trial (at about 53 kg body weight) the pigs were slaughtered. The bodies were dissected and the chemical composition was measured in different fractions.

The experimental observations and the model predictions and the prediction errors are presented in Table 4. The average daily gain, the empty body gain and the carcass gain are overestimated. The prediction errors are due to the overall bias in all cases (B% = 99%). However, the predicted increase in gain upon an increase in lysine content (diet 1 vs. diet 2) was qualitatively in line with observed values, and similarly both observations and predictions indicate the absence of an effect of increasing protein content (diet 2 vs. diet 3) on gain. Although the muscle

Table 4
Comparison of experimental observations of Noblet *et al*. (1987) with model predictions of average daily gain, empty body gain (EBG), carcass gain, muscle gain, organ gain, adipose tissue gain, muscle and carcass protein deposition rates, body protein and fat deposition rates, and protein and fat deposition in empty body gain and in carcass gain

	Diet 1*		Diet 2*		Diet 3*		rootMPSE	relMPSE %	B%	R%	E%
	observed	simulated	observed	simulated	observed	simulated					
Average daily gain (g/d)	649	738	699	799	700	792	93.8	13.74	99.8	0.1	0.1
Empty body gain (EBG, g/d)	625	711	675	772	680	765	89.1	13.50	99.6	0.1	0.3
Carcass gain (g/d)	485	616	527	668	523	661	136.5	26.68	99.9	0.1	0.0
Muscle gain (g/d)	294	281	337	319	338	318	17.0	5.26	97.2	2.5	0.3
Organ gain (g/d)	83	92	85	103	93	102	12.6	14.50	90.5	2.4	7.1
Adipose tissue gain (g/d)	132	142	124	136	118	130	11.3	9.08	98.9	1.1	0.1
Muscle protein deposition (g/d)	51	56	63	64	64	64	2.9	4.96	46.2	51.9	1.9
Carcass protein deposition (g/d)	71	102	85	115	86	115	29.8	36.99	100.0	0.0	0.0
Body protein deposition (g/d)	91	117	104	132	110	132	25.5	25.04	99.0	0.0	0.9
Body fat deposition (g/d)	187	201	175	193	168	187	17.1	9.70	98.4	1.5	0.1
Protein dep. in the EBG (%)	14.5	16.5	15.5	17.1	16.2	17.3	1.58	10.25	94.8	4.1	1.1
Fat dep. in the EBG (%)	29.7	28.3	25.7	25.0	25.1	24.5	0.99	3.68	85.6	14.3	0.4
Protein dep. in carc.gain (%)	14.7	16.5	16.2	17.2	16.3	17.4	1.32	8.36	92.9	6.7	0.4
Fat dep. in carc.gain (%)	34.2	30.8	29.2	27.3	29.4	26.6	2.73	8.84	94.9	2.5	2.6

* Diet 1: low protein low lysine, Diet 2 low protein high lysine, Diet 3 high protein high lysine
rootMPSE is the root of mean square prediction error, relMSPE % is the root MSPE expressed as a percentage of the observed mean, B% is the error attributed to overall bias of prediction, R% is the error attributed to the deviation of the regression slope from one, E% is the error due to the data disturbance

gain is underestimated by on average 17 g/d, the relative MSPE is only 5% of the observed mean. In contrast, the organ and adipose tissue gains are overestimated by 13 and 11 g/d respectively, with a relative MSPE of 15 and 9 % of the observed mean, respectively. Again, the overall bias proportion was the major contributor to the MSPE, whilst the deviation of regression slope from one had minor contribution to the MSPE. The model predicts the muscle protein deposition correctly. The 5 % relative MSPE is primarily caused by the 5 g/d overestimation at diet 1. Carcass protein, body protein and body fat deposition rates are overestimated by 30, 25 and 17 g/d respectively. More than 90 % of the MSPE was attributed to the overall bias. As before, the predictions were qualitatively in line with observations. The distribution of protein and fat in the empty body and the carcass are predicted satisfactorily with root MSPE values being 10 % or less of the observed mean. The differences between observations and predictions are 1.6, 1.0, 1.3 and 2.7 % for percentage of protein and fat deposition in empty body gain, and percentage of protein and fat deposition in carcass gain, respectively. The overall bias contributed most to the MSPE.

The daily muscle protein deposition rate is slightly overestimated (relMSPE = 5 %), while the predicted daily protein deposition rates in carcass and body are 37 and 25 % higher than observed in the trial. This suggests that the protein deposition rates in non-muscle fractions are overpredicted especially in bone and hide. This in turn will give rise to a much higher carcass weight and carcass gain at the end of the simulation than observed in the experiment. Alternatively, the dissection method could cause a difference in anatomical composition between observation and prediction.

Overall, the qualitative behaviour of the model was very much in line with observations. In particular, the muscle and adipose tissue gain, and muscle protein deposition and body fat deposition, and the percentage of protein and fat deposition in gains were predicted accurately (root MSPE is 10 % of observed mean). In general, the overall bias was the most significant contributor to the MSPE. Regarding muscle protein deposition the R% is quite high, but the prediction error is small.

Model response to variation in lysine/DE ratio

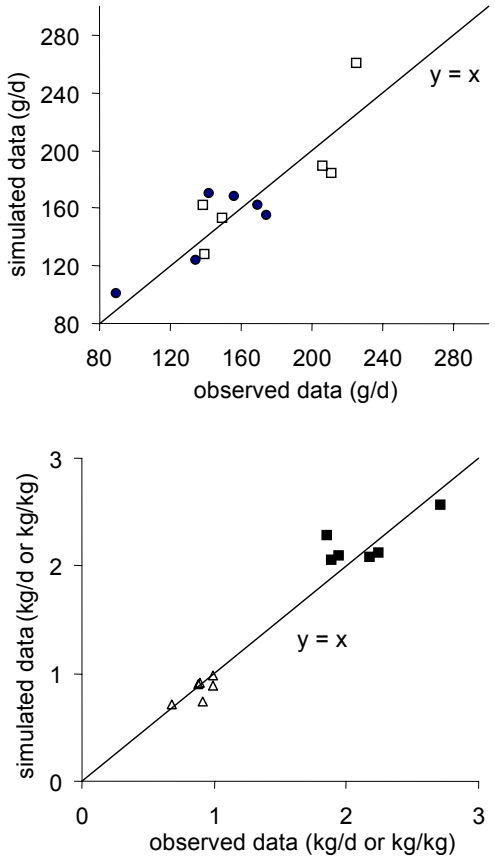
Van Lunen and Cole (1996) examined the effects of dietary lysine/DE ratio on growth performance and body composition of boars, gilts and barrows from 25 to 90 kg live weight. Twelve pigs (four of each sex) were assigned to each dietary treatment consisting of lysine/DE ratios from 0.4 to 1.4, in 0.2 g/MJ increments. Feed was provided at about 0.90 *ad libitum*. The chemical body composition of two pigs per sex per treatment was determined. In the experiment the feed intake, daily gain, feed conversion and the daily protein gain were not effected by sex. Lipid gain however was influenced by sex, and the gilts had a lipid deposition rate in between barrows and boars. The simulations were conducted for a fixed body weight range (25-90 kg) and the feed intake was adjusted to the observed feed consumption in the experiment.

The general agreement of the observed and predicted average daily gain and feed conversion, and daily protein and fat deposition rate can be seen in Figure 4.

The MSPE and the decomposition of the MSPE are presented in Table 3. The model predicted the average daily gain and the feed conversion satisfactorily with a root MSPE of 10 % of the observed mean; these errors are mainly due to the disturbance, attributing 75.2 and 87.0 % of MSPE, respectively (Table 3). The overall bias of body protein and fat deposition rates are estimated correctly. In daily protein deposition, 95.6 % of the prediction error of 16.2 g/day is attributed to the disturbance proportion and 2.7 % of it to the overall bias (Table 3). For daily fat deposition, the root MSPE is 12.6 % of the observed mean, and this error is almost completely attributed to the data disturbance (76.9 %) and to deviation of the regression slope from one (22.6 %).

The study of van Lunen and Cole (1996) was convenient for several reasons: (1) the aim of the trial (to study the effect of increasing lysine/DE ratio on the performance) was in line with the basic approach of the model. According to that, lysine is considered the first limiting amino acid in protein synthesis and the energy supply has an impact on protein synthesis. (2) The weight range of the pigs in the trial represented the whole growing and fattening period. (3) The number of dietary treatments and the experimental contrast were sufficient. The model quantitatively predicted the examined parameters with respect to average daily gain, feed conversion ratio, daily body protein and fat deposition. The errors of prediction were substantially explained by the intra-experimental variance within the trial.

Figure 4
Comparison of experimental observations with model predictions of average daily gain (kg/d, ■) feed conversion ratio (kg/kg, ∆), carcass protein deposition rate (g/d, ●) and carcass fat deposition rates (g/d, □) in the experiment of van Lunen and Cole (1996)
(MSPE analysis performed for each parameter separately can be seen in Table 3)



Model response to variation in energy sources

Beach *et al*. (1991) determined the utilisation of nutrients for energy retention, as affected by the daily fat and starch intake. In this study, 3 diets were used. Diet 1 was based on wheat and soya-bean meal; in diet 2 the wheat was totally replaced by sucrose; diet 3 was formulated using wheat and soya-bean oil. The DE and crude protein content of the diets were 14 MJ/kg and 207 g/kg for diet 1, 15 MJ/kg and 174 g/kg for diet 2 and 15 MJ/kg and 213 g/kg for diet 3, respectively. The diets were fed at the level of 3 times DE maintenance requirement. The trial was carried out with Large White males with an initial body weight of 20 kg. Five

pigs were slaughtered at 20 kg and 10 pigs per treatment slaughtered at 50 kg body weight. Considering that lysine was not the first limiting amino acid in the sucrose diet, the simulations were run for diet 1 (starch) and diet 3 (oil) only. In our simulations, the digestible nutrient content of the diets were recalculated from CVB (1998) table. The experimental contrast in daily nutrient intakes were 1.82 vs. 5.47 g digestible fat/$kg^{0.75}$ and 46.0 vs. 38.9 g digestible carbohydrate/$kg^{0.75}$ in diet 1 and 3, respectively.

Experimental observations and model predictions are presented in Table 5. In the present experiment the decomposition of MSPE is not relevant according to the low number of treatments (n = 2). However, the model predictions are generally in line with the observed values. The model predicts the average daily gain and the carcass gain correctly (MSPE < 5.0 % of observed mean). In both observations and predictions, the energy source affected the fat deposition and the carcass fat content. The model however predicts a larger increase in fat deposition and fat content upon exchanging carbohydrate with fat. Observed and predicted fat deposition rate increases 10 and 19 g/d, respectively. Observed and predicted differences of carcass fat content between pigs fed starch and oil diets are 12 and 23 g/kg, respectively. The protein deposition and the carcass protein content are overestimated by 18 and 17 %. Meanwhile the simulations show slight change between starch and oil treatments in agreement with the observations. The size of prediction errors is within the range of normal inter-experimental variation. The largest difference between observed and predicted values occurred in protein deposition rate and carcass protein content. A reason for this was, that the real intake of ileal digestible lysine and other amino acids were probably reduced in the experiment due to a lower digestibility than it was presumed during the simulation. The difference in observed and predicted values can also result from, for example, a different genotype, sex, or effect of climatic differences.

In order to study the effect of different energy sources on protein and energy metabolism further, a hypothetical starch to fat exchange was performed. The reference simulation used in sensitivity analysis was chosen as a starting point. The daily fat, starch and DE intakes were 5.4 g/$kg^{0.75}$, 41.1 g/$kg^{0.75}$ and 1.48 MJ/ $kg^{0.75}$, respectively. The fat intake was changed by daily 1 g/ $kg^{0.75}$ increments and the starch intake was adjusted to keep the DE intake constant. No other nutrient intake was modified, thus protein intake was the same in each simulation. The simulation was started at 20 kg body weight and it was run for 58 days. At this point the cumulative feed intake was very close to 100 kg. The effect of increasing fat intake on average daily gain, protein and fat deposition ratios are presented in Figure 5. As expected, increasing fat intake decreases the daily protein deposition rate and the average body gain, and increases the fat deposition rate. The protein deposition rate decreases from 163 to 140 g/day upon an increase in daily fat intake from 1.4 to 9.4 g/$kg^{0.75}$ (Figure 5). In the model, glucose arising from starch is metabolised through the acetyl-CoA pool or is linked directly to fat synthesis in the requirements for glycerol and NADPH, whilst fatty acids can be metabolised through acetyl-CoA or directly to body fat. Thus with increasing dietary fat, the acetyl-CoA concentration likely decreases. Since the protein synthesis is energy dependent, a reduced acetyl-CoA concentration reduces the protein synthesis as

well. A decreasing protein synthesis results in a decreasing protein deposition. In the simulations the oxidation of fatty acids hardly changes, even at extreme fat/starch ratio. It is in line with the results obtained by indirect calorimetry (Chwalibog *et al*. 1992; Chwalibog *et al*. 2001). They found that dietary fat was not oxidised when the energy from carbohydrate was sufficient to cover the energy requirements for growth. Consequently, fatty acids are almost quantitatively deposited. Hence, upon a high fat intake, substantial amount of dietary fat are deposited as body fat. As a result of exchanging starch for fat, the decrease in protein deposition, with associated water deposition, is more pronounced than the increase in fat deposition, giving rise to reduced growth rates. In the pig model of Lizardo *et al*. (2002) the conversion of dietary fatty acids to body fat were considered 0.85, indicating that some part of dietary fat used for energy production as well. As they concluded the literature is not convincing as regards to the efficiency of fat utilisation, therefore more study needs to clarify it.

Table 5
Comparison of experimental observations of Beach *et al*. (1991) with model predictions of average daily gain, carcass gain, protein and fat deposition rates and carcass protein and fat content *(*relMSPE % is the root MSPE expressed as a percentage of the observed mean)

	starch		oil		relMSPE
	observed	predicted	observed	predicted	%
Average daily gain (g/d)	668	637	672	638	4.9
Carcass gain (g/d)	528	528	525	527	2.0
Protein deposition (g/d)	98	117	96	112	18.1
Fat deposition (g/d)	109	101	119	122	5.2
Carcass protein content (g/kg)	157	184	154	179	16.8
Carcass fat content (g/kg)	180	156	192	179	10.4

The growth model was not calibrated directly to simulate the pig response to different energy sources, however the model was also evaluated upon exchanging starch for lipids. There are only a few studies to present the effect of energy source on protein and fat deposition. Some of these studies (Chwalibog *et al*. 1992; Chwalibog *et al*. 2001) show a tendency that upon feeding dietary fat or oil, the fat retention increases compared to pigs receiving iso-caloric starch diet. According to indirect calorimetry studies, the mechanism of the energy metabolism seems to be presented reasonably in the model. It has to be noted, however, that more data are needed to quantitatively predict the pig's response to changes in dietary non-protein energy sources.

Conclusion of model testing with independent data

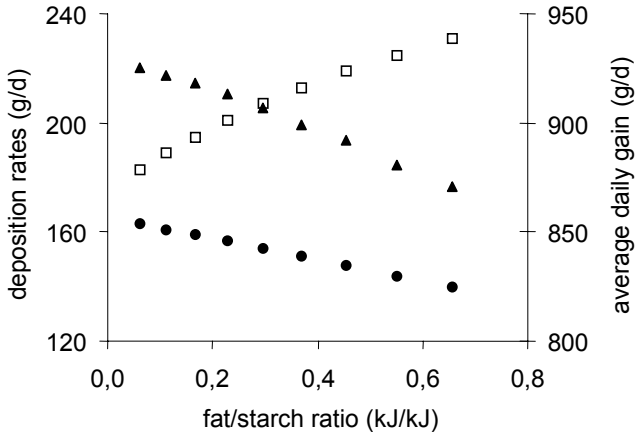
In general, the model satisfactorily predicts the qualitative pig responses to variations in nutrient supply. The predicted chemical and anatomical body

composition and also the distribution of protein and fat were sufficient in model testing. In most cases, the errors due to the deviation of the regression slope one were minor. A major factor contributing to the large bias observed for most growth characteristics is the variation in pig performance among genotypes. Adopting the model for different strains can solve that problem (and is discussed in the companion paper of Halas *et al*., 2004). Based on the comparison of the model simulations with independent data sets it is important to improve the model regarding the effect of energy sources on deposition rates.

Implication of the growth model

The model presented in the companion paper (Halas *et al*. 2004) successfully predicts the qualitative response of pigs to a wide range of variation in nutrient composition. Consequently, the model can be applied to develop feeding strategies to optimise pig production, keeping in mind the restrictions under which it can be applied (see Halas *et al*., 2004). The model predicts the amount and chemical composition of different body parts like lean meat, backfat, and organs. For this reason the model gives a possibility to predict not only the slaughter performance, but also provides a first attempt to simulation of important aspects of meat quality. It simulates the influences of differences in energy sources on energy utilisation in the body and the fat to protein ratio in the meat. However, that prediction should be evaluated with experimental data. By further studies the model can be improved, especially regarding to the rates of protein and energy metabolism in different genotypes.

Figure 5
Effect of variation in the fat/starch ratio on predicted average daily gain (g/d, ▲), protein deposition rate (g/d, ●) and fat deposition rate (g/d, □)



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Chapter 6

Effects of dietary NSP, starch and fat intakes on fat deposition and fat distribution in fattening pigs

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Abstract

The aim of the present paper is to study effects of supplemental energy intake from fermentable NSP, digestible starch and digestible fat on fat deposition and fat distribution under protein limiting conditions. A further aim is to determine whether the extra fat deposition from different energy sources, and its distribution, depends on level of feed intake. Two experiments were completed simultaneously, being a total tract digestibility study (Exp. 1) and a fattening trial (Exp. 2) with identical treatments and experimental diets. Exp. 1 was conducted to quantify the digestible nutrient intakes for the fattening trial. In Exp. 2, a total of 58 individually housed pigs were used with an initial weight of 48±4 kg. The experimental treatments were arranged in a 3x2 factorial design, with three energy sources (fermentable NSP, digestible starch and digestible fat, all added to a control diet) at each of two feeding levels. Within each feeding level, the daily nutrient intakes were the same with regard to digestible protein, ileal digestible lysine and other amino acids, as well as vitamins and minerals. The treatments were achieved by isocaloric addition of daily nutrient intake derived from each energy source (0.2 MJ DE/kg$^{0.75}$) above nutrients from control diet. To obtain initial values, ten pigs were slaughtered at 48±4 and the treatment pigs at 106±3 kg body weight. Each body was dissected into four fractions being 1) lean, 2) organs, 3) hide and subcutaneous fat and, 4) offal. The chemical body composition of each fraction was determined. Differences between fat deposition of body parts in the control group, and the other treatments, resulted in the additional energy derived from short chain fatty acids, glucose or lipid. Results show that under protein limiting conditions, extra energy intake from fermentable NSP, digestible starch and digestible fat resulted in the same fat deposition. The extra fat deposition was similar at both feeding levels. Preferential deposition of extra energy intake in various fat depots didn't depend on the energy source or energy intake.

Keywords: fattening pig, energy sources, fat deposition, fat partitioning

Introduction

Data on the contribution of different energy sources to growth performance, and protein and fat deposition, are limited. This knowledge, however, is crucial because of increased use of by-product feeds and alternative ingredients in pig feeding. Furthermore, essential information is missing on the mechanism by which various energy sources affect fat deposition and its distribution. In the non-protein fraction of the diet, dietary lipids, starch and rapidly fermentable non-starch polysaccharides (NSP) are the major energy sources. Among different types of lipids, long-chain fatty acids are preferentially used for fat production (ARC, 1981). Starch and sugars are absorbed as glucose. Dietary fermentable non-starch polysaccharide (NSP) escapes digestion in the small intestine and is fermented by micro-organisms, mainly in the hind gut. Bacteria produce short-chain fatty acids (mainly C:2, C:3 and C:4) which are absorbed from the gut lumen and can be used as an energy source (Dierick *et al*., 1989). It is well known that the digestibility of nutrients is affected by some diet components, especially by the fat and NSP content of the diet. The main non-protein energy sources such as glucose, long-chain fatty acids, short-chain fatty acids, will enter different metabolic pathways. It has also been reported that the efficiency of utilisation of different energy sources for generating ATP, and retained as body fat, differ (e.g. ARC, 1981; Black, 1995).

Equal intakes of energy from glucose, long-chain fatty acids and short-chain fatty acids will result in differences in fat deposition rates. In addition, it may result in a different distribution of body fat over tissues. There is, however, little quantitative information available about the effect of energy sources on partitioning of body lipids. Unlike the effect of energy source on ATP generating potential, these effects should be established at feeding levels above maintenance energy, and preferably under protein limiting conditions. Also, in many studies (Mershmann *et al*., 1984; Bakker, 1996; de la Llata *et al*., 2001; Rijnen, 2003), increased intake of the energy source is balanced by decreasing the content of another energy source, maintaining the treatments as isocaloric, but nonetheless complicating the interpretation of causal relationships. It has been reported that the energetic efficiency of DE intake for energy retention depends on energy supply (Halas and Babinszky, 2001). Therefore, it is important to distinguish the effect of feeding level from the effects of energy sources. In addition, measurement of digestibility is essential in this type of study.

The aims of the present study were:

1. to study the effect of extra energy intake from fermentable NSP, digestible starch and digestible fat used for fat deposition under protein limiting conditions,
2. to determine the location of fat deposition resulting from extra intake fermentable NSP, digestible starch and digestible fat,
3. to determine whether the supplemental fat deposition from different energy sources depends on the level of feed intake and
4. to quantify the potential interactions between feed intake level and energy source on the location of extra fat deposition of body fat.

Materials and Methods

Two experiments were carried out simultaneously, a total tract digestibility study (Exp. 1) and a fattening trial (Exp. 2) with identical treatments and experimental diets.

Animals, housing and experimental procedure

In Exp. 1 twenty-four barrows of KA-HYB[1] genotype were used in two replicates to determine the effect of energy source and feeding level on apparent faecal digestibility of nutrients and of energy. The mean initial live weight of the animals was 88±3 (sd) kg. A 9-day adaptation period was followed by a 5-day collection period, during which faeces were collected quantitatively. The animals were housed in metabolic cages during both the adaptation and collection periods. Pigs received their diet twice daily and were allowed free access to water. Feed refusals were collected and weighed daily. Fresh faeces production was weighed twice daily (at 8.00 a.m. and at 3.00 p.m.) and stored below -18˚C until analysis. Crude protein was analysed in fresh samples. The remaining faeces were dried and ground (1 mm). Dry matter, crude fat, starch and reducing sugars of the faeces were determined in dried faeces and feed.

[1] Hungarian hybrid, produced by KA-HYB Co. Kaposvár, Hungary

In Exp. 2 fifty-eight pigs (29 gilts and 29 barrows) of KA-HYB hybrid, weighing 48±3 (sd) kg were used. Ten pigs (5 gilts and 5 barrows) were selected and slaughtered at the beginning of the trial as an initial reference group for chemical body analysis. The remaining 48 pigs were allocated to one of eight experimental treatments with 6 pigs per treatment (3 gilts and 3 barrows). All pigs were slaughtered at 106±3 (sd) kg live weight. Pigs were kept in individual pens during the experiment, and live weight was recorded individually once a week. Pigs received their feed twice daily and had free access to water. Feed refusals were collected and weighed daily.

Treatments and experimental diets

The experimental treatments were the same in both Exp. 1 and 2 and were arranged by supplementing fermentable NSP (add. fNSP), digestible starch (add. dStarch) and digestible fat (add. dFat) to a control diet. This control diet was fed at two distinct energy intake levels. The low level was at 2 times maintenance and the high level at 3 times maintenance level. The DE requirement for maintenance was assumed to be 475 kJ/kg$^{0.75}$/d (ARC, 1981). Within each energy level, daily intakes of digestible protein, ileal digestible lysine and other amino acids, vitamins and minerals were similar. The experimental treatments were in addition to the control level, and the contrasts are presented in Table 1. The treatments were achieved by isocaloric addition of each of the three energy sources (0.2 MJ DE/kg$^{0.75}$/d) to a control diet. Addition of energy sources were 11 g/kg$^{0.75}$ /d fermentable NSP (add. fNSP), 11 g/kg$^{0.75}$ /d digestible starch (add. dStarch) or 5 g/kg$^{0.75}$ /d digestible fat (add. dFat). As a consequence of this design, DE intakes in the treatments with the added fNSP, dStarch and dFat were 2.4 and 3.4 times DE requirement for maintenance at the low and high energy intake levels, respectively. The objectives of this experiment required that it be conducted under protein limiting conditions. Due to the lysine controlled protein deposition, the extra energy derived from the additional energy source would certainly be deposited as body fat, and so it was decided to maintain a lysine to DE ratio in both control groups of 0.44g/MJ DE from 48 to 80 kg live weight. To ensure maintenance of protein limitation throughout the entire weight range, the lysine to DE ratio in the control diets was lowered to 0.36 g/MJ DE in the weight range of 80 to 106 kg. These levels are limiting according to NRC (1998) and Dutch feeding standards (CVB, 1998). By supplementation of energy sources to the control diet, protein limitation was ensured in all treatments. The diet was changed on the week when pigs reached 80 kg body weight. Composition and the nutrient content of the experimental diets fed in the weight ranges 48–80 and 80–106 kg body weight are in Tables 2 and 3, respectively.

Table 1
Experimental design with planned nutrient intake in experiment 1 and 2 (g/kg$^{0.75}$ /d)

	Control low feeding level	Control high feeding level	Added energy sources[1]		
			Add fNSP	Add dStarch	Add dFat
Ileal digestible lysine	0.43/0.35*	0.64/0.53*	-	-	-
Fermentable NSP	4.4	7.0	11.0	-	-
Digestible starch	34.0	50.0	-	11.0	-
Digestible fat	2.0	3.0	-	-	5.0
DE intake (x maintenance)	2.0	3.0	0.4	0.4	0.4
Feed intake	67.0	99.0	17.0	13.0	6.0

* in body weight ranges of 48-80 kg / 80-106 kg, respectively
[1] energy additions were in addition to both control treatments yielding 8 dietary treatments in total

The experimental diets consisted of a basal diet (based on cereals and soybean meal). Sugar beet pulp, maize starch and soy oil were used to provide the energy additions. Experimental treatments were achieved as follows: 95.75 and 95.4 % of the control diet consisted of the basal diet in the two weight ranges respectively. The remaining 4.25 and 4.6 % of the control diet was replaced digestible protein and fat present in the energy sources. The basal diet was supplemented by either sugar beet pulp, maize starch or soy oil and corrected to the same nutrient content. Sugar beet pulp, which is an accepted ingredient in pig nutrition, seemed to be an optimal (rapid) rate of fermentation of its NSP. According to calculations from chemical analysis, it contained a large amount of NSP (69 %) with a high degradability, reported to be between 72-95 % (Graham *et al*., 1986; Dierick *et al*., 1989; CVB, 1998). However, it also contained some fat and protein (1.6 and 8.7 %, respectively). In the treatment add. dStarch we used gelatinized maize starch of a high digestibility. The chemical composition of starch was 87.2 % dry matter, 0.6 %protein, 0.14 % ash, 86% starch. Crude fat and reducing sugar content of the starch were below detection. The fatty acid composition (majority of long-chain fatty acids) and the digestibility of soy oil were sufficient for the expected results of the study.

Slaughter procedure and carcass dissection

Pigs were slaughtered at 48±4 (sd) and 106±3 (sd) kg live weight. After electrical stunning, pigs were exsanguinated and blood quantitatively collected. The internal organs and the GI-tract was removed with the abdominal fat and the carcass was split longitudinally. The tail remained on the left half carcass. Subcutaneous fat and skin together were removed from the carcass. The carcass halves, blood, internal organs, full and empty GI-tract (stomach, intestines, gall bladder) and abdominal fat and subcutaneous fat were weighed. The following body fractions were separated: 1. head, feet and tail (offal), 2. subcutaneous fat and skin (hide), 3. intestinal organs, empty GI-tract, abdominal fat and blood (organs) and 4. rest of carcass (lean). Each body fraction was weighted with an

Table 2
Ingredient composition of experimental diets based on equal nutrient intake and the analysed nutrient content (g/kg) in 48-80 kg body weight range

			Low feeding level			High feeding level		
	Basal	Control	Add fNSP	Add dStarch	Add dFat	Add fNSP	Add dStarch	Add dFat
Corn	400,0	400,0	400,0	400,0	400,0	400,0	400,0	400,0
Soybean meal (CP<50%)	164,5	164,5	164,5	164,5	164,5	164,5	164,5	164,5
Wheat	235,0	235,0	235,0	235,0	235,0	235,0	235,0	235,0
Soya oil	18,0	20,0	18,0	20,0	104,0	19,0	20,0	76,0
Sugar beet pulp	-	-	298,0	-	-	199,0	-	-
Maize starch	99,0	125,0	99,0	330,0	125,0	108,0	263,0	125,0
Casein	9,0	20,0	9,0	22,0	21,0	13,0	22,0	21,0
Premix[1]	5,0	5,0	5,0	5,0	5,0	5,0	5,0	5,0
$CaCO_3$	6,5	10,0	6,5	13,0	13,5	8,0	12,0	11,5
MCP	7,5	7,5	9,5	10,5	11,0	9,0	9,5	10,0
Salt	7,0	7,0	7,0	7,0	7,0	7,0	7,0	7,0
$KHCO_3$	6,0	6,0	6,0	6,0	6,0	6,0	6,0	6,0
Total	957,5	1000,0	1257,5	1213,0	1092,0	1173,5	1144,0	1061,0
Analysed nutrient content (g/kg diet)								
Dry matter		897	904	895	903	896	893	900
Protein		232	137	131	143	135	126	131
Fat		41	32	31	106	37	37	112
Fibre		19	47	18	19	48	18	19
Ash		49	49	46	50	45	42	45
N free extract		635	639	669	585	631	670	593
Starch + sugars		505	428	567	471	414	555	472
NSP		148	258	120	133	265	133	140
Ileal digestible lysine[2]		6,7	5,3	5,5	6,1	5,7	5,9	6,3

[1] premix contains vit. A 1204000 NE/kg, vit. D_3 200000 NE/kg, vit. E 2408 mg/kg, Thiamine 199 mg/kg, Riboflavin 504 mg/kg, Niacin 4005 mg/kg, Ca-Panthothenic Acid 1988 mg/kg, Piridoxin 196 mg/kg, vit. B_{12} 3.92 mg/kg, Cholin 22904 mg/kg, Fe 17863 mg/kg, Zn 21600 mg/kg, Mn 17280 mg/kg, Cu 6500 mg/kg, Co 86 mg/kg, I 288 mg/kg, Se 43 mg/kg
[2] calculated value

Table 3
Ingredient composition of experimental diets based on equal nutrient intake and their analysed nutrient content (g/kg) in 80-106 kg body weight range

			Low feeding level			High feeding level		
	Basal	Control	Add fNSP	Add dStarch	Add dFat	Add fNSP	Add dStarch	Add dFat
Corn	440,0	440,0	440,0	440,0	440,0	440,0	440,0	440,0
Soybean meal (CP<50%)	127,0	127,0	127,0	127,0	127,0	127,0	127,0	127,0
Wheat	335,0	335,0	335,0	335,0	335,0	335,0	335,0	335,0
Soy oil	17,0	19,5	17,0	19,5	103,0	18,0	19,5	75,5
Sugar beet pulp	-	-	298,0	-	-	200,0	-	-
Maize starch	6,0	32,0	6,0	236,0	32,0	14,0	169,0	32,0
Casein	-	11,0	-	12,0	11,0	3,0	12,0	11,0
Premix[1]	5,0	5,0	5,0	5,0	5,0	5,0	5,0	5,0
$CaCO_3$	3,5	9,5	3,5	9,5	9,5	5,5	9,5	9,5
MCP	6,5	7,0	6,5	7,0	7,0	6,5	7,0	7,0
Salt	7,0	7,0	7,0	7,0	7,0	7,0	7,0	7,0
$KHCO_3$	7,0	7,0	7,0	7,0	7,0	7,0	7,0	7,0
Total	954,0	1000,0	1252,0	1205,0	1083,5	1168,0	1138,0	1056,0
Analysed nutrient content (g/kg diet)								
Dry matter		895	896	891	897	895	892	894
Protein		149	133	131	135	133	131	137
Fat		37	36	32	102	34	37	80
Fibre		19	45	19	18	44	18	18
Ash		47	46	44	49	45	45	52
N free extract		644	638	666	594	640	662	607
Starch + sugars		531	457	545	490	476	549	541
NSP		132	225	140	122	208	132	84
Ileal digestible lysine[2]		5,4	4,3	4,5	5,0	4,6	4,7	5,1

[1] premix contains vit. A 1204000 NE/kg, vit. D_3 200000 NE/kg, vit. E 2408 mg/kg, Thiamine 199 mg/kg, Riboflavin 504 mg/kg, Niacin 4005 mg/kg, Ca-Panththenic Acid 1988 mg/kg, Piridoxin 196 mg/kg, vit. B_{12} 3.92 mg/kg, Cholin 22904 mg/kg, Fe 17863 mg/kg, Zn 21600 mg/kg, Mn 17280 mg/kg, Cu 6500 mg/kg, Co 86 mg/kg, I 288 mg/kg, Se 43 mg/kg
[2] calculated value

accuracy of 1 gram and stored in plastic bags at –18 °C until chemical analysis. Chemical body analysis was carried out by methods of Kotarbinska (1971). All four body fractions were autoclaved at 134 °C and 0.2 MPa. It took 4.5 h for lean and offal and 3 h for hide and organs. The fractions were ground and homogenised. The homogenized fractions were weighted and sampled and were immediately sent to the laboratory for dry matter, nitrogen, lipid and ash determination.

Chemical analysis
The chemical composition of the diets, faeces and body parts were determined. Dry matter, protein, fat, ash content of the diets, faeces and of each body fraction were determined according to AOAC procedures (1989). The starch and reducing sugar content of the diets and the faeces were determined according to Hungarian Standards (MSZ 6830/18). The total content of fermentable non-starch polysaccharide (NSP) in the diet was calculated from organic matter by subtraction of protein, fat, starch and reducing sugars.

Calculation of DE
The digestibility of energy was calculated from the DE content and the gross energy of the diet. For the energy content of nutrients we assumed 0.0242 (MJ/g), 0.0394 (MJ/g), 0.017 (MJ/g) and 0.017 (MJ/g) for protein, fat, starch & sugars and NSP according to CVB (1998), respectively. Digestible energy (DE) intakes were calculated from the intake of digestible protein, fat, starch and fermentable NSP.

Statistical analysis
Consistent with the objective of the experiment, all effects were expressed relative to the control treatments. Therefore, for all dependent variables, within both energy intake levels, the treatment mean of the control group was subtracted from the observations of the energy sources and sexes. So the marginal results above control were used as dependent variables. Statistical analyses were subsequently completed for these data.

Exp. 1
The effect of dietary energy source, feeding level and repetition on digestibility of nutrients and energy was tested using SAS GLM procedures (SAS, 1990) with the following general model:

$$Y_{ijk} = \mu + EL_i + ES_j + EL_i \times ES_j + R_k + EL_i \times R_k + ES_j \times R_k + e_{ijk}$$

where μ = mean of the treatment
ES_i = energy source; i = 3 (add.fNSP, add.dStarch, add.dFat)
EL_j = feeding level; j = 2 (low, high feeding level)
$R_{k,}$ = repetition; k = 2
e_{ijk} = error

Exp. 2
The effect of dietary energy source, feeding level and sex on fat distribution in the body was tested using SAS GLM procedures (SAS, 1990) with the following general model:

$$Y_{ijk} = \mu + EL_i + ES_j + EL_i \times ES_j + Sex_k + e_{ijk}$$

where μ = mean of the treatment
ES_i = energy source; i = 3 (add.fNSP, add.dStarch, add.dFat)
EL_j = feeding level; j = 2 (low feeding level, high feeding level)
Sex_k = sex ; k = 2 (barrow, gilt)
e_{ijk} = error

Pair-wise comparisons were made when energy sources differed significantly in the analysis of variance, described above, after adjustments according to Tukey (SAS, 1990).

Results

Within each feed intake level, the mean results of the control treatment were subtracted from the treatment prior to statistical analysis. Therefore, the effect of feeding level as represented in Tables 4 to 9 is the effect of a similar energy addition (0.4 x DE requirements for maintenance) averaged among energy sources in addition to the low, versus in addition to the high feeding level.

Digestibility of nutrients and digestible nutrient intake

The effect of feeding level and energy source on faecal digestibility of nutrients and energy is presented in Table 4. There was no significant effect of feeding level on the nutrient and energy digestibility (P>0.05). Although there was no feeding level effect, the effect of energy source on marginal digestibility of nutrients and energy was affected by feeding level (P<0.01), except for reducing sugars. Added fNSP decreased the digestibility of dry matter, protein, fat and energy (P<0.01), while additional dStarch and dFat increased, or did not change, them. The depressing effect of fNSP was higher at low feeding level. Addition of fNSP increased the apparent faecal NSP digestibility at the high (7% units), but not at the low feeding level (Interaction FL x ES; P<0.01). Apparent faecal digestibility of the NSP fraction was reduced by dFat addition at the high feeding level (13% units). However, this effect was not observed at the low feeding level. Averaged over both feeding levels, addition of dStarch improved the apparent faecal NSP digestibility by nearly 4% units. Additional dFat increased the fat digestibility by 3.6 % on average (P<0.01).

The treatment means of digestible nutrient intakes, and that of feed intakes during the fattening study are presented in Table 5 in accordance with the digestibility data. The daily feed and nutrient intakes in different treatments were consistent with expectations.

Growth performance

Two pigs had to be excluded from the experiment due to health problem. Some samples of whole body analyses were disqualified due to technical problems. The effects of energy sources, feeding level and sex on general performance parameters (marginal data per treatment within feeding level) are presented in Table 6. The body composition of pigs in the initial slaughter group was related to the body weight, and these equations were used to determine the initial body composition of pigs in the treatment groups (Table 7). Initial weights,

Table 4
Effect of feeding level and energy source on the change of apparent faecal digestibility of nutrients and energy

	Low feeding level				High feeding level					P-value		
	Control[1]	Add fNSP	Add dStarch	Add dFat	Control[1]	Add fNSP	Add dStarch	Add dFat	RMSE	FL[2]	ES[3]	FLxES
	n=6	n=6	n=6	n=6	n=6	n=6	n=6	n=6				
Dry matter	91.7±0. 5	-5.8 [a]	1.2 [b]	1.5 [b]	90.6±0.4	-2.1 [a]	0.8 [b]	-0.9 [b]	1.9	0.66	0.0001	0.003
Protein	90.0±1.1	-16.1 [a]	1.1 [b]	1.8 [b]	88.6±0.5	-7.1 [a]	0.5 [b]	-2.0 [b]	3.0	0.17	0.0001	0.0002
Fat	91.4±1.1	-10.5 [a]	1.0 [b]	4.8 [b]	92.1±0.7	-7.3 [a]	-0.6 [b]	2.4 [b]	1.9	0.72	0.0001	0.007
Starch	100±0	0	0	0	100±0	0	0	0	.	.	.	.
Reducing sugar	97.0±0.3	-3.3 [a]	-0.4 [b]	0.2 [b]	94.9±0.3	-1.3 [a]	0.7 [b]	1.7 [b]	1.6	0.08	0.001	0.34
NSP	72.4±1.1	0.7 [a]	5.3 [a]	0.6 [b]	65.7±1.5	7.3 [a]	2.6 [a]	-13.5 [b]	5.3	0.10	0.0002	0.001
Energy	93.1±0.4	-6.5 [a]	0.8 [b]	1.5 [b]	94.6±0.5	-2.8 [a]	0.5 [b]	-0.5 [b]	1.7	0.43	0.0001	0.002

[1] Within each feed intake level the mean from the Control treatment was subtracted from the observations prior to the statistical analysis (see text), mean ± SEM
[2] FL = feeding level; represents the effect of a similar energy addition (averaged over energy sources) added to the low, versus the high feeding level
[3] ES = energy source; represents the effect of the source of the energy addition, i.e. fermentable Non Starch Polysaccharides (fNSP), digestible starch (dStarch) or digestible fat (dFat)
a, b - P<0.05

Table 5

Realised feed and nutrient intake during experiment 2 (g/d)

	Low feeding level				High feeding level			
	Control	Add fNSP	Add dStarch	Add dFat	Control	Add fNSP	Add dStarch	Add dFat
Feed intake	1581	2043	1922	1705	2329	2709	2624	2420
Digestible protein	219	205	229	218	307	291	299	283
Fermentable NSP	158	374	192	155	222	479	237	149
Digestible starch	818	903	1070	809	1193	1186	1449	1213
Digestible fat	54	56	55	171	87	82	88	226
DE intake (MJ/d)	24.02	28.87	29.16	28.38	34.91	38.57	39.37	38.88

Table 6

Effect of feeding level, energy sources and sex on the change of general performance

		Low feeding level				High feeding level			Sex			P-value			
	Control[1]	Add fNSP	Add dStarch	Add dFat	Control[1]	Add fNSP	Add dStarch	Add dFat	Barrow	Gilt	RMSE	FL[2]	ES[3]	FLxES	Sex
	n=3	n=6	n=5	n=5	n=4	n=6	n=5	n=5	n=17	n=15					
Body weight gain (g/d)	374±24	102	81	68	747±30	45	10	3	57	45	67.9	0.01	0.41	0.97	0.63
Empty body weight gain (g/d)	328±28	78.3	73.1	42.2	656±35	24.7	19.2	13.7	49.6	34.4	65.8	0.06	0.65	0.86	0.38
Feed conversion (kg/kg)	4.24±0,23	0.13	0.10	-0.34	3.13±0,11	0.32	0.35	0.10	0.14	0.08	0.53	0.13	0.25	0.85	0.75
Initial weight (kg)	45.7±2,4	2.9	2.1	2.2	49.9±1,8	-2.3	-2.3	-2.9	1.3	-1.9	3.88	0.001	0.80	0.95	0.03
End weight (kg)	103.7±0,4	2.6	1.4	2.9	107.0±1,7	-1.5	-2.2	-2.3	0.75	-0.56	2.64	0.0001	0.71	0.83	0.18
Days to slaughter	156±11,7	-34	-27	-20	77±5,0	-4	0	0	-15	-13	16.4	0.0002	0.48	0.78	0.76

[1] Within each feed intake level the mean from the Control treatment was subtracted from the observations prior to the statistical analysis (see text), mean ± SEM

[2] FL = feeding level; represents the effect of a similar energy addition (averaged over energy sources) added to the low, versus the high feeding level

[3] ES = energy source; represents the effect of the source of the energy addition, i.e. fermentable Non Starch Polysaccharides (fNSP), digestible starch (dStarch) or digestible fat (dFat)

end weights and days to slaughter are provided to allow calculation of body composition from tissue deposition rates (Tables 6 and 7). Obviously, the rate of body weight gain of the control pigs at the high feeding level was higher than at the low feeding level. The extra total and empty body weight gain resulting from energy addition was higher at the low feeding level ($P<0.05$ and $P=0.06$, respectively). At low feeding level, the energy additions resulted in 85 g/d, and at high level in 21 g/d, extra body weight gain, being a significant ($P<0.05$) difference. For extra empty body weight gain, these figures were 64 g/d and 19 g/d, respectively. Neither body weight gain nor empty body weight gain were affected by source of energy. There were no differences in extra body weight gain and extra empty body weight gain of barrows and gilts ($P>0.10$). Feed conversion was similar with different dietary additional energy sources and at different feeding levels. There was no sex effect on feed conversion ($P>0.10$). According to the data on body gain, the feeding level affected the length of the fattening period ($P<0.01$), while the source of extra energy, and the sex, did not affect the duration of the fattening study ($P>0.05$). The time taken to slaughter was shortened by 27 days and 1 day by feeding extra energy at the low and high feeding levels, respectively.

Table 7
Linear relationships between body weight (kg) and the weight of the four body fractions (g) and weight of chemical components in four body fractions (g) and empty body (g) in the initial slaughter group (Y [g] = a + b*BW [kg])

	mass		protein		fat		water		ash	
	a	b	a	b	a	b	a	b	a	b
Lean	-829,0	594,9	-338,2	117,3	-384,5	53,5	-260,9	405,5	-79,9	21,5
Organs	-2631,1	209,8	140,3	19,4	275,4	2,8	-3307,9	190,5	20,7	0,9
Hide and subcut. fat	2760,3	50,0	177,5	11,1	1537,9	5,6	521,8	41,9	-2,1	0,5
Offal	1808,8	34,8	137,7	9,7	188,0	5,2	668,2	30,5	-16,9	5,3
Empty body	1108,9	889,5	-315,9	165,4	-1548,8	127,7	209,3	617,8	60,1	25,5

Deposition of body components

In order to minimize calculation error due to variance in initial body weights, linear relationships were computed between the body weight and the weight of the four body fraction masses and the weight of the chemical components of body fractions in the initial slaughter group (Table 7). The mass of body parts, and the mass of chemical components in body parts, were not different between barrows and gilts. The body weight of the initial slaughter group was 47.8 kg (SEM: 2.5). The initial body composition of individual pigs used in the trial was determined by these equations.

The effect of energy sources, feeding level and sex on deposition rates of wet tissues, expressed as marginal values per treatments above control within feeding level, is presented in Table 8. Data indicate that extra lean tissue gain was not affected by energy source (P>0.10). The additional dietary energy increased lean tissue gain at the low feeding level, but decreased it at the high feeding level (P<0.001). Deposition of wet tissue mass in organs was higher when pigs received the additional energy at high feeding level (P<0.001). The extra gain of hide and subcutaneous fat from added energy was affected by sex (P<0.05), with barrows depositing more hide and subcutaneous fat than gilts. The extra gain of the offal fraction was higher at the high feeding level (P<0.05), but was unaffected by energy source or sex.

Table 9 shows the effect of energy sources, feeding level and sex on deposition rates of protein, fat, water and ash in the four body parts. Data are as differences of treatments to controls. The marginal deposition rates of body protein and related components, like water and ash, were affected by feeding level (P<0.05). The additional energy intake increased body protein deposition rates at the low feeding level, but decreased it at the high feeding level. Gilts deposited more protein in their body than barrows (P<0.05). Consistent with our expectations, added energy intake increased the rate fat deposition relative to the control groups. Most of the extra fat deposition occurred as hide and subcutaneous fat (approximately 50 %). The increase in body fat deposition was, however, not affected by feeding level, or source of energy, but it tended to be higher for barrows when compared with gilts (P<0.10). As in the whole body, the deposition rate of protein, water and ash in the lean fraction was increased by additional energy at the low feeding level, but decreased by additional energy at the high feeding level. Similar to body protein, lean tissue protein was also affected by sex. The extra fat deposition in lean from additional energy intake was higher in barrows than in gilts (P<0.05), but was not affected by dietary energy sources and feeding level. The extra organ protein deposition rate was affected by energy source (P<0.05); additional fNSP increased the gain of this fraction, but only at the high feeding level (interaction FLxES P=0.08). The extra energy intake at the high energy level increased daily protein (P=0.06), water (P=0.001) and ash deposition (P<0.001) in organs as a result of the fNSP treatment. The energy source feeding level interaction was significant (P=0.04) for extra ash deposition rates. Barrows deposited 5.2 g/d more fat in their organs than gilts (P=0.06). Deposition rates of chemical components in hide and subcutaneous fat were independent of the dietary treatments. However, barrows deposited more fat in the subcutaneous area than gilts (P=0.07). At the high feeding level, extra energy intake resulted in more fat, water and ash deposition in offal than at the low feeding level (P<0.05). Neither dietary energy source nor sex affected the deposition rates of chemical components of the offal fraction (P>0.10).

Table 8
Effect of feeding level, energy sources and sex on marginal deposition rate of wet tissues in four body fractions (g/d)

		Low feeding level				High feeding level			Sex			P-value			
	Control[1]	Add fNSP	Add dStarch	Add dFat	Control[1]	Add fNSP	Add dStarch	Add dFat	Barrow	Gilt	RMSE	FL[2]	ES[3]	FLxES	Sex
	n=3	n=6	n=5	n=5	n=4	n=6	n=5	n=5	n=17	n=15					
Lean	176,2±13,2	28,6	39,8	26,6	353,7±18,9	-24,5	-47,1	-41,4	-9	3,96	39,69	0.0001	0,86	0,62	0,64
Organ	50,5±6,2	-0,2	-0,1	-10,3	75,3±3,8	28,3	9,7	10,2	9,77	5,86	12,82	0,0003	0,12	0,23	0,41
Hide and subcut. fat	55,0±14,6	50,8	29,1	23,3	179,3±23,8	14,6	44,4	32,3	42,59	18,26	32,45	0,56	0,55	0,20	0,042
Offal	46,5±4,0	-0,9	4,3	-1,6	48,1±6,2	6,3	12,2	11,9	5,95	6,31	13,48	0,021	0,54	0,50	0,81

[1] Within each feed intake level the mean from the Control treatment was subtracted from the observations prior to the statistical analysis (see text), mean ± SEM
[2] FL = feeding level; represents the effect of a similar energy addition (averaged over energy sources) added to the low, versus the high feeding level
[3] ES = energy source; represents the effect of the source of the energy addition, i.e. fermentable Non Starch Polysaccharides (fNSP), digestible starch (dStarch) or digestible fat (dFat)

Table 9
Effect of feeding level, energy sources and sex on marginal deposition rates of chemical components in the four body fractions (g/d)

		Low feeding level				High feeding level				Sex			P-value			
		Control[1]	Add fNSP	Add dStarch	Add dFat	Control[1]	Add fNSP	Add dStarch	Add dFat	Barrow	Gilt	RMSE	FL[2]	ES[3]	FLxES	Sex
		n=3	n=6	n=5	n=5	n=4	n=6	n=5	n=5	n=17	n=15					
Total deposition	protein	58,1±6,1	7,2	7,7	-0,3	100,4±2,7	-3,7	-6,2	-7,6	-4,66	4,58	9,79	0,0074	0,49	0,84	0,031
	fat	65,2±13,0	54,0	46,8	47,5	199,9±19,6	36,0	77,9	54,9	65,07	38,84	40,09	0,59	0,59	0,42	0,096
	water	195,0±8,9	17,7	15,3	-3,9	336,6±17,9	-3,7	-46,0	-29,2	-8,61	-7,1	46,64	0,033	0,38	0,58	0,83
	ash	12,6±1,4	1,1	2,2	0,7	23,8±2,2	-4,7	-6,0	-5,3	-3,18	-0,88	3,53	0,0001	0,88	0,79	0,18
Deposition in lean	protein	35,4±3,9	5,8	6,4	3,5	68,2±2,1	-8,8	-8,7	-8,9	-5,55	2,41	7,27	0,0001	0,95	0,91	0,012
	fat	16,2±2,8	11,5	13,5	13,0	43,1±2,9	9,1	18,2	11,9	14,99	10,12	7,21	0,98	0,21	0,59	0,081
	water	116,4±6,8	10,4	17,2	9,3	227,5±13,6	-22,8	-53,5	-40,7	-17,13	-8,5	30,51	0,0001	0,62	0,37	0,73
	ash	8,6±1,1	1,2	2,1	0,9	16,5±2,3	-3,5	-3,8	-3,3	-2,1	-0,24	2,99	0,0001	0,87	0,94	0,19
Deposition in organ	protein	7,6±1,0	-0,1	-0,2	-1,7	11,0±0,8	2,5[a]	-1,0[b]	0[b]	-0,41	0,43	1,66	0,06	0,01	0,08	0,26
	fat	5,4±0,7	5,6	7,4	6,8	19,2±2,6	5,2	10,6	6,5	9,26	4,14	7,25	0,79	0,48	0,92	0,066
	water	37,0±4,7	-5,7	-7,2	-14,5	44,7±2,1	20,1	0,1	3,4	0,7	1,69	12,38	0,0007	0,12	0,25	0,79
	ash	0,5±0	0	0	-0,1	0,6±0,1	0,4[a]	0,1[b]	0,2[b]	0,11	0,1	0,154	0,0001	0,04	0,04	0,57
Deposition in hide and subcut. fat	protein	7,1±1,6	1,3	0,6	-1,5	13,1±0,9	1,5	2,2	1,8	0,99	0,67	2,89	0,21	0,29	0,70	0,72
	fat	28,9±9,9	36,5	23,6	24,2	124,0±17,6	12,3	38,9	30,4	36,47	17,22	27,86	0,83	0,83	0,28	0,070
	water	19,3±3,0	14,0	4,6	-1,8	42,2±5,4	0,8	3,4	-0,3	5,3	0,37	14,44	0,24	0,20	0,61	0,26
	ash	0,2±0	0	0	0	0,5±0,1	0,1	0,1	0,1	0,04	0,02	0,166	0,31	0,49	0,97	0,70
Deposition in offal	protein	7,4±0,4	-0,6	0,9	-0,2	7,5±0,9	0,9	1,0	-0,4	0,011	0,79	2,74	0,41	0,75	0,88	0,44
	fat	12,2±1,8	1,3	2,7	3,0	11,9±2,1	7,5	7,6	6,1	4,52	5,59	7,32	0,04	0,9	0,98	0,57
	water	24,0±2,2	-1,8	0,4	-4,5	22,9±4,0	-0,4	6,2	8,4	2,33	1,8	8,57	0,02	0,4	0,15	0,75
	ash	3,4±0,4	-0,2	0,1	-0,1	6,2±0,7	-1,6	-2,3	-2,3	-1,25	-0,66	0,76	0,0001	0,82	0,46	0,11

[1] Within each feed intake level the mean from the Control treatment was subtracted from the observations prior to the statistical analysis (see text), mean ± SEM
[2] FL = feeding level; represents the effect of a similar energy addition (averaged over energy sources) added to the low, versus the high feeding level
[3] ES = energy source; represents the effect of the source of the energy addition, i.e. fermentable Non Starch Polysaccharides (fNSP), digestible starch (dStarch) or digestible fat (dFat)
a, b - P<0.05

Discussion

Digestibility of nutrients and energy

The objective of the digestibility measurements was to quantify digestible nutrient intakes for integration with results of the slaughter experiment. Results of the digestibility study show that adding a similar quantity of energy (averaged among energy sources) either in addition to the low, or in addition to the high feeding level did not affect nutrient digestibility. Quiniou *et al*. (1995) also found no effect of feeding level on N digestibility. However they found a positive effect of feeding level on energy digestibility. There was no difference in nutrient digestibility as a result of feeding additional energy at low or high feed intakes. Thus, no difference was expected for digestibility of energy at different feeding levels.

Many studies have shown that the dietary NSP (either total or fermentable NSP) reduces both the faecal and ileal digestibility of nutrients (Drochner, 1984; Dierick *et al*., 1989; Bakker, 1996). In our study, protein digestibility was dramatically decreased by fNSP. That can be explained by different factors, notably that high NSP intakes increase endogenous secretion of N (Furuya and Kaji, 1992; Schulze, 1994; de Lange *et al*., 1989). Furthermore, N present in the NDF matrix is largely unavailable (Schulze, 1994). Finally, differences in bacterial protein synthesis might decrease the apparent total tract protein digestibility (Mosentin *et al*., 1992; Bakker, 1996). From this difference, it can not be concluded that amino acid availability would be decreased (i.e. ileal digestibility). Although the reduced protein gain at high intake levels with added NSP may suggest this to be true. Fat digestibility was reduced by fNSP, but increased by dFat (Table 4). Dierick *et al*. (1989) and Bakker (1996) also reported that fat digestibility was reduced with fermentable carbohydrates in the diet. The reason could be the effect of NSP on bile acids and other micellar components (Furda, 1990), and also that increased fermentation rates result in a higher rate of microbial lipid synthesis (Bakker, 1996). Since the fat source with additional dFat was soy oil, which is highly digestible, the digestibility of fat increased. Similar results were found by Bakker (1996b), with inclusion of a pure, highly digestible, fat source increasing the overall fat digestibility in all types of diets. According to our results, the apparent faecal digestibility of starch is complete (Bakker, 1996; Everts *et al*, 1996). The digestibility of NSP differs according to the composition of the NSP. Sugar beet pulp contains rapidly fermentable NSP, mainly pectins, which increases the overall digestibility of NSP at fNSP groups at the high feeding level. This was similar to results reported on faecal digestibility of NSP fractions from sugar beet pulp from studies of Graham *et al*. (1986), Schrama *et al*. (1996, 1998). Dietary dFat reduced NSP digestibility when added to the high feeding level, but not when added to the low feeding level. Additional fat might affect the process of fermentation, however no interaction was expected. The pre-ceacally non-digested fat may reduce the number of bacteria in the large intestine (Mallett and Rowland, 1983). Due to the reducing effect of NSP on nutrient digestibility, the digestibility of energy was expected to be reduced in fNSP groups. The reducing effect of fNSP is higher at a low feeding level. Christensen and Thorbek (1987) confirmed that methane production per unit of dry matter intake of pigs fed at low feeding levels was higher

than at high feeding levels. It suggests that bacterial activity, and hence the reducing effect on nutrient digestibility, is also higher at low feed allowances.

Deposition of chemical components in body and body parts

In our experiment, additional energy intake was expected to result in only extra fat deposition, since the protein and ileal digestible lysine intake was adjusted to be limiting for protein deposition. In order to explain the changes in (empty) body weight gain, and gain of body parts, the deposition rates of chemical components must be examined.

Protein, water and ash deposition

Total body protein deposition was somewhat higher at the low feeding level when pigs received additional energy intake from fNSP and dStarch, compared to the control group. If the theory of protein and energy dependent phases of linear-plateau concept is accepted, then no effects of energy addition on protein deposition would have been expected. A high lean genotype was used in the trial and so the energy supply at the low feeding level might have been too low for this breed. An intensive hybrid might suffer more upon a very low nutrient supply than an extensive one. At the high feeding level, protein deposition was lower when pigs received additional energy compared to the control group. Presumably protein deposition at high feeding levels was limited by the slightly reduced digestible protein intake compared to the control group (Table 5). Protein deposition was not affected by the energy source (Table 9), although faecal digestibility of protein was dramatically reduced by added fNSP (Table 4) and the digestible protein intake was much lower in the fNSP group at low feeding level than in other groups. This suggests that faecal digestibility data underestimated protein availability, perhaps due to the high amount of excreted bacterial protein (Bakker, 1996). More than half of body protein is located in lean, therefore any change in body protein deposition will appear in lean protein deposition. The extra deposition of body protein in groups fed additional energy at low feeding levels appeared almost exclusively in the lean fraction. At the high feeding level, reduced protein deposition in groups fed additional energy intake originated from reduced lean protein deposition. The energy source affected organ protein deposition (P=0.01) only, feeding a high level of fNSP increased the protein accretion in organ fraction, but mainly at the high feeding level. Supplementing diets with NSP has been shown to increase weight of the small and large intestine by 40 % in poultry, presumably due to increased protein synthesis in the gastrointestinal tract (Simon, 2001).

Water and ash deposition rates were closely related to protein deposition rates in the body (Table 9). The water to protein deposition ratio in the body was 3.4 in control groups and ranged between 3.1-3.5 in groups receiving additional energy. This is consistent with results of Bikker *et al*. (1996), who found that the water to protein deposition ratio varied between 2.9-4.7, with an average of 3.3. Emmans and Kyriazakis (1995) suggested that this ratio is constant for all pigs. The water to protein deposition ratio in fractions of lean, hide and offal are similar than that in the whole body and the organs contained more water than the whole body. In the present study the ash to protein deposition ratio was approximately 0.2

in agreement with the generally accepted value (de Lange, 1995). Organs, hide and subcutaneous fat fractions contain less ash than lean and bony tissues, and so the ash to protein deposition ratio was 0.06 and 0.03 for organs and the hide and subcutaneous fat fractions, respectively.

In our study the higher protein deposition rate in lean of gilts resulted in a higher net body protein deposition than in barrows. The literature is inconsistent regarding the effect of sex on protein deposition rate, but difference in protein deposition between gilts and barrows is usually not reported. Indirect calorimetry results of Noblet *et al*. (1989) suggested that males retained more energy as protein than females, but there was no difference between females and castrates. Another study, using a comparative slaughter method, showed that protein deposition was independent of sex of the pigs (van Lunen and Cole, 1996).

Fat deposition

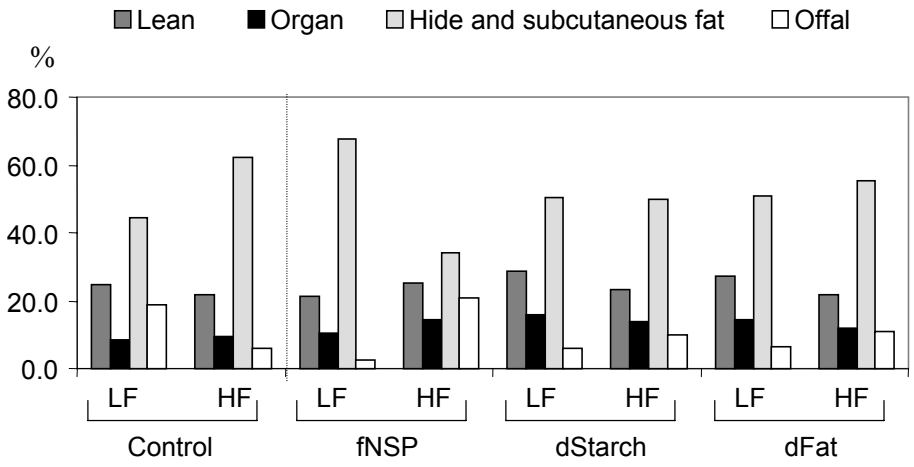
According to our hypothesis, the extra energy intake from different sources would result in different fat depositions and also in different fat distributions within the body. Furthermore, the effect of different energy sources would change at low and high feeding levels. However, results of Table 9 do not support this hypothesis. In the present study, feeding extra energy gave similar marginal body fat deposition at both low and high feeding levels. This is consistent with several studies which showed that increasing energy intake increased body fat deposition rate linearly (Campbell *et al*., 1985; Bikker *et al*., 1995; Quiniou *et al*., 1995, 1996a, Dunshea *et al*., 1998). A relatively small number of *in vivo* studies have been conducted to study the effect of different energy sources on body protein and fat deposition. In the present experiment, protein deposition was limited by lysine intake and therefore it didn't vary among energy sources. Alternatively, our data suggests that the equal amount of energy from short chain fatty acids, long chain fatty acids and glucose resulted in similar daily fat deposition. Consistent with our results, Urquhart *et al*. (1991) showed by indirect calorimetry that increasing fat inclusion with isocaloric feed intake had no effect on the protein and fat deposition ratio. Contrary to that, another indirect calorimetry study with pigs fed semipurified diet without oil or with 90 g/kg soya bean oil in proportion of daily 1357 and 1410 kJ of metabolisable energy/kg$^{0.75}$, showed that the calculated fat retention was about 30 % higher on the additional oil diet vs. the semipurified diet (Chwalibog *et al*., 1992). In contrast to that, Bakker and Dekker (1991) and Bakker (1996) in a comparative slaughter study, found that fat inclusion in a diet with isocaloric intake on a net energy basis reduced fat retention. In the latter study, the authors concluded that the energy intake from the fat-free part of the diet was not sufficient to meet maintenance energy requirements and, therefore, dietary fat was used as an ATP source with low efficiency. The generally accepted efficiency of fat generating ATP is about 66 %, while that for fat retention is 90 % (Black, 1995). It should be noted, however, that the energy retention in the study of Bakker (1996) reflected to the DE intake. Thus, it emphasised how carefully the NE system should be used (Whittemore, 1999).

In agreement with our data from the comparative slaughter study, indirect calorimetry data suggested that the daily protein and fat retention from a diet with

high-starch and high easily fermentable NSP (from sugar beet pulp) content did not differ when feed intake was isocaloric on ME basis (Longland *et al*., 1991; Schrama *et al*., 1996). However, Rijnen (2003) used isocaloric on ME intake, with an increasing proportion of solvent-extracted coconut meal from 5 % to 50 % of the feed, and found a slightly decreasing protein retention and similar fat retention. The efficiency of utilization of fermentable carbohydrates for energy gain was found to be between 65-80 % (Müller *et al*., 1989; Roth *et al*., 1988; Black, 1995). Higher values, close to the efficiency of starch (reported as 74-85% by Schiemann *et al*., 1972 and Black, 1995), were found when volatile fatty acids were infused into the cecum directly. Consequently, the combination of these results and ours indicate that isocaloric intake of fermentable NSP could result in a fat retention similar to that of digestible starch, especially if the source of NSP is highly degraded and produces a small amount of methane. Schrama *et al*. (1996, 1998) reported a reduction in activity related heat production of pigs fed a highly fermentable NSP rich diet, compared to pigs fed a high starch diet. Possibly the energy released due to the reduced physical activity compensated for the lower energetic efficiency of short-chain fatty acids in fat retention.

The fat deposition rate in different body parts, similar to that in the whole body, seems to be linear as a function of energy intake and the extra fat deposition in body compartments seems not to be affected by feeding level or by energy source. Figure 1 shows the distribution of fat deposition over tissues in the control group (% of total fat deposition) and distribution of extra fat deposition over tissues as affected by the intake of fNSP, dStarch and dFat (in % of extra fat deposition). The distributions of fat deposition in the dStarch and dFat groups are similar and correspond to the control groups. Additional digestible starch and fat resulted in approximately 50 % of the body fat deposited as subcutaneous fat at both feeding levels. Similar to our results, fat distribution in the study of de Greef (1992) did not differ in pigs fed 16.3 MJ DE compared to pigs fed 12.6 MJ DE above maintenance. Figure 1 shows that fNSP results in a different distribution of fat deposition, especially at the high feeding level. This suggests some differences in fat distribution within the body with different fat sources. The subcutaneous fat deposition was 68 and 34 % of total fat deposition at the high and low feeding levels, respectively. However, the 32 g/d lower rate of whole body fat deposition is almost quantitatively reflected in a lower rate of fat deposition in subcutaneous tissue (12 g/d, NS). As mentioned above, the end products of fermentation of NSP are short-chain fatty acids, mainly with 2 and 3 carbon atoms. Stanko *et al*. (1989) reported that dietary addition of trioses (dihydroxyacetonate and pyruvate) reduced carcass fat deposition of pigs fed isocaloric feed intake of a basal corn-soybean diet. The pigs were fed approximately 3.2 times their DE maintenance requirements, and the ones receiving a triose mixture had a lower percentage of fat in leg and loin tissue samples, and also a lower percentage of fatty cuts in the right carcass. In another study with rats, the mechanism of action of trioses involved an increase in resting energy expenditure and an inhibition of trygliceride synthesis in adipose and hepatic tissue (Stanko and Adibi, 1986). The mechanism could explain the reduction of subcutaneous fat and body fat, but this effect presumably exists only at the high feeding level. Based on our results, the

Figure 1
Distribution of fat deposition (g/d) over tissues in the control group (% of total fat deposition) and distribution of extra fat deposition over tissues as affected by extra intake of fNSP, dStarch and dFat (in % of extra fat deposited) at low (LF) and high feeding levels (HF)



metabolism of short-chain fatty acids seems to be more efficient at a low feeding level, at least, as far as fat deposition is concerned.
In our study, barrows tended to deposit more fat in their body than gilts (P=0.10). The sex effect was dominant in fractions of lean (P=0.08), organ (P=0.07) and subcutaneous fat (P=0.07) and hence in the total fat deposition rates. Literature data have generally agreed that fat deposition differs in gilts and barrows (Noblet *et al*., 1989; van Lunen and Cole, 1996). The lower fat deposition rates of gilts results in a lower fat content in the body. Data of Jorgensen *et al*. (1985) confirmed that female pigs contained less fat in the dry matter of all anatomical fractions (entrails, carcass, muscle, fat and bone) than barrows.

Growth performance and wet tissue deposition

Protein deposition is accompanied by water and ash deposition, and thus determines the major portion of weight gain. Fat deposition was approximately 20 and 30 % of empty body gain in the control groups at low and high feeding levels, respectively. Since body fat deposition was not affected by dietary treatments, changes in protein deposition in the total body, and also in different body parts, resulted in changes of empty body weight gain and gain of wet tissues.

In our study, neither protein deposition nor average daily gain was influenced by dietary energy source. Rijnen (2003) also showed that the weight gain of pigs fed isocaloric dietary intake (733kJ/kg$^{0.75}$/d) from a high starch (457 g/kg), or NSP rich diet (315 g/kg), did not differ. The source of the NSP was solvent-extracted coconut meal, in which the NSP was highly digested (73 %). Anugwa *et al*. (1989)

completed a study, in which pigs were fed a commercial corn-soybean diet or a diet with high alfalfa meal containing a relatively high acid detergent fibre (4.5 *vs*. 16.2 %) and lignin (1.3 *vs*. 4.3 %) level. The average daily gain and the feed conversion ratio in pigs between 55-106 kg body weight range (i.e. 66 days) were 0.77 kg/d and 3.45 kg/kg on average, irrespective of the dietary treatments. The effect of starch and fat, as the energy source, on growth and efficiency of feeding growing pigs were studied by Mersmann *et al*. (1984), who found that isocaloric feed intake of different types of diets, with additional cornstarch (18.7 %) or lard (12 %), to a basal corn-soybean diet resulted in no differences in gain. In agreement with these results, de la Llata *et al*. (2001) found that at isocaloric feed intake, an additional 6 % fat in the diet did not affect average daily gain. The feed conversion ratio improved in both studies due to the higher energy density diets with high fat levels. In both studies, the authors suggested that fat deposition increased with high fat diets, although only backfat thickness, and/or fatty cuts of the carcass side, was measured (Mersmann *et al*., 1984; de la Llata *et al*., 2001). Knowles *et al*. (1998) also found that isocaloric intake of a control corn-soybean diet with inclusion of different fat sources, such as 3.85 % of soybean oil or 2.45 % of poultry fat, resulted in no difference in performance of pigs, or in the mass of the fatty tissues. These data suggest that the equal energy from fat or starch possibly resulted in similar weight gain, although the composition of the body gain should have been measured directly. In another experiment of de la Llata *et al*. (2001), isocaloric feed intake with increasing fat content (added dietary fat increased from 0 to 6%) increased average weight gain and backfat thickness, while decreasing lean percentage and improving the gain to feed ratio.

There is little literature dealing with nutritional effects on body compartments such as wet tissue of lean, organs and subcutaneous fat. Since the lean fraction is approximately half of empty body, changes in empty body generally correspond to changes in lean. According to data on protein deposition rates, energy addition to the low feeding level resulted in extra lean deposition, whereas a similar addition decreased lean deposition at the high feeding level. Jorgensen *et al*. (1985) found that muscle and bone mass, as a percentage of carcass mass, decreased with increasing energy density (MJ ME/kg dry matter) and feeding intensity (MJ ME/d). However, in this study, protein intake was not limiting, unlike in our study. In the present study, the depressed extra lean gain was compensated by increased organ gain at the high feeding level, and so resulted in a positive, but lower, extra empty body gain vs. the low feeding level. According to gain of the chemical entities, source of added energy did not affect daily deposition of lean tissue. However, additional energy intake resulted in higher extra wet tissue gain of organs at the high feeding level. This effect was caused mainly by high fNSP intake. The hypertrophic effect of high fibre diets on the gastrointestinal tract in growing pigs has been reported repeatedly (e.g. Pekas *et al*., 1983; Pond *et al*. 1989). Literature is limited, but consistent, concerning daily gain of hide and subcutaneous fat as affected by energy intake. The marginal deposition of hide and subcutaneous fat was similar at both feeding levels, making our data consistent with Walstra (1980), Jorgensen *et al*. (1985), Godfrey *et al*. (1991), Quiniou *et al*. (1996b), who all suggested a linear effect of energy intake on gain of this fraction. In our

experiment, subcutaneous fat deposition of added fNSP, dStarch and dFat groups did not differ from each other. In a fattening trial of Scipioni *et al*. (1991), lower backfat thickness, and a smaller proportion of fatty cuts in the right side of the carcass, was obtained from pigs fed a diet with a high proportion of pressed beet pulp silage. Several other studies, however, did not confirm that carcass fat could be reduced by high dietary fermentable NSP. The backfat thickness, and the fatty cuts in the right side of the carcass, was not affected by inclusion of different types of beet pulp in the study of Parisini *et al*. (1991) and Martelli *et al*. (1999, 2000).

The literature is rather consistent in respect to the effect of sex on average daily gain and feed conversion. In agreement with our results, no effect of sex was obtained by van Lunen and Cole (1996) with boars *vs*. gilts *vs*. barrows, and Chen *et al*. (1999) with gilts *vs*. barrows, on average daily gain and feed conversation. In several other studies, the reason for the higher growth rate of barrows was higher feed intake capacity (Friesen *et al*., 1994; Grandhi and Cliplef, 1997), which is not relevant in our case. Walstra (1980), however, found a slight difference in daily gain between gilts and barrows at restricted feed allowance. Nonetheless, protein deposition was slightly higher in gilts and daily gain was similar in both sexes since barrows had a higher fat deposition in their body. In agreement with our results, Walstra (1980) found no difference between slopes of the growth curve for bone and muscle mass in gilts vs. barrows. The difference in fat deposition rates in hide and subcutaneous fat, however, resulted in differences in wet tissue deposition rates between barrows and gilts.

In conclusion, under protein limiting conditions, supplemented energy intake from fermentable NSP, digestible starch and digestible fat resulted in similar body fat deposition. Preferential deposition of the supplemental energy intake in various fat depots did not depend on the energy source, and the extra fat deposition from fermentable NSP, digestible starch and digestible fat deposited as body fat, was similar at the low and high levels of feed intake.

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GENERAL DISCUSSION

Introduction

Knowledge of the growth process has increased during the last decades. Understanding of nutrient metabolism, however, is still far from complete. Modelling of the growth of animals is intended to address these shortcomings, by providing a systematic representation of the biological process. A mechanistic approach implies a representation of the principles underlying the mechanisms governing metabolism (France *et al*., 1987). As shown in Chapters 1 and 2 the quantitative understanding of the relationships between nutrient intake and animal performance in the literature is presented at different levels (Burlacu *et al*., 1989; Moughan, 1989; Pomar *et al*., 1991; Lange, 1995; Lavotto and Souvant, 2003). Gill *et al*. (1989) suggested that models be developed to predict animal performance on a biochemical bases, since this approach enables extrapolation of model predictions beyond the initial data set. Another objective of those models is to increase understanding of metabolic integration. A further benefit is that their construction helps to identify gaps in current knowledge, and in the design of appropriate experiments to fill those gaps (Gill *et al*., 1989).

This kind of approach has already been used to model growth in cattle (France et al. 1987), lactating sows (Pettigrew et al., 1992) and pre-ruminant calves (Gerrits et al. 1997). The present model was developed on a biological, rather than a statistical, basis. Some consequences of the mechanistic approach are discussed first in the present chapter. In this chapter attention is focussed on the practical aspects of using the model, which predicts animal performance from nutrient intake. However, it would be useful if a model could predict the required amount of feed, or nutrients, to obtain a pre-defined level of animal production. It will be demonstrated, through an example, why nutrient intake cannot be estimated from body composition. The latter part of this General Discussion focuses on the representation of different energy sources in the model. The energetic efficiency of the different dietary energy sources is discussed and, based on data from Chapter 6, the growth model is further evaluated with results of the fattening trial. Moreover, data from the fattening trial are analysed relative to the distribution of fat deposition. Environmental conditions, and health status also determine pig production as presented in Chapter 1. Inclusion of health status and environmental conditions can be achived by understanding the reasons for differences in animal response to various environmental conditions. This may involve either changes in parameter values or inclusion of mechanisms to account for such differences. In the last section of the General Discussion, a new application of the present model is introduced in addition to the development of feeding strategies and improvement of understanding in research. Finally, the main conclusions from each chapter are summarized.

Approach of the model

There are several consequences of using a mechanistic approach in model development. Similarly to the pig model of Whittemore and Fawcet (1976), the current model describes protein synthesis and degradation is a function of protein mass. This approach suggests that protein deposition does not require a constant energy requirement per unit of protein gain. Thus a certain protein deposition rate

does not completely determine the energy requirement for deposition. For instance, this will be the case with reduced protein synthesis together with reduced protein degradation (i.e. low turnover). Several situations can result in the same net protein deposition and, in case of low turnover, it is associated with less energy costs compared to a situation with a high turnover. In most growth models, the fractional protein degradation rate is fixed and protein degradation is related to protein mass. Consequently, in such models the nutrient supply affects only protein synthesis. Such approximations may contain some error as far as the representation of energy metabolism. The model of Lovatto and Sauvant (2003) represents both long-term control (homeorhesis) and a short-term control (homeostasis) of the animal response. In this model both anabolism and catabolism of body proteins are influenced by age and plasma metabolite concentrations. This is likely to be more a accurate representation of turnover. Alternatively, assuming a fixed catabolism rate makes the model simpler. It is not clear yet how important that is, because protein degradation changes only slightly with changing protein consumption in conditions of non-extreme nutrient supply (e.g. Simon, 1989).

A major assumption of the present model is that concentrations of metabolites have a major effect on nutrient fluxes. As a consequence of the principle of saturation behaviour used to represent most nutrient flows, there is some flux in each transaction. This is consistent with experimental results. For example, Chwalibog et al. (1992) measured lipid metabolism using indirect calorimetry. In their, study some lipogenesis occurred simultaneous with fat oxidation from the body, even with a diet that had a very low carbohydrate, and high fat, level. In the situation with low fat and high carbohydrate intake, lipolysis still occurred. In the first case, lipogenesis indicates that there is synthesis of fat, while in the second case, oxidation of fat means that a part of energy comes from fat (Chwalibog et al., 1992). According to the major equations, there is always some synthesis of protein and fat during the simulation. However, these synthesis rates must be higher than the degradation rates, or else the model becomes instable. It was found that lipid deposition is zero when pigs are fed at a level of 1.3 times ME for maintenance (Campbell and Traverner, 1988 and Bikker, 1994). Theoretically, the lowest level of the nutrient input in the model should be at a feeding level of 1.3 times maintenances. The growth model was calibrated from feed intake of 1.7 maintenances to *ad libitum* intake (Chapter 4). As mentioned in Chapter 4, the model will likely predict the pig response less accurately when the nutrient intake is below 1.7 times the maintenance energy requirement.

In many pig growth models, a minimum fat to protein deposition ratio is suggested as an input parameter (Whittemore and Fawcet, 1976; Moughan et al., 1987; Pomar et al., 1991; De Lange, 1995). The concept of a minimum fat to protein deposition ratio has been defined as a constant ratio of fat deposition to protein deposition in the body when pigs are fed below their protein deposition capacity. This is assumed to be determined by genotype, and sex, of the pig (van der Peet-Schwering et al., 1999). By the model's nature, partitioning of nutrients between protein and fat deposition, and therefore the fat to protein deposition ratio, are influenced by nutrient intake. As shown in Chapter 4, increasing energy intake increased simulated body fatness. The effect of energy supply was different,

however, at different weight ranges (see Chapter 4). Therefore the composition of gain in model simulation depends on energy intake and body weight, in agreement with experimental results of de Greef (1992).

Due to the saturation kinetics used to model protein synthesis, the marginal efficiency of protein synthesis decreases as it nears to its maximum. As a consequence, protein deposition in muscle follows a maximum curve as a function of lysine intake. Deposition of other tissue proteins, such as organs, bone and hide, are dependent on muscle protein deposition and result in a maximal curve of total protein deposition as a function of lysine intake. This phenomenon can be described by a linear-plateau development, which is one of the principles of empirical models. The linear-plateau concept defines two phases of protein deposition, protein or lysine dependent and energy dependent phases. The mechanism of the limitation of protein deposition by energy supply is also included in the model. Protein synthesis depends on concentrations of both lysine and acetyl-CoA, in which the latter supplies the energy. Therefore, as shown in Chapter 4, the limitation of protein deposition occurs at insufficient lysine, and also at insufficient energy intake. However, the effect of lysine and acetyl-CoA concentration on protein synthesis cannot be separated in the model. Subsequently, as shown in Chapter 5, protein deposition differed when the energy source in the diet changed. In the simulation, lysine was not limiting for protein deposition, and dietary starch intake was replaced by isocaloric fat intake, on a DE basis. The higher acetyl-CoA generating potential of glucose, from dietary starch, resulted a slight increase in protein deposition when dietary starch was increased.

If neither lysine nor energy intake is limiting to protein synthesis, the genetically determined maximal protein deposition (PDmax) will occur. In many models, PDmax is considered constant between 20 and 110 kg live weight (van der Peet-Schwering et al., 1999). When neither lysine nor energy limit muscle protein synthesis in the model, the maximal velocity of protein synthesis determines protein deposition. Thus a maximal muscle protein deposition rate determines a maximal body protein deposition rate. As a result, PDmax increases with the maximal velocity of the muscle protein synthsis, cousing increased muscle protein mass (see Chapter 4). This is consistent with NRC (1998), which suggested a curvilinear response of PDmax on body weight, rather than a constant value. It can be concluded, that PDmax and also the minimum LD/PD approaches are very attractive because of simplicity, but our model approach is closer to biology.

A mechanistic model is very flexible by its nature, while an empirical model is valid only in a narrow range of circumstances. However, it is always possible to find an empirical model that gives a better fit to a specific set of data than a mechanistic model (France and Thronley, 1984). In the future, however, mechanistic models will be more useful because this approach allows for better quantification of the contribution of the different processes involved in energy metabolism (van Milgen, 2003).

One way prediction

The first generation of growth models were able to define the nutrient requirements of farm animals (Blaxter, 1962; ARC, 1965). These static models are still in use (e.g. NRC, 1998), and calculate the nutrient requirement of pigs at any live weight with certain housing conditions, such as temperature and space per pig. Another purpose of growth models is to predict performance in time. All dynamic models, whether empirical or mechanistic, predict traditional indicators of pig growth, to which end-users are accustomed. Tese include growth rate, feed conversion, days to slaughter, weight of carcass at slaughter, body protein and fat deposition, etc. From a practical aspect, a backward prediction might be required as well, to provide an estimation of the nutrient intake required to achieve a desired production level. However it should be noted that a given growth rate, and body composition at final body weight, can be realised throught different nutritional strategies. An example is shown in Table 1. Three different feeding strategies were simulated as: in strategy A pigs received a diet with an adequate nutrient content (15.1 MJ DE/kg feed, 169 g/kg ileal digestible protein, 11.2 g/kg ileal digestible lysine). The daily proportion increased weekly from 1 kg with 100 g increments. In strategy B, the nutrient content of the diet was as in feeding strategy A, but the daily proportion of the feed increased from 1 kg with weekly increments of 90 g/d until the 8^{th} week and with 120 g/d thereafter. In feeding strategy C, the feeding schedule was the same as in strategy A, but the lysine content of the diet was increased by 10% for 9 weeks, and than reduced by 10 %. These feeding strategies were designed to evaluate model responses to different allocations of a fixed amount of feed over time. Furthermore, they vary in quantity (strategy A vs. B) but also in quality (strategy A vs. C) of dietary nutrient intake. The initial body weight of the pigs was 25.3 kg and the simulation time was 109 days in all strategies. Due to the feeding schedule, cumulative feed intakes were the same in each feeding strategy. There was no difference in final live weight of pigs, nor in growth performance, anatomical or chemical composition. Feeding strategy B resulted in a higher growth rate during the first 8 weeks of the simulation, and a lower rate thereafter, when compared to feeding strategy A. Results suggest that a reduced nutrient consumption can be compensated later by extra feed intake. It is well known that pigs have a compensatory ability for growth during this period of life. Bikker (1994) found also that pigs fed at low energy level, between 20-45 kg, deposited as much lean and fat tissue between 45-85 kg as the pigs receiving high energy intake between 20-45 kg body weight. Strategy A and C gave a slightly different fat deposition, due to the two-phase lysine supply. The recommendation for dietary lysine during growth is that it can be reduced with time according to NRC (1998) in line with feeding schedule C. However, the growth performance (i.e. average daily gain, feed conversion, time taken to slaughter) is similar in both feeding strategies.

As a consequence, theoretically a certain body composition can be realised by different feeding strategies. Such feeding strategies may be evaluated further on practical application and financial consequences. By changing the nutrient intake frequently, the nutrient requirement can be met by optimal supply. It should be noted however, that the digestion tract of animals needs to adapt to each change

in dietary components, so in practice there is a limit to dietary changes because a high frequency may not have more benefit to growth performance.

Table 1
Simulated effects of different feeding strategies on growth and body composition

	Feeding strategy*		
	A	B	C
Initial body weight (kg)	25.3	25.3	25.3
Final body weight (kg)	113.6	113.8	113.8
Days to slaughter	109	109	109
Average daily gain (g/day)	809	810	810
Cumulative feed intake (kg)	188.5	187.39	188.5
Feed conversion ratio (kg/kg)	2.13	2.12	2.13
Body protein deposition (g/day)	145	146	146
Body fat deposition (g/day)	162	161	158
Muscle mass (kg)	62.5	62.6	62.4
Lean %	55.0	55.0	54.9
Organ mass (kg)	16.2	16.2	16.3
Hide mass (kg)	36.7	36.6	36.5
Bone mass (kg)	9.4	9.5	9.5
Protein in the muscle (kg)	9.49	9.52	9.56
Fat in the muscle (kg)	3.88	3.86	3.82
Fat to protein ratio in the muscle	0.409	0.405	0.400

* A - 1 kg feed/day in the 1st week, weekly increments of 100 g/day; B – 1 kg feed/day in the 1st week, weekly increments 90 g/day between 2nd and 8th weeks, and 120 g/day thereafter;
C – daily feed intake is as strategy A, the ileal digestible lysine intake increased 10 % until week 9, and reduced by 10% thereafter compared to ileal digestible lysine intake in strategy A.

Effect of different energy sources on animal and model responses
Further evaluation of the growth model from an energetic view

The effect of different energy sources at two energy levels on energetic efficiency was simulated, and the predictions were compared with observed data from the fattening study (Chapter 6). Energy retention (RE, kJ/d) was tested first by retained energy as protein (REp, kJ/d) and retained energy as fat (REf, kJ/d). The different parameters of energetic efficiency calculated from the fattening trial, and those taken from the model simulation, were also compared. In this way the results of the study were used for model validation. This evaluation included utilisation of DE intake for energy retention (RE/DE, kJ/kJ) and utilisation of protein free DE intake for energy retention as fat (REf/DEpf, kJ/kJ). The energetic values of 1 g protein, fermentable NSP, starch and fat were assumed to be 24.2, 17.0, 17.0 and 39.3 kJ, respectively, according to Schiemann et al. (1971) and CVB (1998). The experimental treatments and design of the trial are described in Chapter 6. For the purpose of comparison, only the data of gilts were selected. As an indicator of the

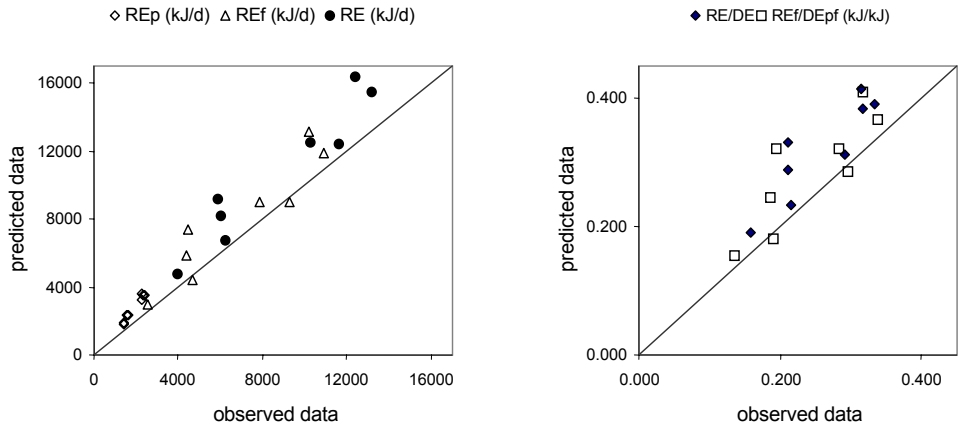
error of the predicted values relative to observed values, the mean square prediction error (MSPE) was calculated according to Bibby and Toutenburg (1977):

$$MSPE = \Sigma (Oi - Pi)^2 / n$$

in which Oi and Pi are the observed and predicted values; i = 1, …, n, and n = number of experimental observations. In data analysis, the relative MSPE (relMSPE), the errors attributed to overall bias (B%), the deviation of regression slope from one (R%), and the disturbance proportion (E%) were calculated as defined in Chapter 5.

The general agreement of predictions and observations of the six parameters are presented in Figure 1. The MSPE and the decomposition of MSPE are in Table 2. As shown by the figure, the model slightly over-predicts the energy retention in terms of total energy and energy retention as both protein and fat. The prediction error attributed to the overall bias with 48, 24 and 27 % of the MSPE for energy retention as protein, fat and total, respectively (Table 2). The remainder of the MSPE is the error asociated with deviation from regression and non-defined error resulting from data disturbance. The deviation from regression slope was nearly 10 % in all parameters. The utilisation of DE for energy retention, and the protein free DE for fat retention, were over-predicted by 28 and 26 %, respectively. The majority of MSPE was attributed to overall bias (76 and 49%), and 16 and 37% of MSPE were attributed to the non-defined error for RE/DE and REf/DEpf, respectively.

Figure 1
Observed and predicted data on energy metabolism of gilts in the fattening study (Chapter 6)



REp (kJ/d) retained energy as protein, REf (kJ/d) retained energy as fat, RE (kJ/d) retained total energy, RE/DE (kJ/kJ) utilisation of digestible energy intake for energy retention, REf/DEpf (kJ/kJ) utilisation of protein free digestible energy intake for energy retention as fat

Table 2
The relative MSPE (relMPSE, %) and the distribution of MSPE of retained energy and energy utilisation in the fattening trial within all treatments (see in Chapter 6)

	relMSPE	B%	R%	E%
REp (kJ/d)	48	89.4	10.1	0.5
REf (kJ/d)	24	48.6	10.5	40.9
RE (kJ/d)	27	74.8	8.5	16.7
RE/DE (kJ/kJ)	28	75.6	8.0	16.5
REf/DEpf (kJ/kJ)	26	48.7	14.5	36.8

B% - errors attributed to overall bias, R% - deviation of regression slope from one, E% disturbance proportion, REp - retained as protein, REf - retained energy as fat, RE - retained total energy, RE/DE - utilisation of digestible energy intake for energy retention, REf/DEpf - utilisation of protein free digestible energy intake for energy retention as fat

As discussed in Chapter 5, the prediction is considered successful when the MSPE is mainly attributed to overall bias and data disturbance, which comprised at least 85 % of the MSPE in the present simulation. Among the examined parameters, quantitative prediction of energy retention as protein was the least accurate. Pigs in the fattening trial were less efficient, and retained less protein and somewhat less fat compared to those predicted by the model. The difference in energetic efficiency may be due to the different genotypes and, probably, the different environmental conditions which were not considered by the model. As discussed in a previous chapters (Chapter 1 and 4) the protein deposition capacity of different genotypes is different. In our experiment, a high lean hybrid was used, but its protein deposition capacity was probably lower than that of the strain used in model calibration. Genotype can affect the absolute capacity for protein deposition, as well as its efficiency (Batterham, 1994). Therefore nutrient, and particularly protein, intake resulted in lower protein deposition in the trial as compared to that predicted.

It can be concluded from the discussion above, and from the model evaluation (Chapter 5), that the present growth model is valid in a wide range of nutrient intake. However, it is also emphasized that some additional factors need to be taken into account, such as genotype.

The marginal energetic efficiency of different dietary energy sources

In many studies (Mershmann et al., 1984; Bakker et al., 1996; de la Llata et al., 2001; Rijnen et al., 2003), increased intake of one energy source is balanced by decreasing the content of another energy source, and so maintaining the treatments as isocaloric, but in so doing complicating the interpretation of causal relationships. The design of the experiment presented in Chapter 6 is appropriate

for studying fat retention of different pure energy sources such as starch, VFAs and lipids. Briefly, isocaloric intake of fermentable NSP, digestible starch and digestible fat were added in addition to a control dietary supply at low and high feeding levels (2.0 and 3.0 times DE maintenance, respectively). The effect of these pure energy sources on energy retention is computed by subtracting the energy retentions in control from that in each added energy source treatments. Calculation of the energetic efficiency of fermentable NSP, digestible starch and digestible fat for fat retention is presented in Table 3. Protein intake was similar in all treatments, including control groups at low feeding level (see in Chapter 6), therefore a slight difference occurred between the additional total and protein free DE intakes. However, protein intake was unintentionally higher in the high control group, compared to the other treatments at the high feeding level (see in Chapter 6). The marginal RE/DE ratio was calculated as the extra retained energy (protein and fat) above the control group divided by the additional DE intake. This ratio expresses the efficiency of the energy source for energy retention. Due to differences in realised nutrient intake, a corrected efficiency was also calculated as the marginal efficiency of protein free DE for fat retention (marginal REf/DEpf).

Table 3
Intakes , retentions and marginal energetic efficiencies of conversion fermentable NSP (fNSP), digestible stach (dStarch) and digestible fat (dFat)

	Low feeding level			High feeding level		
	fNSP	dStarch	dFat	fNSP	dStarch	dFat
Added DE intake (kJ/d)	4965	4977	4611	4005	4080	4182
Added protein free DE intake (kJ/d)	5469	4958	4376	4400	4662	4436
Extra retained energy (kJ/d)	2120	1840	1866	1414	3062	2333
Extra retained fat (kJ/d)	2291	2022	1858	1327	2914	2155
Marginal efficiency of DE for energy retention (%)	49	42	46	32	70	54
Marginal efficiency of protein free DE for fat retention (%)	41	38	48	31	64	55

Experimental data on the marginal efficiency of DE for energy retention, and also that of protein free DE for fat retention, show similar values for fermentable NSP, digestible starch and digestible fat at the low feeding level (Table 3). Marginal efficiencies of starch and fat increased at the high feeding level, at the same time the value of fermentable NSP was lower. However, fat deposition from different energy sources did not differ between the low and high feeding levels (Chapter 6). It was also found in a previous study that efficiency of DE intake for energy retention increased with increasing energy supply when the pigs were fed by a corn-soybean diet (Halas and Babinszky, 2001). Data in Table 3 are much lower

than the generally reported efficiencies for fat retention of 90 % for dietary fat, 70-80 % for starch and 60-70 % for digestible NSP (ARC, 1981; Black, 1995; Noblet et al., 1994, Milgen et al., 2001). The reason might be that the experiment was completed in winter, when the mean ambient temperature was 17°C at the beginning of the trial. The critical temperature for pigs of 60-100 kg body weight has been reported to be 19-20°C and 14-16°C when fed at 2 and 3 times of maintenance requirements, respectively (Holmes and Close, 1977). Considering these values, the overall efficiency of energy retention at the low feeding level is low relative to other results. The efficiency of fermentable NSP was higher at the low feeding level *vs.* at the high feeding level. This seems logic when animals at the low control feeding level were sometimes below their lower critical temperature. In a cold environment, additional heat released during digestion and metabolism of fibre may be used to meet the animal's elevated thermoneutral needs, thus sparing other nutrients for tissue synthesis (Dierick et al., 1989). A similar low energetic efficiency for conversion of fermentable NSP (43%) for lipid gain was reported by Bakker et al. (1996) when feeding different fibre sources. They explained the low efficiency due to an increased maintenance energy requirement. In our study, the organ protein deposition also increased in pigs which were fed a high amount of high fermentable NSP (Chapter 6). Thus, as discussed earlier, feeding high NSP diets has a consequence on energy requirements for maintenance. The marginal efficiency of starch at the high feeding level is compareble with generally reported values of 75 % (Black, 1995; Milgen et al., 2001). In our data, the most surprising result was the case of fat addition, where the marginal efficiency of fat was only 55 %. An explanation is difficult, although the low efficiency may be due to effects of specific effect of fatty acids. As the source of fat was soya oil, which contains high amounts of linoleic acid (average of 400-500 g/kg) (Kinney, 1999), it will contain some conjugated linoleic acid (CLA). It has been shown repeatedly that CLA results in reduction of fat deposition (Ostrowska et al., 1999; Wiegand et al., 2001; 2002; Thiel-Cooper, 2001). Some brioler trial also confirmed that the dietary fatty acid profile, particularly the polyunsaturetad fatty acids intake, modifies abdominal fat deposition (Crespo and Esteve-Garcia, 2001).

In order to see the model response to pure energy sources, the experimental treatments were used in simulations. The input data were identical to the planned nutrient intakes in the trial, and so the protein intake was standardised during the simulation. Consequently, there was no difference between additional DE and additional protein free DE intakes among treatments (i.e. it was 4880 kJ/d). The values of marginal efficiencies (RE/DE and REf/DEpf) were computed similar to the fattening trial, and results are shown in Table 4. The order of magnitude of energetic efficiency of different energy sources, from model simulation, is generally consistent with values reported in the literature. Furthermore, data from the simulations suggest that the efficiency of any certain energy source is independent of feeding levels. Some differences occur between the RE/DE and REf/DEpf due to the different protein deposition rates. As discussed earlier (in the section *Approach of the model* and also in Chapter 5) energy source slightly modified the protein deposition. The marginal efficiency of fermentable NSP was consistent with the

mean of our observations at the low and high feeding levels (Table 3 and 4), and the REf/DEpf of starch corresponds to the theoretical value of 75 %. The value exceeding 100 % efficiency of fat for fat synthesis seems unrealistic, because it suggests that more fat was deposited than provided by the diet. It should be noted, however, that simulated protein deposition was somewhat lower in the case of the additional fat diet than with the control. Differences between the extra retained energy as fat, and additional DE intake, are 229 and 150 kJ/d, respectively. These are the *de novo* extra energy (fat) retained in the body from sources other than dietary fat. The difference between retained energy, and retained fat, is the retained protein which is 72 kJ/d in both cases. Protein, however was not deposited when pigs were fed with a high fat diet, and therefore it was available for fat synthesis. If no difference in protein deposition had occurred, 229 and 150 kJ energy would have been available for protein deposition of 72 kJ in low and high feeding levels, respectively. These values correspond to the net cost for protein deposition of 0.31 (72 kJ/229 kJ) and 0.48 (72 kJ/150 kJ), respectively. Moughan and Verstegen (1988) and Milgen et al. (2001) suggested 0.445 and 0.484 of net energy cost for protein deposition, respectively. By that correction the efficiency of dietary fat for fat retention is still 100 %. Noblet & Henry (1993) reported 99.2 % of ME/DE and 99.1 % conversion of NE/ME for animal fat, which resulted in 98 % efficiency of DE for net energy supposedly for fat retention. The theoretical value of efficiency of fat retention from digestible fat is also 98 % (Armstrong, 1969; Schiemann, 1972). In general, however, the efficiency of fat retention from dietary fat confirmed by experiments is 90 % (ARC, 1981; Black, 1995).

Table 4
Extra retained energy and fat and marginal efficiency of extra energy sources, fermentable NSP (fNSP), digestible stach (dStarch) and digestible fat (dFat) computed by model simulation

	Low feeding level			High feeding level		
	fNSP	dStarch	dFat	fNSP	dStarch	dFat
Extra retained energy (kJ/d)	1835	3912	5036	1817	3885	4958
Extra retained fat (kJ/d)	1690	3694	5109	1769	3812	5030
Marginal efficiency of DE for energy retention (%)	38	80	103	37	80	102
Marginal efficiency of protein free DE for fat retention (%)	35	76	105	36	78	103

Fat deposition and fat distribution and its consequences on the model development

It was concluded in Chapter 5 that the model is sensitive to the dietary energy source of the diet. The prediction showed that more protein, and less fat, was deposited with isocaloric DE intake when the fat intake was replaced by starch (Chapter 5). In the simulation, protein synthesis increased due to the higher acetyl-

CoA generating potential of starch, and the higher protein deposition left less energy for fat deposition with the high starch diet. It should be noted, however, that in our fattening trial protein deposition was limited by lysine intake and thus protein deposition was similar in pigs fed different energy sources. Therefore, due to the lysine limited protein deposition, less glucose was probably required to produce ATP, and more remained to produce fat. Depositions from dietary fat and starch were confirmed to be lower, by our comparative slaughter trial, than was expected.

Results of partitioning of body fat deposition show a constant distribution over the body irrespective of the energy source in our trial. As was expected, subcutaneous fat had priority for deposition, followed by lean fat and organ fat deposition. Partitioning of the observed daily fat deposition among hide, lean and organs is presented in Table 5 and Figure 2. It is apparent that distribution of daily body fat deposition follows an allometric pattern in each compartment, irrespective of dietary energy intake and energy source. Although the range of the body fat deposition rate differed for gilts and barrows, as confirmed in Chapter 6, the allometric function is similar for these two sexes. Result of the Student-test showed that the equations did not differ between barrows and gilts. Figure 2 presents curves of distribution of deposited fat in the body, found in the fattening study (Chapter 6) and also in pigs of the basic dataset used for model calibration (Chapter 4). It shows that pigs used in the model calibration deposited more fat in their hide, and apparently less fat in their muscle and organs. It should be noted, however, that lean fat deposition in our fattening study occured in the muscle and also a considerable amount in bone tissues.

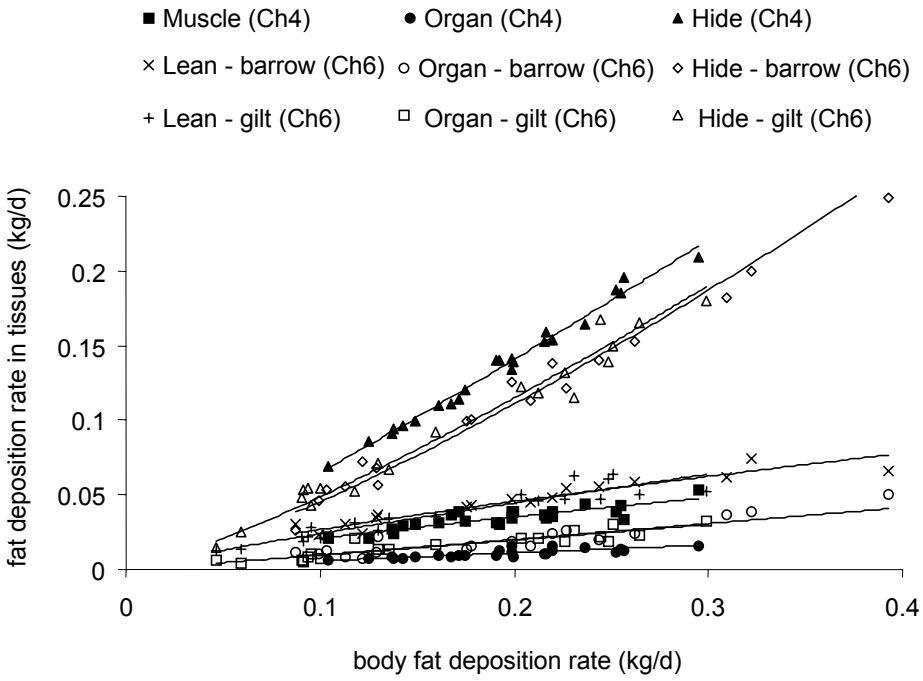
As a result of the fattening study (Chapter 6) and in agreement with our basic data set for the model calibration (Chapter 4), partitioning of daily fat deposition follows a well determined pattern irrespective of nutrient intake. The body fat deposition, however, is obviously determined by energy intake. Based on these results, it was confirmed that the representation of fat distribution in the model was correct. Furthermore, inclusion of sexes into the model would not require changes to the allometric equations of distribution of fat deposition in barrows. However, more data are required to study the effect of genotype on distribution of fat deposition.

Table 5
Allometric distribution of daily fat deposition (FD) in different tissues (y = a FD^b) in barrows (n = 20) and gilts (n = 19) (based on the fattening trial)

	Sex	a	s.e.	b	s.e.	Adj R^2	Fit std.error
Lean fat	Barrows	0,1483	0,0135	0,7294	0,0595	0,904	0,0046
	Gilts	0,1740	0,0254	0,8453	0,0902	0,869	0,0059
Organ fat	Barrows	0,1568	0,0269	1,2792	0,1264	0,881	0,0041
	Gilts	0,0987	0,0207	0,9914	0,1326	0,820	0,0036
Hide fat	Barrows	0,7578	0,0455	1,1888	0,0435	0,983	0,008
	Gilts	0,7519	0,0730	1,1702	0,0631	0,969	0,009

s.e. – standard error, adj R^2 – adjusted correlation coefficient, Fit std.error – fitted standard error of the equation

Figure 2
The daily partitioning of body fat deposition among body fractions in the basic data set for model development (Chapter 4) and in the fattening trial (Chapter 6)



Effect of health status and environmental conditions on model parameters

The effect of health status and environmental conditions are rarely included in nutrient partitioning models, including the present one. The pig model of Black et al. (1986) is an exception. Environmental circumstances involve factors that can result in stress to the animal (i.e., cold/heat stress, any mental stress). During infection or stress, animals may consume less feed and/or the digestibility of nutrients may be depressed. Moreover a lower health status results in a changed metabolism. Due to the reduced digestible nutrient intake, and less efficient nutrient conversion, the daily weight gain drops. It has been demonstrated that the energy requirements of a low-health-status animal are higher than those of a healthy animal (Baracos et al., 1987; Verstegen et al., 1991; van Dam et al., 1996). Deviation from the optimal temperature will increase the energy requirement of pigs (Verstegen et al., 1995). In a modelling context, an extra energy cost occurs in cases of infection or stress. It can be represented by increasing the maintenance energy requirement, or rather the oxidation of acetyl-CoA, as an extra energy drain. The effect of an increased acetyl-CoA oxidation is expected to modify the energy metabolism and result in less protein and fat deposition. According to Close (1996) upon stress conditions the protein and fat deposition and so the daily gain as depressed. Depression of body gain rate, protein and fat deposition rates, and also the amount of energy required to compensate for extra heat loss below thermoneutrality, have already been quantified (Verstegen et al., 1995). These data could be used to calibrate the model response to different ambient temperatures. However, the quantification of the extra energy needed during infection has not been completed in pigs. An increase in urinary N losses post infection has been reported, which may result from increased protein catabolism to provide energy and for a demand for amino acids used in immune responses (Reeds et al., 1994). An increased protein requirement for defence mechanisms could be represented in the model, such as an additional drain on the amino acid and lysine pools. However, the profile of such proteins has been reported to differ considerably from the body protein profile (Reeds et al., 1994 and 2000; Kidd, 2000; Borbolla et al., 2000) which cannot be accounted for by the present model construction.

Implication of mechanistic models

Mechanistic models are used in practice as well as in research. Production models are integrated into farm management programmes, and are used by nutritionists and feed producers (Chapter 1). The mechanistic pig growth model described (Chapter 4) and evaluated (Chapter 5) in this thesis successfully predicts chemical and anatomical body composition from nutrient intake. A novel feature of the model is that the amount of meat, and the fat to protein ratio in the meat can be estimated at slaughter. Hence it could be used for development of feeding strategies with inclusion of new production aspect, being the prediction of slaughter and meat quality. Prediction of meat quality could be included by considering more traits such as drip loss, glycogen content, estimation of pH and tenderness.

The advantages of mechanistic models are that they are more flexible than empirical ones. The capability of the present model to distinguish between dietary

nutrients, such as protein, fat, starch and NSP fractions, makes it a valuable tool for use in practice. By its nature - being developed on the basis of biological, physiological or biochemical principles - a mechanistic model can be used in research. It highlights areas in which knowledge is inadequate. During the evaluation of the present model by experimental results (Chapter 5), an interesting topic occured regarding the effect of energy source on energy metabolism and fat deposition. As discussed in Chapter 5 and 6, the results from the literature referring to the effect of feeding different energy sources are contradictory.

A further implication can be suggested since the model establishes a relationship between feed and pig production. Mechanistic growth models can also be integrated into feed evaluation systems. A new concept was developed by Boisen (2003) for feed evaluation based on properties of the feed itself. It is suggested to use (potential) physiological energy (PhE), instead of DE, ME or NE (Boisen and Verstegen, 2000; Boisen, 2003). Present feed evaluation systems are generally based on regression analysis of animal production results for estimating general energy coefficients for the different nutrient fractions (Boisen and Verstegen, 2000). Therefore the energy content of the diet does not completely determine production, since it also depends on animal factors and environmental effects (Whittemore, 1999). The ideology behind the physiological energy is consistent with the present model. Physiological energy corresponds to the production of a universal energy source at the cellular level (ATP) in animals (Boisen and Verstegen, 1998; Chudy, 2000). It is assumed that the absorbed energy is conserved in deposited nutrients or is used for actual production (in which the classical term “maintenance”, as well as urinary energy and extra energy costs for production are included). Energy used for actual production is separated into a basal component, which describes the basal (minimal) requirement according to live weight, sex and genotype estimated from specific production, and an extra component found under sub-optimal feed or sub-optimal environmental conditions (Boisen and Verstegen, 2000). The present growth model represents nutrient metabolism in accordance with principles of physiological energy. The key metabolite is acetyl-CoA, and non deposited nutrients are converted to acetyl-CoA and yield energy. The absorbed non-deposited energy used for maintenance is dependent on chemical composition and weight of the different compartments. As discussed in the Chapter 4, the maintenance energy requirement in the model was influenced indirectly by sex, and genotype, and also live weight. The term “extra energy above the basal energy used for actual production”, corresponds to the extra energy for growth in our model. It depends on feed composition and this flux can correspond to sub-optimal environmental conditions, as discussed above. A substantial part of energy expenditure is due to protein metabolism. The model represents the increased energy cost of protein metabolism upon surplus dietary protein supply, as it is required from the physiological energy system. Boisen (2000) suggested that it was necessary to complete a step-wise feed evaluation procedure, including computer modelling of the actual utilisation of the feed, in relation to actual feeding conditions.

Main conclusions from the thesis
From the present thesis, the following main conclusions can be drawn:

1. A mechanistic-dynamic model for growing and fattening gilts (20-105 kg) was developed. The model predicts the chemical body composition at slaughter, and also the protein and fat deposition, from nutrient intake (Chapter 4).

2. The model was evaluated with independent data sets. It was confirmed that model prediction was appropriate concerning distribution of protein and fat deposition, and the anatomical body composition from nutrient intakes. Therefore it can be used to estimate the amount of meat, and the fat to protein ratio, in the meat as a trait of meat quality (Chapter 4 and 5).

3. The model is sensitive to changes in both maintenance energy requirements and energy requirements for growth. Either of them - preferentially the latter – is an appropriate tool to include environmental effect on model response. The sensitivity of the model depends on nutrient supply, but the model seems to be responsive to change in protein metabolism, especially in muscle (Chapter 5 and General Discussion).

4. The accuracy of the model is high considering the predicted change in animal response on changed nutrient intake. The predicted chemical and anatomical body composition correspond to the observed experimental data (Chapter 5).

5. The present growth model is a valuable tool for development of feeding strategies. It considers new aspects of the effect of nutrient intakes on quantitative and qualitative production traits (Chapter 5 and General Discussion).

6. It was confirmed that nutrient intake determines body composition, but a pre-defined body composition can be realised by different nutritional strategies (General Discussion).

7. There is a possibility to integrate the present model into a new feed evaluation system called physiological energy. According to its principles, the present model supply the expectations of the physiological energy system, but further improvements have to be completed to allow different sexes and genotypes and the effect of environmental circumstances on the model response (General Discussion).

8. Under protein limiting conditions, extra energy intakes from fermentable NSP, digestible starch and digestible fat resulted in similar fat deposition (Chapter 6).

9. The extra fat deposition from isocaloric fermentable NSP, digestible starch and digestible fat are similar on both low and high levels of feed intake (Chapter 6).

10. The energy source has no influence on partitioning of body fat deposition between 48-106 kg body weight, when it originates from fermentable NSP, digestible fat and starch (Chapter 6).

11. The distribution of fat deposition rate can be accurately described by allometric functions that are irrespective of the dietary energy intake and energy source. Integration of sex into the model would not require changes to the equations of the distribution of fat deposition for barrows (General Discussion).

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New Scientific Results

The following new scientific results are obtained in the present thesis

1. A mechanistic-dynamic model for growing and fattening gilts (20-105 kg) has been developed, which predicts the body composition in terms of chemical and anatomical composition at slaughter and the protein and fat deposition in different body compartments from nutrient intake. Therefore it can be used for estimation of the amount of meat and the fat to protein ratio in the meat as a trait of meat quality. The accuracy of the model is high considering the predicted change in animal response on changed nutrient intake. (Chapter 4 and 5).

2. There is a possibility to integrate the present model to a new feed evaluation system called physiological energy. According to its principles, the present model supply the expectations of the physiological energy system, but further improvements has to be done to imply different sexes and genotypes and the effect of environmental circumstances on the model response (General Discussion).

3. Under protein limiting conditions, extra energy intakes from fermentable NSP, digestible starch and digestible fat resulted in similar fat deposition. Different dietary energy sources resulted in similar extra fat deposition at low and high feeding levels (Chapter 6).

4. The partitioning of body fat deposition between 48-106 kg body weight was not affected by the dietary energy source, when it originates from fermentable NSP, digestible fat and starch (Chapter 6).

5. The distribution of fat deposition rate can be accurately described by allometric functions that are irrespective of the dietary energy intake and energy source. Integration of sex into the model would not require changes to the equations of the distribution of fat deposition for barrows (General Discussion).

Summaries

Summary

Prediction of pig performance from data on nutrient intake and animal properties makes it easier to obtain a better productivity. It provides tools to arrive at desired outputs, or to calculate required inputs. Thus it enables production to be flexible, safe and less erratic. It is to be expected that the results will give a more profitable pig production. In practice, different types of models are used, mostly by feed producers, but also in farm management programmes. Each of these existing models was designed to meet a certain objective. Some of the models are able to establish the nutrient requirement of a pig, while others predict production, and some others are used to achieve a better understanding of the physiological processes. Literature on growth modelling showed a large variety of approaches. The classification of different types of models, and the benefits of using them, are presented in the literature overview of the thesis (Chapter 1). It was shown that the following principles should be considered in modelling: 1) description of the animal, 2) description of the diet, 3) distribution of nutrients within the body, and 4) quantification of the impact of dietary nutrients on animal performance. The general modelling process is the same in all types of models, as regards to data collection and analysis, model development, and testing. After a general overview of modelling in Chapter 1, a critical evaluation was provided on existing models in Chapter 2. Most pig growth simulation models consider protein and energy as separate entities. As acknowledged in more recently developed models, this ignores effects of differences in the source of the dietary energy. In addition to models predicting body chemical composition, prediction of anatomical body composition is of great interest, as it relates chemical body composition to meat quality. It was concluded that a comprehensive model that precisely predicts anatomical body composition in terms of muscle, bone, hide and organs in pigs did not yet exist. Some research groups have developed models to predict anatomical body composition, depending on feed intake and diet composition, however these models are almost exclusively based on empirical relationships. It was also concluded in Chapter 2 that a mechanistic approach should be used to modelling growth. The conceptual basis of a mechanistic model was developed in accordance with basic properties of protein and lipid metabolism. It was clear from the literature that protein metabolism had been studied more thoroughly than lipid metabolism. Body protein turnover differs among tissue types and it can be manipulated by nutrition. Dietary protein, amino acid and energy supply influence protein turnover of the tissues to differing extents, that result in different protein accretion rates in muscle, bone, organs and hide. It was shown that nutrition clearly influences fat deposition, but there is insufficient data to determine the rate of synthesis, and degradation, of lipids under different nutritional conditions, and not even in different fat stores. Since nutrients are almost exclusively absorbed in the hydrolyzed form, simulation of use of nutrients for growth should, at least to some extent, make use of biochemical pathways. Therefore, a biological approach to simulation of anatomical body composition is pretended as it follows nutrients from ingestion through intermediary metabolism to deposition as body fat and protein,

preferably in distinct tissues or tissue groups. Prediction of anatomical body composition therefore has to be based on deposition of the chemical entities.

Therefore the scope of the present thesis was 1) to develop a mechanistic-dynamic model for growing and fattening pigs which predicts anatomical and chemical body composition at slaughter; 2) to determine which model parameters are sensitive to changes in the model; 3) to determine the model accuracy by quantitative and qualitative prediction of the model tested with independent data; 4) to complete an experiment to define fat production potential of different energy sources at low and high feeding levels, and 5) to study the effect of different energy sources at two feeding levels on the distribution of fat deposition during the fattening period.

After defining the scope of the study, the general outline of the thesis is presented in Chapter 3. The aim of Chapter 3 is to introduce the work that has been completed. It clarifies the layout of the project and explains the data process of model development. This chapter also summarises the methodologies used in the various parts of the thesis, and presents the sequence of the chapters. However, detailed methodology is presented in each chapter. The developed model, introduced in Chapter 4, predicts growth rate as well as chemical and anatomical body compositions of gilts in the 20-105 kg live weight range, from nutrient intake. The model represents partitioning of nutrients from feed intake through intermediary metabolism to synthesis of body protein and body fat. State variables of the model are lysine, acetyl-CoA equivalents, glucose, VFA, and fatty acids as metabolite pools, as well as protein in muscle, hide, bone and viscera and body fat as body constituent pools. It is assumed that fluxes of metabolites follow saturation kinetics depending on metabolite concentrations. Anatomical body composition is predicted from chemical body composition and accretion. Partitioning of protein, fat, water and ash into muscle, organs, hide and bone fractions are described by allometric equations, driven by rates of muscle protein and body fat deposition. Muscle protein deposition rate was chosen as a driving force for the protein deposition rate in organs, bone and hide. Water and ash are linked to protein in the body and therefore protein deposition rates determine water and ash deposition rates in the different body parts. Allometric relationships between chemical constituents in different body parts have frequently been used in the literature. By that approach, it is assumed that at zero muscle protein deposition rate none of the other protein pools, and hence neither the water and ash deposition, would change. The allometric form of deposition rates also supplies a positive accretion in all body constituent pools, if muscle protein and body fat deposition are positive. Therefore, the growth model is valid only when the nutrient supply is sufficient to meet maintenance energy requirements.

The equations describing metabolite fluxes contained parameters which were either calculated from, or calibrated to, experimental data. The maximal velocity of a certain reaction (e.g. lysine oxidation, protein synthesis from lysine) was calculated from available data sets, but occasionally assumptions were necessary. Other model parameters, such as affinity and inhibitor constants and steepness parameters, were adjusted to obtain a good fit of the model outcome to the available experimental data. The basic data sets of model calibration, with regard

to predicting the muscle protein and body fat deposition rate from nutrient inputs were derivd from chemical composition of different body parts of individually housed gilts. Two experiments were used in the model calibration process, one with 95 growing pigs (20-45 kg) fed different ileal digestible lysine intakes at two feeding levels, and another with 100 growing and fattening pigs (20-105 kg), which received different energy intakes. Differential equations were solved numerically for a given set of initial conditions and parameter values. The integration interval used was 0.01 day, with the fourth-order fixed-step-length Runge-Kutta algorithm. The muscle protein and body fat deposition rates were considered in different weight ranges and for the whole fattening period. Results presented were not sensitive to small changes in initial conditions, or to smaller integration step sizes.

In the model evaluation in Chapter 5, the predicted response of the pigs to changes in model parameters, and to changes in nutrient intakes, are shown. As a result of the sensitivity analysis, the model was responsive to changes in a number of the model parameters examined. Changes in maintenance energy requirements, and the fractional degradation rate of muscle protein, have the largest impact on tissue deposition rates. The model is highly sensitive to changes in the maximal velocity and steepness parameter of lysine utilisation for muscle protein synthesis. Those parameters which directly affect the size of the lysine pool generally have a considerable influence on model predictions. For instance, when reducing the maximal velocity of protein synthesis by 20 %, the daily protein deposition, and average daily gain, decreased approximately 50 g/d and 210 g/d, respectively. Furthermore, it should be noted that results of this sensitivity analysis depend on nutrient intakes of the reference simulation. The model was relatively insensitive to changes of parameters regarding energy metabolism. It was concluded that the probable reason was that protein and/or lysine was more limiting within the simulated conditions. The model was further tested by independent published data. In general, the model satisfactorily predicted qualitative pig responses to a wide range of variations in nutrient supply. The predicted chemical and anatomical body composition, and also the distribution of protein and fat, were satisfactory in model testing. In most cases, errors in the predicted parameters attributed to the deviation of the regression slope were minor. It was assumed that the major factors contributing to the relatively large bias, observed for most predicted growth characteristics, was variation in pig performance among genotypes, or differences in environmental conditions. Based on the comparison of model simulations with independent data sets, it was recommended to improve the model regarding prediction of protein and fat deposition rates from nutrient intake of different energy sources.

It was found that literature data on the effect of different energy sources on fat deposition was limited. Apart from the importance of having accurate estimates for the effect of different feed intake to be used in the modelling approach, it is also important to have accurate estimates due to the substantial increase in use of by-product feeds and alternative feed ingredients in pig nutrition. In non-protein energy fraction of the diet, dietary lipids, starch and rapidly fermentable non-starch polysaccharides (NSP) are major energy sources. Lipids are absorbed as long-chain fatty acids and starch as glucose. Dietary NSP is fermented by the microbial

population mainly in the hind gut, and the short-chain fatty acids produced enter intermediary metabolism as an energy source. Glucose, long-chain fatty acids, and short-chain fatty acids will enter different metabolic pathways. Equal intakes of energy from glucose, long-chain fatty acids and short-chains fatty acids will therefore result in different fat deposition rates, and quite likely, result in different distributions of body fat over the tissues. There is, however, little quantitative data available on effects of energy source on partitioning of body lipids. Unlike the effect of energy source on ATP generating potential, these effects are of special interest at feeding levels above maintenance, and under protein limiting conditions. Furthermore, it is important to distinguish the effect of energy intake level from the effects of energy sources.

Therefore a fattening trial was completed to: 1) study the effect of extra energy intake from fermentable NSP, digestible starch and digestible fat used for fat deposition under protein limiting conditions; 2) determine the location of the fat deposition resulting from extra intake fermentable NSP, digestible starch and digestible fat; 3) determine if the extra fat deposition from different energy sources depends on the level of feed intake, and 4) quantify potential interactions between feed intake level and energy source on the location of extra body fat deposition.

All details concerning the experiment were presented in Chapter 6. Briefly, a total of 58 hybrid individually housed pigs were used in the trial with an initial body weight of 48±4 kg. The experimental treatments were arranged in a 3x2 factorial design, with three energy sources (i.e. fermentable NSP, digestible starch and digestible fat, all added to a control diet) at each of two energy levels. Within each energy level, daily nutrient intakes were the same with regard to digestible protein, ileal digestible lysine and other amino acids, vitamins and minerals. Treatments had an isocaloric proportion of daily nutrient intake derived from each energy source (0.2 MJ DE/kg$^{0.75}$), in addition to the nutrients from control diet. It was equal with 11 g/kg$^{0.75}$ highly fermentable NSP, 11 g/kg$^{0.75}$ starch or 5 g/kg$^{0.75}$ digestible fat daily. The DE intakes were 2.0 and 3.0 maintenance requirement in control groups. The additional energy from different sources increased DE intake up to 2.4 and 3.4 times maintenance requirement at low and high feeding levels, respectively. To obtain initial values, ten pigs were slaughtered at 48±4 kg and the treatment pigs at 106±3 kg body weight. Each body was dissected into four fractions being: 1) lean, 2) organs, 3) hide and subcutaneous fat, and 4) offal. Chemical body composition was determined in each body fraction. The differences between fat deposition of body parts in the control group, and the other treatments, resulted in the additional energy derived from each energy source. Due to the design of the experiment, the priority for fat deposition could be studied from the different energy sources, such as short chain fatty acids, glucose or lipid, at each feeding level. As a conclusion from the study, under protein limiting conditions, extra energy intake from fermentable NSP, digestible starch and digestible fat resulted in similar fat deposition. Preferential deposition of extra energy intake in various fat depots did not depend on the energy source. The extra fat deposition from fermentable NSP, digestible starch and digestible fat deposited as body fat was similar at both the low and high levels of feed intake.

In the General Discussion, some consequences of the mechanistic approach were discussed and then substantial attention was devoted to the practical aspects of the model. Although the present model predicts animal performance from nutrient intake, it would be useful if it could also predict the required amount of feed or nutrients to obtain a pre-defined level of production. It was demonstrated by an example why nutrient intake cannot be estimated from body composition. The later part of the General Discussion focuses on representation of different energy sources as an aspect of the model. The energetic efficiency of the different dietary energy sources is discussed, based on data from Chapter 6. The growth model is further evaluated by results of the fattening study. Moreover, data from the fattening study are analysed regarding the distribution of fat deposition. Consequences of the fattening study on the model is discussed regarding the effect of energy sources on energetic efficiency, and on location of fat deposition in the pig. The environmental conditions and the health status also determine the pig production, as it was presented in Chapter 1. The inclusion of health status and environmental conditions is possible by understanding the reasons for the differences in animal response to various environmental conditions. Finally, a new application of the present model is introduced in addition to development of feeding strategies identifying research priorities. The model may also be used to include a new feed evaluation system, called physiological energy.

The following main conclusions are drawn from the present thesis:

1. A mechanistic-dynamic model for growing and fattening gilts (20-105 kg) was developed. The model predicts the chemical body composition at slaughter, and also the protein and fat deposition, from nutrient intake (Chapter 4).

2. The model was evaluated with independent data sets. It was confirmed that model prediction was appropriate concerning distribution of protein and fat deposition, and the anatomical body composition from nutrient intakes. Therefore it can be used to estimate the amount of meat, and the fat to protein ratio, in the meat as a trait of meat quality (Chapter 4 and 5).

3. The model is sensitive to changes in both maintenance energy requirements and energy requirements for growth. Either of them - preferentially the latter – is an appropriate tool to include environmental effect on model response. The sensitivity of the model depends on nutrient supply, but the model seems to be responsive to change in protein metabolism, especially in muscle (Chapter 5 and General Discussion).

4. The accuracy of the model is high considering the predicted change in animal response on changed nutrient intake. The predicted chemical and anatomical body composition correspond to the observed experimental data (Chapter 5).

5. The present growth model is a valuable tool for development of feeding strategies. It considers new aspects of the effect of nutrient intakes on quantitative and qualitative production traits (Chapter 5 and General Discussion).

6. It was confirmed that nutrient intake determines body composition, but a pre-defined body composition can be realised by different nutritional strategies (General Discussion).

7. There is a possibility to integrate the present model into a new feed evaluation system called physiological energy. According to its principles, the present model supply the expectations of the physiological energy system, but further improvements have to be completed to allow different sexes and genotypes and the effect of environmental circumstances on the model response (General Discussion).

8. Under protein limiting conditions, extra energy intakes from fermentable NSP, digestible starch and digestible fat resulted in similar fat deposition (Chapter 6).

9. The extra fat deposition from isocaloric fermentable NSP, digestible starch and digestible fat are similar on both low and high levels of feed intake (Chapter 6).

10. The energy source has no influence on partitioning of body fat deposition between 48-106 kg body weight, when it originates from fermentable NSP, digestible fat and starch (Chapter 6).

11. The distribution of fat deposition rate can be accurately described by allometric functions that are irrespective of the dietary energy intake and energy source. Integration of sex into the model would not require changes to the equations of the distribution of fat deposition for barrows (General Discussion).

Samenvatting

Wanneer men uit gegevens over opname van nutriënten en over diereigenschappen van het varken de productie (groei, verhouding groei/voer en slachtkwaliteit) kan voorspellen zou dit het goed mogelijk maken om de productie te optimaliseren. Het maakt het mogelijk om een gewenste output te halen uit input of andersom om de vereiste input te berekenen uit de output. Dit maakt het dus mogelijk om een productie te behalen, die flexibel is en voorspelbaar. Men kan dan ook verwachten dat een goed groeimodel kan helpen om een optimale en winstgevende varkensproductie te bereiken. Groeimodellen worden tot nu toe veelal gebruikt door voedingsproducenten maar kunnen ook heel goed gebruikt worden in bedrijfsmanagementprogramma's. Er is een aanzienlijk verschil in de soort modellen, dat wordt toegepast in de praktijk. Elk van deze bestaande modellen is ontwikkeld met een speciaal doel. Sommige programma's zijn ontwikkeld om de nutriëntenbehoefte van het varken vast te stellen, anderen worden toegepast om de productie te voorspellen en weer andere worden gebruikt om een duidelijker beeld van fysiologische processen te krijgen. Groeimodellen die in de literatuur zijn gepubliceerd, laten een grote variatie zien in de benaderingswijze met betrekking tot de wijze van modellering. De classificatie van verschillende types van modellen en de voordelen van deze modellen worden in een literatuuroverzicht van dit proefschrift beschreven (Hoofdstuk 1). De volgende onderwerpen worden in de modellering behandeld: 1) karakterisering van het dier; 2) beschrijving van het rantsoen, 3) distributie van nutriënten en aanzet in het lichaam en 4) kwantificering van het effect van nutriënten uit het rantsoen op de dierprestatie. Het algemene modelleringsproces is in bijna alle verschillende modeltypen vergelijkbaar met betrekking tot dataverzameling en analyse, modelontwikkeling en testen. Na een algemene beschrijving van de modellering (Hoofdstuk 1) worden sommige bestaande modellen kritisch geëvalueerd (Hoofdstuk 2). De meeste groeisimulatiemodellen bij varkens behandelen eiwit en energie aanzet als twee verschillende processen. Zoals in meer recentere literatuur over modellen wordt vermeld, houdt deze benadering geen rekening met energieverschillen tussen verschillende rantsoenen. Het zou zeer interessant zijn om in navolging van de modellen, die de chemische lichaamssamenstelling voorspellen, ook de voorspelling van de lichaamssamenstelling en dan voornamelijk de relatie tussen de chemische lichaamsamenstelling en de slacht- en vleeskwaliteit te kunnen voorspellen .

De conclusie uit de literatuur is dat een veelomvattend model dat de lichaamssamenstelling voorspelt van de spieren, botten, huid en organen niet bestaat. Enkele onderzoekinstituten hebben modellen ontwikkeld die de lichaamssamenstelling voorspellen op basis van voeropname en rantsoensamenstelling. Deze modellen zijn slechts gebaseerd op empirische relaties. In hoofdstuk 2 wordt geconcludeerd dat een mechanistische benadering gebruikt zou moeten worden. De basis van het mechanistische model is logisch omdat dit gebaseerd is op basis van eigenschappen van het eiwit- en vetmetabolisme. Op basis van een literatuuronderzoek is het duidelijk dat eiwitmetabolisme op veel meer aspecten is bestudeerd dan vetmetabolisme. Eiwit

turnover is verschillend in verschillende lichaamsweefsels en kan worden gemanipuleerd door de voeding. Rantsoeneiwit, aminozuren en energievoorziening hebben invloed op de eiwit turnover in lichaamsweefsels. Dit resulteert in verschillende ratio's van eiwitgroei in respectievelijk spieren, botten, organen en de huid. Het is aangetoond dat voeding de vetdepositie duidelijk kan beïnvloeden, maar er zijn te weinig geschikte data met dat soort ratio's voor vetaanzet en vetafbraak in het lichaam wanneer verschillende rantsoenen worden gegeven. Dit geldt ook voor vetdepots. Omdat de meeste nutriënten na hydrolyse uit eiwitten, vetten en zetmeel als aminozuren, vetzuren en glucose worden geabsorbeerd, zou gebruik gemaakt moeten worden van biochemische methodes om het gebruik van deze nutriënten voor groei te omschrijven en kwantificeren. Door een biologische benadering kunnen de nutriënten gevolgd worden na de opname uit het voer en metabolisme via intermediaire stofwisseling tot de vastlegging in lichaamsvet en lichaamseiwit. Eigenlijk zou dit ook in uiteenlopende weefsels en weefselgroepen moeten gebeuren. De voorspelling van de lichaamssamenstelling moet daarom gebaseerd worden op basis van vastlegging in eiwit en water en vetten.

Nadat de achtergrond van deze studie is beschreven wordt de algemene opbouw van de studie gepresenteerd in hoofdstuk 3. De opbouw van het model en de data processing in het model worden uitgelegd. Dit hoofdstuk is ook een samenvatting van de verschillende methoden van de verschillende onderdelen van het proefschrift. Dit (hoofdstuk 3) wordt gevolgd door de omschrijving van het ontwikkelde model in hoofdstuk 4. Het voorspelt de groeisnelheid en de chemische- en anatomische lichaamssamenstelling van gelten van 20 tot 105 kg levend gewicht vanuit de nutriëntopname. Het model geeft weer hoe de nutriënten na de opname via intermediaire stofwisseling worden vastgelegd in het lichaamseiwit en lichaamsvet. Belangrijke variabelen van het model zijn lysine, acetyl-CoA-equivalenten, glucose, VFA, vetzuren als bron, en eiwit in spieren, huid, bot en organen en lichaamsvet als metabolisch component. Er wordt aangenomen dat het gebruik van metabolieten voor een bepaalde reactie verloopt via de verzadigingskinetiek en afhangt van de metabolietenconcentraties. De anatomische lichaamssamenstelling kan dan worden afgeleid uit de aanwezige hoeveelheden vet en eiwit en hun toename. De verdeling van eiwit, water, vet en eiwit wordt beschreven via allometrische formules .In deze formules komt de toename in lichaamseiwit en in vet voort uit spiereiwit en lichaamsvet. Toename in spiereiwit is gekozen als drijvende kracht voor eiwitgroei in organen, skelet en huid. Water en as worden in vaste verhouding tot lichaamseiwit vastgelegd. Daarom bepaalt eiwitgroei ook de groei van water en as in de verschillende lichaamsdelen in het model. De allometrische relatie tussen chemische componenten worden heel vaak in de literatuur gebruikt. Dit houdt ook in dat bij afwezigheid van spiereiwit groei er ook geen verandering in de eiwitpool plaats vindt en dus ook geen verandering in water en as. Deze allometrie betekent ook dat bij positieve groei in spiereiwit en in vet er ook ander lichaamseiwit en as wordt aangezet. Dat betekent ook dat het groeimodel alleen dan werkt als de nutriëntenvoorziening en ook energievoorziening hoger is dan het onderhoudsniveau van het dier. De vergelijkingen die de fluxen van metabolieten beschrijven bevatten parameters die voortkomen uit ijkingen en uit proefgegevens. De maximale snelheid van een

bepaalde chemische reactie (b.v. lysine oxidatie, eiwitsynthese uit lysine) werd berekend uit bekende data sets dus met praktisch geen aannames. De andere modelparameters zoals affiniteit en remmingconstante werden aangepast om het model goed te laten aansluiten bij de experimentele gegevens. Als uitgangspunt voor het voorspellen van spiereiwit aanzet en vetaanzet werd een basis dataset gebruikt van een proef met individueel gehuisveste gelten waarvan behalve de chemische samenstelling van de verschillende lichaamsdelen ook de nutriënten input bekend was. Gegevens uit twee proeven met dieren werden gebruikt voor het calibratieproces. Een data set was met 95 groeiende dieren van 20-45 kg. Zij kregen verschillende niveaus aan darmverteerbare lysine in het voer elk bij twee energieniveau´s. De differentiaalvergelijkingen werden opgelost (nummerical) voor een set van begin condities en de bijgehorende waarden voor de parameters. Het integratie-interval had een lengte van 0.01 dag met een 4^{e} orde "fixed step length" en Runga-Kutta algoritme. Spiereiwit- en vetaanzet snelheid werden bestudeerd over verschillende gewichtstrajecten en over het gehele mesttraject.De resultaten werden niet beinvloed door kleine veradereingen in uitgangswaarden en ook niet door kleinere intervallen. De evaluatie van het model vindt plaats in hoofdstuk 5. Hierin wordt aangegeven hoe het voorspelde varken reageert op veranderingen van modelparameters en ook op veranderingen in nutriëntopname. Uit de gevoeligheidsanalyse blijkt dat het model goed reageert op veranderingen van een aantal modelparameters. Veranderingen in onderhoudsbehoefte en ook een gedeeltelijke afbraak van spiereiwit hebben de meeste invloed op de relatieve weefselaanzet. Het model is zeer nauwkeurig indien veranderingen optreden in de maximale capaciteit waarin lysine gebruikt kan worden voor de spieropbouw. Deze parameters, die invloed uitoefenen op de omvang van het lysineaanbod, hebben in het algemeen een aanzienlijke invloed op de modelvoorspellingen. Een verlaging van de snelheid van de eiwitsynthese met bijvoorbeeld 20%, verlaagt de dagelijkse eiwitaanzet en de dagelijkse groei met respectievelijk ongeveer 50 g/d en 210 g/d. Verder is duidelijk dat de resultaten van deze gevoeligheidsanalyse afhangen van de nutriëntenopname in de desbetreffende simulatie. Het model reageerde nauwelijks op veranderingen van parameters die betrekking hebben op het energiemetabolisme. Geconcludeerd werd dat het beperkte eiwit- en/of lysineaanbod onder de gesimuleerde omstandigheden hiervan waarschijnlijk de reden zijn. Het model werd verder getest door datasets uit onafhankelijke publicaties. In het algemeen was de voorspelling van de gevolgen van een grote variatie in verstrekking van nutriënten door het model goed . De voorspelling van zowel de chemische- en anatomische lichaamssamenstelling als de verdeling van eiwit en vet tijdens het testen van het model was naar tevredenheid.In de meeste gevallen was de afwijking van 1 (error) van de ratio tussen de regressiecoefficient bepaald met het model en die uit de proefgegevens model erg klein. Er werd aangenomen dat de factoren die hoofdzakelijk bijdragen aan de bias in de voorspelling van de groei bestaan uit variatie in genotype en omgeving. Men kan stellen dat vergelijking van de modelsimulatie met onafhankelijke datasets betere resultaten zou kunnen opleveren wanneer de voorspelling van eiwit en vet met verschillende energievormen (zetmeel, vet en fermentatie) verbeterd kan worden. Uit de gevonden data van de literatuur werd duidelijk dat de invloed van

verschillende energiebronnen op de vetaanzet beperkt is. Naast het feit dat een goede schatting van de effecten in de modelbenadering zeer belangrijk is, is het ook nog om een andere reden belangrijk. De reden is een belangrijke toename van het gebruik van bijproducten en andere alternatieve ingrediënten in het varkensvoer. De niet-eiwitfractie van het rantsoen, de vetten, zetmeel en het makkelijke fermenteerbare niet-zetmeel polysacchariden (NSP) zijn belangrijke energiebronnen. Vetten worden geabsorbeerd als langketenige vetzuren en zetmeel wordt als glucose geabsorbeerd. Niet zetmeel polysachariden (NSP) worden gefermenteerd door micro-organismen. De hierdoor geproduceerde kortketenige vetzuren komen meteen beschikbaar voor de intermediaire stofwisseling en zijn op die manier een energiebron voor varkens. Glucose, langketenige vetzuren en kortketenige vetzuren volgen verschillende metabolische wegen. Een gelijke energieopname uit glucose, langketenige vetzuren en kortketenige vetzuren leidt tot verschillen in vetaanzet. Hierdoor is het ook aannemelijk dat dit leidt tot een andere verdeling van lichaamsvet over de weefsels. Hierover is echter slechts zeer weinig kwantitatieve informatie beschikbaar. Met name is niet bekend wat het effect van de energiebron is op de verdeling van lichaamsvet. Ondanks het potentieel van de energiebron op de ATP-voorziening, zijn deze effecten zeker interessant bij voedingsniveaus boven onderhoud en bij voorkeur ook onder eiwitlimiterende omstandigheden. Daarnaast is het belangrijk om een onderscheid te maken tussen het effect van de mate van energieopname en het effect van de energiebron.

Om de bovengenoemde redenen is een groeiproef uitgevoerd met de volgende doelen:
1) Bestudering van het effect van extra energieopname aan verteerbaar vet, zetmeel en fermenteerbare NSP dat gebruikt wordt voor vetaanzet onder eiwitlimiterende omstandigheden; 2) Vaststelling van de plaats waar vetaanzet plaatsvindt als gevolg van de extra opname van verteerbaar vet, zetmeel en fermenteerbare NSP; 3) Bestudering van de efficiëntie waarmee extra energie, afkomstig van verschillende energiebronnen gebruikt wordt, afhangt van de hoogte van de energie-opname; 4) Tenslotte de kwantificering van mogelijke interacties tussen voeropname en energiebron op de locatie waar extra vetaanzet in het lichaamsweefsel plaatsvindt.

Alle details die betrekking hebben op het experiment zijn weergegeven in hoofdstuk 6. In het kort: er werden 58 hybride individuele gehuisveste varkens gebruikt in het experiment Hun begin gewicht was 48±4 kg. De experimentele behandelingen werden gerangschikt volgens een 3x2 factorieel ontwerp, met drie verschillende energiebronnen (fermenteerbare NSP, verteerbaar zetmeel en verteerbaar vet, allen toegevoegd aan een controlerantsoen) op twee verschillende energieniveaus. Binnen elk energieniveau was de hoeveelheid verteerbaar eiwit, ileaal verteerbare lysine en andere aminozuren, vitamines en mineralen hetzelfde. De behandelingen werden als volgt uitgevoerd: De dieren in de verschillende behandelingen ontvingen een isocalorische hoeveelheid van ofwel fermenteerbare NSP, ofwel verteerbaar vet, ofwel zetmeel als dagelijkse extra nutriënten. Dit was 0.2 MJ verteerbare energie, DE per $kg^{0.75}$ boven dat in het controle dieet. Het was gelijk aan een extra gift van dagelijks ofwel 11 $g/kg^{0.75}$ hoog fermenteerbaar NSP,

ofwel 11 g/kg$^{0.75}$ zetmeel ofwel 5 g/kg$^{0.75}$ verteerbaar vet. De DE-opname was 2.0 en 3.0 maal de onderhoudsbehoefte in de controlegroepen. De toegevoegde energie afkomstig van de verschillende bronnen verhoogde de DE-opname tot 2,4 en 3,4 maal de onderhoudsbehoefte op het respectievelijk lage en hoge voedingsniveau. Om de initiële waardes te verkrijgen, werden 10 varkens geslacht op 48(ds±4)kg en de behandelde varkens op 106±3 kg lichaamsgewicht. Elk lichaam werd gedissecteerd in 4 verschillende delen namelijk 1) Mager vlees, 2) Organen, 3) Huid en subcutaan vet en 4) De restfractie (offal). De chemische lichaamssamenstelling werd bepaald volgens Kotarbinska (1971). De verschillen tussen de vetaanzet in verschillende lichaamsonderdelen in de controle groep en de andere behandelingen was het resultaat van de extra energie afkomstig van de verschillende energiebronnen. Met deze opzet kan de prioriteit voor vetaanzet bestudeerd worden. Deze kan worden afgeleid uit de resultaten na voeren van verschillende energiebronnen zoals kortketenige vetzuren, glucose en vet. Bovendien kan men dit nagaan op twee energieniveaus. Een conclusie die uit het experiment getrokken kon worden, was dat onder eiwitbeperkende omstandigheden extra energieopname afkomstig van fermenteerbare NSP, verteerbaar zetmeel en verteerbaar vet met dezelfde efficiëntie werd gebruikt om vet aan te zetten. Preferente aanzet van extra opgenomen energie in verschillende vetdepots hing dus niet af van de energiebron.

De efficiëntie waarmee de extra opgenomen energie (uit fermenteerbare NSP, verteerbaar zetmeel en verteerbaar vet) werd aangezet in lichaamsvet, was voor de beide voerniveaus gelijk. Bij hoge voeropname werd de extra vetaanzet als subcutaan vet relatief lager indien de energiebron fermenteerbaar NSP was. Dit was niet het geval bij de energiebronnen verteerbaar vet of zetmeel.

In de algemene discussie worden eerst een aantal consequenties van de mechanistische benadering bediscussieerd. Dit gebeurt voordat er substantiële aandacht aan de praktische onderdelen van het model wordt geschonken. Het huidige model voorspelt de dierprestaties vanuit nutriëntenopname. Het model zou echter nog beter toepasbaar zijn indien het kon voorspellen in welke mate nutriënten nodig zijn voor een bepaald gedefinieerd productieniveau. Met een voorbeeld is aangetoond dat de nutriëntenopname de lichaamssamenstelling niet kan voorspellen. Het huidige model was ontwikkeld voor gelten afkomstig van een commercieel ras (VOC, Nieuw-Dalland, Venray, Nederland), hoewel het model in de praktijk gebruikt zou kunnen worden voor verschillende seksen en genotypen. De omgevingsfactoren en de gezondheidsstatus bepalen ook de productie van de dieren zoals dat al in hoofdstuk 1 naar voren is gekomen. De aanpassing voor elk van deze factoren (sexe, genotype, gezondheidsstatus en omgevingsfactoren) kan worden verwezenlijkt indien de verschillen tussen de seksen en rassen en het reactiemechanismes van het varken begrepen worden onder veranderde gezondheids- en omgevingsfactoren. Men zou dat kunnen doen door b.v. hiervoor eerst de vergelijkingen voor eiwitmetabolisme aan genotype aan te passen. Dit zou kunnen door de maximumsnelheid van de reactie aan te passen Dit zou ook kunnen door de affiniteit/remming constante aan te passen. Ook kan de steilheidparameter voor eiwitsynthese of fractionele afbraak van de spiereiwit pool aangepast worden. De flux van acetyl-CoA oxidatie is een belangrijk hulpmiddel

om omgevingseffecten in te passen en om model respons te beïnvloeden. Tenslotte wordt in de algemene discussie ingegaan op de representatie van verschillende energiebronnen als een nieuw onderdeel in het model. De consequenties van de resultaten van het hiervoor besproken groei-experiment worden bediscussieerd. Hierin wordt het effect van de energiebron op energie-efficiëntie en de locatie van de vetaanzet betrokken. Uiteindelijk wordt een nieuwe toepassing van het huidige model geïntroduceerd. Naast ontwikkeling van voedingsstrategieën en verbetering van het inzicht in onderzoek kan het model mogelijk ook in nieuwe voedingsevaluatiesystemen ingepast worden. Dit zou wellicht "fysiologische energie" kunnen gaat heten.

De belangrijkste conclusies die in dit huidige proefschrift zijn getrokken zijn:

1. Een mechanistisch-dynamisch model is ontwikkeld dat toegepast kan worden op groeiende en afmetende gelten (20-105 kg). Het model voorspelt de chemische lichaamssamenstelling van slachtrijpe dieren en de eiwit- en vetaanzet als gevolg van de verschillen in voeropname (Hoofdstuk 4).

2. Het model is geevalueerd met onafhankelijke data sets Hieruit blijkt dat het geschikt is om de verdeling van de eiwit- en vetaanzet in het lichaam en de daaruit volgende chemische anatomische lichaamssamenstelling uit de voeropname te voorspellen. Het kan gebruikt worden om de vleesaanzet in te schatten. Ook kan de ratio eiwit/vet in het vlees als een maat van vleeskwaliteit geschat worden (Hoofdstuk 4 en 5).

3. Het model is gevoelig voor de energie die nodig is voor het onderhoud en ook voorenergie nodig voor de groei . Beide factoren, maar bij voorkeur energie voor de groei kan gebruikt worden om het effect van de omgeving in het model te verwerken. De gevoeligheid van het model hangt af van de nutriënt voorziening uit het rantsoen. En het is ook gevoelig voor veranderingen in het eiwitmetabolisme, met name die in de spieren (Hoofdstuk 5).

4. Het model voorspelt de groei van varkens vrij nauwkeurig; ook als er veranderingen in voeropname optreden. De voorspelde chemische en anatomische lichaamssamenstelling die correspondeert met de resultaten van de data sets uit de proeven. (Hoofdstuk 5).

5. Het huidige groeimodel is een waardevol middel dat gebruikt kan worden voor de ontwikkeling van nieuwe voerstrategieën. Het model houdt rekening met de effecten van de voeropname op de kwantitatieve en kwalitatieve productiekenmerken (Hoofdstuk 5 en de Algemene discussie).

6. In overeenstemming met andere literatuur blijkt dat de voeropname de lichaamssamenstelling bepaalt. Eenzelfde lichaamssamenstelling kan echtere bereikt worden met verschillende voerstrategieën (Algemene discussie).

7. Integratie van dit huidige model in een nieuw voerevaluatie systeem genaamd de fysiologische energie , behoort tot de mogelijkheden. Volgens de principes waarop model gebaseerd zou op grond van dit model fysiologische energie kunnen worden berekend. Echter, het model moet verder ontwikkeld worden om factoren als sekse, genotype en omgevingsfactoren ook kunnen opnemen in de voorspelling van de response (Algemene discussie).

8. Onder eiwitbeperkende omstandigheden kan met een extra energieopname afkomstig van isocalorische hoeveelhden van ofwel fermenteerbare NSP,ofwel zetmeel ofwel verteerbaar vet een gelijke extra vetaanzet worden bereikt (Hoofdstuk 6).

9 De efficiëntie waarmee extra vet wordt aangezet uit isocalorische hoeveelheden fermenteerbare NSP, verteerbaar zetmeel en verteerbaar vet in het lichaamsvet gelijk bij verschillend energieopnameniveaus (Hoofdstuk 6).

10 De energiebron (fermenteerbaar NSP, verteerbaar vet en zetmeel) heeft geen invloed op de verdeling van de extra vetaanzet in het lichaam tussen 48-106 kg lichaamsgewicht. (Hoofdstuk 6).

11 De verdeling van de vetaanzet kan nauwkeurig beschreven worden door allometrische functies, deze zijn onafhankelijk van energieopname en –bron Bij aanpassing van het model voor sexe zou het model niet veranderd hoeven te worden voor gecastreerde dieren (Algemene discussie).

Összefoglalás

A sertéseknek a táplálóanyagfelvételre valamint az állatok jellemzőire (kor, ivar, genotípus) alapozott teljesítménybecslése nagymértékben hozzájárul a hústermelés javításához és egy kívánatos eredmény eléréséhez, valamint a szükségleti értékek pontosabb meghatározásához is. További előnye a teljesítmény matematikai úton való becslésének, hogy használatával a termelés biztonságosabbá és tervezhetővé válik, csökkenthető a hústermelés kockázata és ennek következtében javítható a termelés gazdaságossága. A gyakorlatban különböző típusú modellek terjedtek el, melyeket elsősorban a takarmánygyártó cégek használnak, azonban megtalálhatók ezen modellek a farm-management programokban is. A meglévő modellek különböző céllal készültek: néhány ezek közül a sertések táplálóanyag igényének meghatározására szolgál, de léteznek olyan modellek is, melyek a termelést prognosztizálják vagy a fiziológiai folyamatok jobb megértését szolgálják. A modellek csopotosítását és használatuk előnyeit a disszertáció irodalmi áttekintésében foglaltam össze (1. fejezet). Az 1. fejezetből kitűnik, hogy egy új modell kifejlesztésekor a következőket kell figyelembe venni: 1) az állat jellemzői, 2) a takarmány jellemzői, 3) a táplálóanyagok eloszlása a szervezetben, valamint 4) a napi táplálóanyagfelvétel hatásának kvantifikációja az állat termelése alapján. A modellek kifejlesztésének folyamata általánosan az alábbiakban foglalható össze: adatgyűjtés és -értékelés, a modell felállítása és ellenőrzése. A disszertáció témájához tartozó irodalom áttekintése után (1. fejezet) egy kritikai értékelést adtam a meglévő modellekről (2. fejezet). Az irodalmi adatok értékelése alapján megállapítható, hogy az eddig kifejlesztett modelleknek több hiányosságuk van. A legtöbb sertés növekedési modell a fehérjét és az energiát egymástól független értékként kezeli. A fehérje mentes energiának (DE, ME, NE) modellbemenetként való használata figyelmen kívül hagyja a takarmány energiaforrásának hatását, valamint nem számol a fehérje által képviselt energia mennyiségével. Az eddigi sertésmodellek csupán a test kémiai összetételére adnak becslést, de a fehérje és zsírbeépülés eloszlását (anatómiai testösszetétel: izom, csont, szervek) nem tudják jelezni. Ennek fontossága azonban napjainkban egyre nyilvánvalóbb, mivel ez teszi lehetővé például a húsminőség becslését. Az irodalmi áttekintésből kiderül, hogy nincs olyan sertés modell, melynek az un. output adatai között szerepelne az anatómiai testösszetétel. Létezik ugyan néhány modell, mely a vágási kihozatalt és a színhús %-t is megbecsüli, azonban ezeket empírikus egyenletekre alapozták, azaz a táplálóanyagfelvétel és a testösszetétel közötti kapcsolatot használták a modell egyenleteként. Az effajta modellek hibája, hogy megváltozott feltételek esetén az eredmények igen pontatlanok. Ezért a 2. fejezet egyik következetése, hogy a modern sertésmodellekben az un. mechanisztikus megközelítést kell alkalmazni, ugyanis ezzel biztosítható a fehérje- és a zsíranyagcsere pontosabb leírása. Az irodalom tanulmányozása során az is világossá vált, hogy míg a fehérjemetabolizmust számos aspektusból vizsgálták, addig a zsírmetabolizmusra vonatkozó vizsgálatok száma kevés. Ismeretes, hogy a fehérjeturnover mértéke eltérő az egyes szövettípusokban, s hogy ez a tápálóanyag felvétel útján megváltoztatható. Irodalmi adatok bizonyítják, hogy a fehérje, az aminósav és az energiafelvétel különböző mértékben hat az egyes

szövetek fehérjemetabolizmusára, minek következtében a fehérjebeépülés különböző lesz a test egyes részeiben (pl. izomban, szervekben). Azt is tudjuk, hogy a takarmányozás befolyásolja a zsírbeépülés mértékét, azonban nincsenek egyértelmű adatok arra vonatkozólag, hogy miként változik a zsír szintézis és degradáció különböző táplálóanyagfelvétel esetén. Arról pedig csak nagyon kevés információnk van, hogy hogyan alakul a zsírturnover a különböző szervekben. Mivel a tápálóanyagok hidrolizált formában szívódnak fel, ezért a táplálóanyag hasznosítás szimulációjakor a biokémiai folyamatoknak legalább részbeni matematikai leírására szükséges. Ezért, az anatómiai testösszetétel változásának biológiai szimulációjakor javasoltam, hogy a különböző testrészek (szövetek vagy szövettípusok) fehérje- és zsírbeépülését a táplálóanyagfelvételből az intermedier anyagcsere főbb folyamatain keresztül határozzák meg. Így az anatómiai testösszetétel becslése a fő kémiai komponensek eloszlása alapján történhet (fehérje, zsír, víz, hamu).

A disszertáció célja tehát a következő:

1) egy dinamikus mechanisztikus modell felállítása, mely alkalmas a növendék és hízósertések kémiai és anatómiai testösszetételének (izom, csont, szervek, bőr) vágáskori becslésére;
2) a modell érzékenység-vizsgálatának elvégzése;
3) a modell kvantitatív és kvalitatív becslési pontosságának meghatározása független adathalmazzal;
4) egy modell hízlalási kísérlet beállítása, melyben a különböző energiaforrások (nem keményítő szerű poliszacharidok – NSP valamint keményítő és zsír) zsírbeépítő képességét vizsgáljuk egy alacsony és egy magas energiaellátási szinten;
5) annak vizsgálata, hogy a különböző energiaforrások (NSP, zsír, keményítő) két energiaellátási szinten, hogyan hatnak a hízósertések zsírbeépülésének lokális eloszlására.

A 3. fejezet a dolgozat általános felépítését valamint a fejezetek közötti logikai kapcsolatot mutatja be. Az egyes fejezetekben a kísérletek módszere részletes tárgyalásra került. A kialalított növekedési modell leírása a 4. fejezetben, míg a modell érvényességének vizsgálata az 5. fejezetben található. A munkám során sikerült egy olyan modellt kialakítani, amely alkalmas a gyarapodás valamint a kémiai és anatómiai összetétel becslésére a táplálóanyagfelvételből 20-105 kg közötti élősúlyú nőivarú sertések esetében. A modell a táplálóanyagok eloszlását mutatja be a takarmányfelvételtől az intermedier anyagcserén keresztül a fehérje és zsír szintézisig. A modellben a szervezet meghatározó metabolitjait poolokba soroltam, ezen poolok egymással kapcsolatban állnak, a deponálódó fehérje és zsír ezen metabolitpoolok “irányítása” alatt áll. A modell állapotváltozói: lizin, acetil-CoA, glükóz, rövid szénláncú zsírsavak, hosszú szénláncú zsírsavak, fehérje mennyisége az izomban, a szervekben, a csontokban és a bőrben valamint a testzsír mennyisége. A modell kialakítása során feltételeztem, hogy a metabolitok áramlásának kinetikája (egymásba való átalakulása) telítődési görbével írható le és hogy az áramlás mértéke a metabolit koncentrációtól függ. Az anatómiai testösszetételt a kémiai összetételből származtattam. A fehérje, a zsír, a víz és a hamu eloszlásának leírására minden testfrakcióban (izom, szervek, csont, bőr)

allometrikus egyenleteket használtam. Az egyenletek független változója a fehérjék esetében az izomfehérje, a zsír esetében pedig a testzsír volt. A víz és a hamu a fehérjéhez kötötten található a szervezetben, ezért a fehérjebeépülés meghatározza a víz és a hamu beépülését is. Allometrikus egyenleteket gyakran használnak az irodalomban is a különböző testfrakciók kémiai összetételének egymás közötti viszonyának leírására. Ezen összefüggést használva ugyanis, ha nincs izomfehérje gyarapodás, akkor sem más fehérjepool, sem pedig az ezekhez kapcsolódó víz és hamu mennyisége nem változik. Az anatómiai testösszetétel allometrikus alapegyenletei azt is biztosítják, hogy az egyes frakciók mindaddig gyarapodnak, míg az izomfehérje és a testzsír beépülés pozitív. Következésképpen a modell csak a létfenntartó szükséglet kielégítése feletti táplálóanyag-ellátás esetén működik.

A metabolitok áramlásának egyenletei olyan paramétereket tartalmaznak, melyeket vagy kísérleti adatokból számoltam, vagy kísérleti adatokhoz kalibráltam. A maximális reakciósebességet egy adott folyamatban (pl. lizin oxidáció, fehérje szintézis) meglévő kísérleti adatok alapján számoltam ki, de néhány esetben irodalmi adatokat is felhasználtam. További paramétereket, mint az affinitási és inhibítor konstanst vagy a meredekségi determinánst, úgy határoztam meg, hogy a modell outputja illeszkedjen a meglévő kísérleti adathalmazra. A modell kalibráció alapadatai olyan kísérletekből származtak, melyekben az egyedileg tartott emsék testének összetételét testrészenként határozták meg. Két kísérletsorozat adatait használtam fel a modell kifejlesztése során. Az egyikben 95 növendéksertést (20-45 kg) állítottak be, melyek különböző lizinfelvételben részesültek két energia szinten. A másik kísérletet 100 növendék és hízósertés (20-105 kg) bevonásával végezték, melyek különböző energiaellátásban részesültek. A modell differenciálegyenleteit adott kezdő feltételekkel és paraméterértékekkel oldottam meg. Az integrációs intervallum 0.01 nap volt, melyhez negyedik hatványú állandó lépéstávolságú Runge-Kutta algoritmust használtam. A kalibrációt az izomfehérje és a testzsírbeépülés mértéke alapján végeztem különböző testsúlykategóriákban valamint a teljes hízlalási időszakban. A model outputját minden egyes paraméter kombinációnál összevetettem az *in vivo* vizsgálatok eredményeivel. A modell szempontjából rendkívül fontos, hogy eleget tesz annak a kritériumnak, hogy az nem érzékeny a kezdeti körülmények (metabolit koncentrációk) kis mértékű változtatására, valamint kisebb integrációs intervallumra.

A model ellenőrzése során, a modell válaszát vizsgáltam minden egyes paraméter és a táplálóanyagfelvétel megváltoztatása esetén (5. fejezet). A érzékenység-vizsgálat eredménye azt mutatta, hogy a modell néhány paraméter változására különösen érzékeny. A létfenntartó energiaszükséglet és az izomfehérje frakcionális degradációs ráta változtatása nagymértékben megváltoztatta a gyarapodás mennyiségét és összetételét. A modell nagy érzékenységet mutatott a az izomfehérje szintézis maximális sebességi állandójának valamint az izomfehérje szintézis meredekségi determinánsának változtatásákor is. Az izomfehérje szintézis maximális sebességi állandójának 20%-kal való csökkentése például 50 g/nap illetve 210 g/nap csökkenést okozott a napi testfehérje beépítésben illetve a napi súlygyarapodásban. Meg kell továbbá azt is jegyezni, hogy a szenzitivitás-vizsgálat eredményei nagymértékben függnek a kiinduló állapottól (referencia

szimuláció). Azon paraméterek, melyek közvetlenül hatnak a lizin poolra, általában nagyobb hatással bírtak a szimuláció eredményére is. A model viszonylag érzéketlen volt azon paraméterekre, melyek az energiametabolizmus egyenleteiben szerepelnek. Ezen fejezet következtetése az volt, hogy valószínűleg a fehérje és/vagy lizin limitáló tényező volt a szimuláció során. A modell további ellentőrzését független adathalmazzal végeztem. Általánosan megállapítható, hogy a modell megfelelő kvalitatív becslést ad széles spektrumú táplálóanyagfelvétel esetén is. A becsült kémiai és anatómiai testösszetétel, valamint a fehérje és a zsír eloszlása a testben jó eredményeket mutatott. A legtöbb esetben a regresszióból adódó becslési hiba az összes hibának kevesebb, mint 10 %-a volt. Eredményeink alapján elmondható, hogy a mért és becsült értékek közötti különbségek fő oka főleg a genotípusokból adódó különbségekkel magyarázható, bizonyos esetekben azonban a környezeti hatások is felelősek lehetnek a modell és a kísérlet eredményének különbözőségéért. A modell ellenőrzése független adathalmazzal arra is felhívta a figyelmet, hogy a modell fejlesztésének egyik iránya lehet a különböző energiaforrások hatásának vizsgálata a fehérje és a zsírdepozícióra.

Az irodalom tanulmányozása során kiderült, hogy kevés megbízható adat áll rendelkezésünkre a különböző energiaforrásoknak a zsírbeépülésre gyakorolt hatásáról. Ez a kérdés nem csak a növekedési modellek szempontjából fontos, hanem azért is, mert az utóbbi időben a gyakorlati sertéstakarmányozásban a különböző melléktermékek és az un. alternatív takarmánykomponensek (pl: kukorica glutén, cukorrépa pellet) használata nagymértékben megnőtt. A takarmány nem fehérje eredetű energia tartalmának döntő hányadát a lipidek, a keményítő és a könnyen fermentálható NSP adják. Ismeretes, hogy a lipidek hosszú szénláncú zsírsavakként, a keményítő pedig glükózként szívódik fel. A takarmánnyal felvett NSP-t a - főként a vastagbélben élő - mikrobák fermentálják. Az így keletkező rövid szénláncú zsírsavak részt tudnak venni az intermedier metabolizmusban és energiát szolgáltatnak a sertés számára. A glükóz és a hosszú, valamint a rövid szénláncú zsírsavak különböző “anyagcsere utakon” keresztül hasznosulnak, ezért azonos mennyiségű DE felvétel glükózból és a hosszú, valamint a rövid szénláncú zsírsavakból különböző mennyiségű zsírbeépülést eredményez, s valószínű, hogy a zsíreloszlás lokális eloszlásában is tapasztalhatunk változást. Azonban az energiaforrások ATP potenciáljának meghatározásával ellentétben, a zsírbeépülés lokális eloszlásának vizsgálatát létfenntartó szükséglet feletti energiaellátás és a fehérjebeépítés limitálása mellett érdemes vizsgálni, mert a különböző energiaforrások transzformációs hatásfoka eltérő, attól függően hogy az energianyerésre vagy zsírbeépülésre fordítódik. Az is nagyon fontos továbbá, hogy el tudjunk különíteni egymástól az energiafelvétel és az energiaforrás hatását.

Ezért a beállított modellkísérletünk célja annak megállapítása volt, hogy 1) azonos mennyiségű extra energia felvétel (DE) fermentálható NSP-ből, keményítőből és zsírból (növényi olajból) milyen mértékű zsírbeépülést eredményez, ha a fehérje depozíció limitált, 2) meghatározzuk a zsírbeépülés lokális eloszlását 3) a különböző energiaforrásokból származó zsírbeépülés mértékét különböző energiafelvétel esetén, valamint 4) megvizsgáljuk, van-e

kölcsönhatás a napi energiaellátás és az energiaforrások között a zsírbeépülés lokális eloszlását illetően.

A kísérletbe összesen 58 egyedileg tartott és takarmányozott, vegyes ivarú hibrid sertést állítottunk be, melyek élősúlya a vizsgálatok indulásakor 48±4 kg volt (6. fejezet). A kísérleti kezelések 2x3-as faktoriális elrendezésűek voltak, három energiaforrással (fermentálható NSP, keményítő és zsír, mindegyik egy alap diétához adva) egy alacsony és egy magas energia ellátás mellett. Mindkét energiaellátásnál azonos volt a napi emészthető fehérje, ileálisan emészthető lizin és más aminósavak, valamint a vitaminok és ásványi anyagok mennyisége. Az alap diétát fogyasztó csoportok (kontroll) napi takarmányfelvétele a létfenntartó szükséglet 2.0 illetve 3.0-szorosát fedezte. A különböző energiaforrásokból napi 200 kJ/kg$^{0.75}$ DE-t biztosítottunk, mely megfelelt 11 g/kg$^{0.75}$ fermentálható NSP-nek, 11 g/kg$^{0.75}$ keményítőnek és 5 g/ kg$^{0.75}$ emészthető zsírnak. Így a hozzáadott energiaforrások esetében az állatok a létfenntartó energiaszükségletük 2.4 illetve 3.4-szorosát kapták. A kísérlet kezdetén 10 véletlenszerűen kiválasztott egyedet levágtunk (48±4 kg), melyek referenciacsoportként szerepeltek a teljestes analízishez. A fennmaradó 48 állatot a kísérlet végén, 106±3 kg testsúlyban vágtuk. A testeket 4 frakcióra bontottuk: 1) csontos hús, 2) szervek, 3) bőr és subcutan zsír (szalonna) és 4) az un. maradék frakció (fej, lávégek, farok). A teljestest-analízist Kotarbinska (1971) módszerével végeztük, a frakciókat autoklávoztuk, ledaráltuk és homogenizaltuk, majd meghatároztuk az egyes frakciók kémiai összetételét. Adtatainkból kiszámoltuk a kontroll csoportok és a többi kezelést fogyasztó állatok kémiai összetételében lévő különbségeket, melyet a hozzáadott energiaforrás okozott. A vizsgálataink eredményei alapján megállapítható, hogy ha a fehérjebeépülés limitált, az extra energiafelvétel fermentálható NSP-ből, keményítőből és zsírból azonos mértékű zsírdepozíciót eredményez és hogy a zsírbeépülés lokális eloszlása független a felvett energia forrásától. Adataink azt is mutatták, hogy a zsírbeépülés fermentálható NSP-ből, keményítőből és zsírból azonos mértékű függetlenül attól, hogy a sertések alacsony vagy magas energiaellétásban részesültek.

A fejezeteket összefogó általános megbeszélésben (*General Discussion*) először a modell mechanisztikus megközelítési módjának néhány konzekvenciáját, majd a növekedési modell gyakorlati aspektusait tárgyalom. A kialakított modell a táplálóanyagfelvétel alapján ad becslést a teljesítményre, azonban hasznos volna az is, ha meg tudnánk határozni egy termelési színvonal eléréséhez szükséges táplálóanyagfelvételt is. Ebben a fejezetben egy példán keresztül mutatom be, hogy miért nem lehet a táplálóanyagfelvételt egyértelműen meghatározni a teljesítményből. Példánkban 3 takarmányozási stratégiát hasonlítottam össze, melyek mindegyike azonos idő alatt azonos termelést eredményezett. A diszkusszió további része a különböző energiaforrások energetikai hatékonyságával foglalkozik a 6. fejezetben leírt kísérlet eredményeinek alapján. Megvizsgáltam továbbá a zsíreloszlás allometrikus egyenleteink helytállóságát is. A táplálóanyagfelvételen túl a környezeti hatások valamint az állat egészségi állapota is nagymértékben befolyásolja a termelést. A diszkusszió további része a takarmányozástól független determináns tényezőknek a modellbe való integrálásának lehetőségét, majd pedig a modellnek egy újabb felhasználási

területét tárgyalja. Több irodalmi utalás is van arra, hogy a jelenlegi energiaértékelési rendszerek hiányosságai miatt egy újabb, összetettebb szempontokra épülő redszer felállítására lenne szükség. Ezen új energiaértékelési rendszer kidolgozásán – melyet fiziológiai energiának neveznek – több munkacsoport is dolgozik. A modell alkalmas lehet arra, hogy ezen rendszer kialakításában és működtetésében részt vegyen, hiszen alapelvei megegyeznek a fiziológiai energiával szemben támasztott követelményekkel.

A disszertációból az alábbi főbb következtetések vonhatók le

1. Egy olyan dinamikus mechanisztikus modell került kialakításra, mely a táplálóanyagfelvétel alapján alkalmas a nőivarú növendék és hízósertések vágáskori kémiai és anatómiai testösszetételének, valamint a a fehérje és zsírbeépülésének becslésére.

2. Független adathalmazokkal végzett vizsgálatok alapján megállapítható, hogy a modell becslése megfelelő pontosságú mind a fehérje és zsírdepozíció megoszlásának, mind pedig az anatómiai testösszetétel tekintetében.

3. A modell kellően érzékeny a létfenntartó energia szükséglet valamint a növekedés extra energiaigényének változtatására. Elsősorban ez utóbbi, lehet alkalmas eszköz a sertéseknek a környezeti hatásokra adott válaszának modellezésére. A modell érzékenység-vizsgálatának eredménye nagyban függ a referenciaszimulációban használt táplálóanyagellátástól, de a fehérje-metabolizmusban történő változtatások - főként az izom esetén - mindenképpen nagy változást okoznak a szimuláció eredményében.

4. A modell pontossága megfelelő, mivel kísérleti eredményekkel összehasonlítva a legtöbb esetben a táplálóanyag-felvétel változása azonos mértékű változást eredményezett a szimulációkban, mind a kémiai mind pedig az anatómiai testösszetétel tekintetében.

5. A kialakított model jól alkalmazható a takarmányozási stratégiák kialakításában. További előnye ezen modellnek, hogy a termelékenység növelésének egy új aspektusát is figyelembe veszi, mivel a táplálóanyag-felvétel mind a kvantitatív, mind pedig a kvalitatív tényezőkre hatással van.

6. Tesztszimulációk alapján megállapítható, hogy egy adott táplálóanyagfelvétel egy adott test-összetételt eredményez, azonban ez a testösszetétel többféle takarmányozási stratégiával is elérhető.

7. Lehetőség nyílhat arra, hogy a kialakított növekedési modellt egy új energiaértékelési rendszerbe – az un. fiziológiai energia rendszerbe – integráljuk, mivel alapelvei megegyeznek a fiziológiai energiával szemben támasztott követelményeknek. Ez is indokolja, hogy szükséges a modell további fejlesztése a különböző genotípusok, ivarok és a környezeti hatások megjelenítéséhez.

8. Vizsgálataink eredményei azt mutatják, hogy ha a fehérjebeépülés limitált, akkor a fermentálható NSP-ből, keményítőből és zsírból származó extra energiafelvétel ugyanolyan mértékű zsírdepozíciót eredményez.

9. A vizsgált energiaforrásokból származó zsírbeépülés azonos mértékű volt függetlenül attól, hogy a sertések alacsony vagy magas energiaellátásban részesültek.

10. A 48-106 kg élősúly közötti sertések zsírbeépülésének lokális eloszlását nem befolyásolta a takarmány energiaforrása, ha az fermentálható NSP-ből, keményítőből vagy zsírból származott.

11. A testzsír eloszlását nagy pontossággal allometrikus egyenletekkel lehet leírni, mely egyenletek függetlenek az energiafelvételtől és a felvett energia forrásától. Az is megállapítható, hogy a modellben a különböző ivar (emse és ártány) esetében nem szükséges a zsíreloszlás allometrikus egyenleteit megváltoztatni.

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Curriculum Vitae

Veronika Halas was born on the 19th of May in 1975 in Dombóvár, in Hungary. She graduated from the secondary education in 1993. After completing her studies in the Pannon University of Agriculture in Kaposvár (Hungary) she received her degree majoring in Agricultural Engineering with Animal Husbandry Specialisation (MSc) in 1999. In the same year she entered the PhD education in University of Kaposvár Faculty of Animal Science (formerly the Pannon University of Agriculture). In 2000 she obtained her second degree of Animal Nutritionist from University of Kaposvár Faculty of Animal Science. During her PhD she studied 13 months in Wageningen University Animal Nutrition Group at different periods. Officially she was admitted in a sandwich PhD in March of 2002. She has been in study trips in Germany, Canada and USA.
Since September of 2002 she has been employed by University of Kaposvár Faculty of Animal Science Department of Animal Nutrition as an assistant lecturer.

Abstract

The objective of present thesis was to develop a growth model for pigs, with a new approach such as to predict anatomical body composition from nutrient intake. The developed growth model predicts the partitioning of nutrients from intake to body protein and body fat. It was confirmed by model testing that the predicted chemical and anatomical body composition and also the distribution of protein and fat were sufficient. The benefit of using models that these kinds of tools give opportunities to develop feeding strategies to optimise desired output. Knowing the response of the animals to nutrient intake is crucial and therefore a fattening trial was carried out to generate vital information that is yet missing. Therefore a further aim of the PhD thesis was to conduct an experiment to study the effect of fermentable NSP, digestible fat and starch on fat deposition and location of fat deposition at low and high feeding levels in fattening pigs. It was confirmed that under protein limiting conditions, extra energy intakes from fermentable NSP, digestible starch and digestible fat resulted in similar fat deposition. The extra fat deposition from isocaloric fermentable NSP, digestible starch and digestible fat were similar on both low and high levels of feed intake. The energy source has no influence on partitioning of body fat deposition between 48-106 kg body weight, when it originates from different energy sources.

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