PROTEIN AND LIPID ACCRETION IN
BODY COMPONENTS OF GROWING PIGS:
effects of body weight and nutrient intake

Promotor: **Dr. ir. M.W.A. Verstegen**
Buitengewoon hoogleraar op het vakgebied van de Veevoeding,
in het bijzonder de Voeding van de Eenmagigen

Co-promotor: **Dr. R.G. Campbell**
Research Scientist, Animal Research Institute, Werribee, Australia
Present position: Bunge Meat Industries, Corowa, Australia

PROTEIN AND LIPID ACCRETION IN BODY COMPONENTS OF GROWING PIGS:

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Paul Bikker

Proefschrift

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Bikker, P. 1994. Protein and lipid accretion in body components of growing pigs: effects of body weight and nutrient intake (Aanzet en verdeling van eiwit en vet bij groeiende varkens: effecten van lichaamsgewicht en nutriëntenopname).
In pig production, optimization of the conversion of animal feeding-stuffs into body components, especially lean meat, requires knowledge of the response relationships between nutrient intake and animal performance. In this study, the separate effects of protein and energy intake on rate and composition of body gain have been determined, in pigs with a high genetic capacity for lean tissue gain, from 20 to 45 kg. In addition, the response in body gain to energy intake has been investigated from 20 to 45 kg and from 45 to 85 kg, and the effects of body weight and previous nutrition on this response were examined. The relationship between protein intake and protein accretion was described well with a linear-plateau model, reflecting a protein and an energy dependent phase in protein deposition. The amino acid pattern of body protein was influenced by protein and energy intake. The optimal lysine/energy ratio was not significantly affected by the level of feed intake. Protein and lipid accretion responded linearly to energy intake, both from 20 to 45 kg and from 45 to 85 kg. The increase in protein gain per unit increase in energy intake, decreased with increasing body weight. The ratio between lipid and protein deposition, and consequently body lipid content, responded curvilinearly to energy intake and increased with increasing body weight. The percentage of lean tissue decreased curvilinearly with increasing energy intake. Pigs which were restricted in energy intake from 20 to 45 kg, gained faster from 45 to 85 kg. However, this gain was largely explained by an increase in digestive tract contents and in organ gain. The percentage lean tissue at 85 kg was higher in these previously restricted pigs, but this was the result of their higher lean percentage at 45 kg, and not of a compensatory gain from 45 to 85 kg. Consequences of these results for defining an optimal feeding strategy have been discussed.
Ph.D. thesis, Department of Animal Nutrition, Wageningen Agricultural University, Haagsteeg 4, 6708 PM Wageningen, The Netherlands.

This study was largely financed by Eurolysine S.A., Paris, France, and Orffa-Nederland Feed B.V., Giessen. Mengvoeder UT-Delfia B.V., Maarssen partly financed the investigations described in the Chapters 4 to 6. Their contributions are gratefully acknowledged.

7 Het vervangen van voedertabellen door simulatiemodellen kan bijdragen aan een doelmatiger dierlijke produktie.

8 Het fokken van dieren die niet op normale wijze hun volwassen gewicht kunnen bereiken miskent de intrinsieke waarde van het dier.

9 In veevoedingsonderzoek wordt teveel van multiple comparison tests gebruik gemaakt.

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11 Het voorstel tot afschaffen van de voetoverheveling is een ongewenste inmenging in het gezinsleven en getuigt van onderwaardering van het ouderschap.

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13 De ontkenning van de beschermwaardigheid van een kind vanaf de conceptie maakt de uterus van veilige moederschoot tot "the most dangerous place to be".

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Protein and lipid accretion in body components of growing pigs: effects of body weight and nutrient intake.
Wageningen, 13 september 1994.

STELLINGEN

1 Om de eiwitbenutting van varkens te kunnen verhogen moet meer rekening gehouden worden met de eiwit- en energieafhankelijke fasen in de eiwitaanzet.

Dit proefschrift

2 Zolang de intrinsiek bepaalde maximale dagelijkse eiwitaanzet niet is bereikt, wordt de optimale eiwit/energie verhouding in het voer weinig beïnvloed door het voerniveau.

Dit proefschrift

3 Een lineaire toename in zowel eiwit- als vetaanzet bij een toenemende energieopname impliceert meestal een kromlijnige stijging in de verhouding tussen vet- en eiwitaanzet.

Dit proefschrift

4 Een lineaire relatie tussen energieopname en energieretentie, bij een stijgende verhouding tussen vet- en eiwitaanzet, impliceert nog geen variatie in k_p of k_f.

Dit proefschrift

5 De verhouding tussen vet- en eiwitaanzet stijgt bij een toenemend diergewicht. Deze stijging is groter bij een hogere energiegift.

Dit proefschrift

6 De gunstigere lichaamssamenstelling (meer vlees, minder vet) bij slachten, zoals soms gevonden na een voerbeperking in het eerste deel van het mesttraject, is geen gevolg van compensatoire groei, maar een direct gevolg van de eerdere voerbeperking.

Dit proefschrift

VOORWOORD

Dit proefschrift is het resultaat van vier en een half jaar onderzoek bij de vakgroep Veevoeding van de Landbouwuniversiteit te Wageningen. Terecht staat deze vakgroep bekend om haar prettige werksfeer, goede collegiale verhoudingen en teamgeest. Hierdoor was het ook mogelijk piekperioden tijdens de experimenten op te vangen. Allereerst bedank ik dan ook ieder die tijdens deze periode aan de vakgroep verbonden was voor de plezierige tijd die ik hier als AIO heb gehad. Natuurlijk zijn er een aantal mensen die een bijzondere bijdrage aan dit onderzoek hebben geleverd. Ik wil mijn waardering en dank voor hun betrokkenheid uitspreken door hun inbreng kort te noemen.

Gedurende het eerste jaar van mijn onderzoek werd ik enthousiast begeleid door Bas Kemp. Na zijn vertrek werd de dagelijkse begeleiding overgenomen door mijn promotor, Martin Verstegen, terwijl Bas Kemp en Marlou Bosch het onderzoek wat meer op de achtergrond bleven volgen. De gezamenlijke discussies, jullie adviezen en jullie commentaar op onderzoekvoorstellen en concept artikelen waren een bron van motivatie en hebben in belangrijke mate bijgedragen aan dit onderzoek.

Het vertrek van mijn begeleider ging uiteraard niet ongemerkt voorbij. Martin, ik ben je veel dank verschuldigd voor de geweldige manier waarop je dit hebt opgevangen. Je deed dit op je eigen manier: niet altijd gestructureerd, wel altijd enthousiast. Je deur stond altijd open en een concept verhaal was meestal de volgende dag al van commentaar voorzien. Zonder je steun zou dit onderzoek niet tot een goed eind zijn gebracht.

Dear Roger, 18000 km is a great distance, but only one day per fax. Your scientific work was an important starting point. I highly appreciate your comments, criticism, and encouragements. I enjoyed the times we met each other somewhere in Europe, to present and discuss scientific results. Thanks for your support.

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De basis van dierexperimenteel onderzoek wordt gelegd in de stal. De medewerkers van proefaccomodatie "De Haar" vormden dan ook een belangrijke schakel in dit onderzoek. Met name de deskundige inbreng van André Jansen en Ries Verkerk mag hier niet onvermeld blijven. Bij de ileale verteringsproef, uitgevoerd op het ILOB, heeft met name Kasper Deuring een belangrijke rol gespeeld. Piet Roeleveld en Karel Siebers produceerden een deel van de proefvoeders. De inzet van Peter van der Togt en Tamme Zandstra bij de organisatie en uitvoering van tal van activiteiten, zoals het wegen, slachten en cutteren van de varkens, was in twee woorden geweldig en onmisbaar. Karel de Greef heeft mij in de destructieve kant van de slachtproeven ingewijd. Na het experimentele werk werd het personeel van het lab van onze vakgroep ingeschakeld voor de verwerking van een groot aantal monsters. Met name Marianne van 't End heeft zich kranig geweerd bij de analyse van ongeveer 500 diermonsters. Bedankt.

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Een groot deel van de engelse tekst van dit manuscript werd gecorrigeerd door Barbara Williams. Bedankt.

Tenslotte, een wetenschappelijke prestatie als het schrijven van een proefschrift komt slechts tot stand als de huiselijke omstandigheden hiervoor optimaal zijn. Zonder enige twijfel heeft mijn echtgenote dan ook een cruciale bijdrage aan het gereed komen van dit proefschrift geleverd. Tegelijk is zij ook degene die de nadelen van deze soms asociale bezigheid heeft ondervonden. Coby, bedankt voor je geduld en steun. Aan jou draag ik dit proefschrift op.

Bennekom, juli 1994.

Paul Bikker

Geprezen zij de naam van God van eeuwigheid tot eeuwigheid, want Hem behoort de wijsheid en de kracht. ... Hij verleent wijsheid aan wijzen en kennis aan hen die inzicht hebben.
(Daniël 2:21,22)

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GENERAL INTRODUCTION

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PIG PRODUCTION

The primary aim of pig production is to provide food for human consumption. Meat is an important component of the daily menu of most western people. In The Netherlands, the yearly meat consumption is about 80 kg per head, of which about 50% is pork (LEI-DLO and CBS, 1993). Worldwide pig meat production is about 40% of the total meat production (F.A.O., 1990).

Historically, pigs were kept in small populations and used to valorize waste- and by-products of human food production. During the last decades, the number of pigs per farm and the total production of slaughter pigs has been tremendously increased and the feed composition changed towards industrial by-products, e.g. grain by-products and soybean meal. In The Netherlands the number of slaughter pigs raised yearly increased from 5 million in 1960 to over 20 million in 1990. Simultaneously, the average farm size increased from 20 to 450 pigs per farm. Industrialization, the increase in world population, the increased consumption of (pig)meat per head, and the use of new rational production techniques are some of the important factors that stimulated and enabled these drastic changes in the nature of pig production. In addition, the geographical situation, the good structure of the pig husbandry and feed industry, and the professional skills of the people involved, facilitated a competitive pig industry in The Netherlands.

Despite the valuable contribution of animal husbandry to the human food package, concerns have risen with regard to the quality of the end-products, the welfare of the animals and the negative impact on the environment. There is an increasing awareness that an economical production of large quantities of meat, milk, and eggs does not guarantee a sustainable animal husbandry. It is more and more recognized that on a global scale attention should be paid to the position of the producers, the health and welfare of the animals, the quantity, quality, variety and price of the products, and the consequences for the environment. In pig production, some of these criteria (e.g. amount and quality of produced carcasses, the economic efficiency and environmental consequences) are substantially influenced by the biological efficiency of conversion of nutrients into edible body tissues. In our opinion, the optimal utilization of nutrients for the valorization of edible products of high quality is an important aspect of a more sustainable animal production. Therefore, in pig production, attention should be focused on an efficient utilization of nutrients for the production of lean meat of high quality, rather than on the increase and exploitation of the animals' capacity for body gain. This requires detailed knowledge of the response relationships between nutrient intake and animal performance in terms of nutrient retention and body composition. These relationships have been studied in this thesis for pigs of a modern genotype. The results, together with clearly defined goals and restrictions in pig production, will contribute to the design of biologically and economically efficient feeding strategies.

In order to define an optimum feeding strategy for growing pigs, different criteria can be used to determine optimum protein and energy allowances, e.g. maximum body or lean tissue gain, maximum efficiency of body or lean tissue gain, maximum body lean content, and minimum nitrogen excretion. The use of different criteria presumably leads to different optimum protein and energy allowances, depending for example on market conditions and legislation. Furthermore, results may depend on the aggregation level at which these optima are calculated, e.g. animal, farm or regional level. Therefore, concepts for the response relationships between nutrient intake and tissue deposition as determined in this study, presumably can best be applied when they are included in simulation models.

RESPONSES TO PROTEIN AND ENERGY INTAKE

During the last decade, the emphasis in animal production has switched from maximizing daily gain to improving the efficiency of gain and increasing the lean tissue growth or protein deposition. These changes were stimulated by the increasing consumers demand for lean meat. Secondly, the enhancement of daily protein gain at the same feed intake is associated with an increase in rate and efficiency of body gain and a decrease in carcass lipid content (Campbell, 1988). It has been long recognized that protein accretion can be determined by intrinsic factors, i.e. age or body weight, sex and genotype of the pig (e.g. Mølgaard, 1955; Thorbek, 1975) and extrinsic, mainly nutritional factors, i.e. energy intake, protein intake and protein quality (Miller and Payne, 1963). Contrasting views and experimental results exist concerning the relative importance of intrinsic and extrinsic factors.

Black and Griffiths (1977) and (Campbell et al., 1984, 1985b) reported a linear-plateau relationship between protein intake and protein accretion. These results gave rise to the development of the concept of protein- and energy-dependent phases in protein deposition. At a constant energy intake, protein accretion increases linearly with increasing protein intake until the required protein/energy ratio has been reached. A further increase in protein intake above the inflection point has no beneficial effect on protein gain. At a higher energy intake level, protein accretion responds to higher levels of daily protein intake (Figure 1a). Others described the relationship between protein intake and protein accretion at constant energy intake as linear (Zhang et al., 1984), curvilinear (ARC, 1981; Fuller and Garthwaite, 1993) and two-phase linear (Batterham et al., 1990). These different response relationships will be discussed in Chapter 2. The slope of the relationship between nitrogen intake and nitrogen accretion represents the marginal efficiency of protein utilization for protein gain. According to the ARC (1981), this marginal efficiency is determined by the digestibility and quality of the dietary protein, the amino acid availability, protein supply, and animal factors such as body weight and genotype.

For diets adequate in amino acids, the response to incremental amounts of feed reflect the effect of energy intake on protein deposition. The response of protein accretion to energy intake has been described as linear, curvilinear and linear-plateau. Campbell and Dunkin (1983) and Close et al. (1983), reported a linear increase in protein deposition with increasing energy intake for pigs below 40 kg live weight. Consequently, protein gain was restricted by energy intake. On the other hand, the linear-plateau response relationships (Figure 1b) reported by

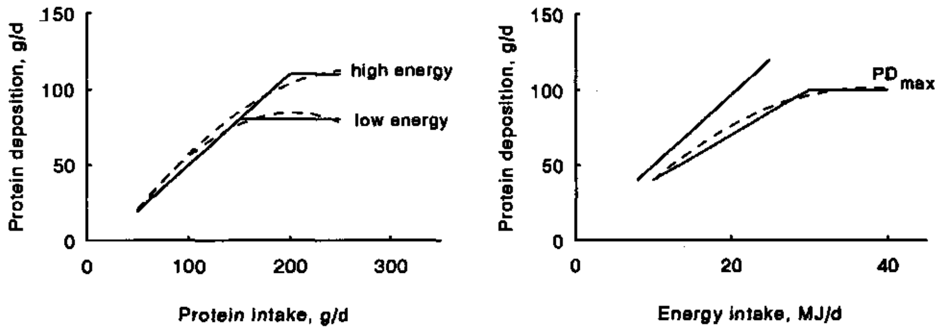

Figure 1. (a) Linear-plateau and curvilinear relationships between protein intake and protein deposition at two levels of energy intake. (b) Linear and linear-plateau relationships between energy intake and protein deposition.

Campbell et al. (1983, 1985a) and Dunkin et al. (1986) and the curvilinear response in Schneider et al. (1982) indicate that in these studies a maximum protein deposition was reached at high energy intake levels. This maximum was caused most likely not by a lack of certain nutrients since energy intake was varied by feeding incremental amounts of a protein adequate diet. These studies support the concept of Whittemore and Fawcett (1976) that pigs have a maximum capacity for protein deposition. It depends on the protein and energy allowances and the feed intake capacity of the pig, whether this PD_{max} is reached. The chance that PD_{max} can be reached is biggest for older and heavier pigs, castrates and pigs of a poor genotype for protein accretion. The slope of the response relationship between energy intake and protein accretion reflects the assignment of dietary energy to protein and lipid accretion. This slope can be affected by the sex and the genotype of the pig (Campbell and Taverner, 1988). Furthermore, Black and Griffiths (1975) reported a diminishing slope with increasing body weight in lambs. However, in pigs the effect of body weight on the relationship between energy intake and protein deposition is unclear. This effect was studied in this thesis.

Whittemore and Fawcett (1976) assumed that no protein was retained at energy equilibrium (maintenance energy intake). This assumption implies that with a linear increase in protein (PD) and lipid (LD) accretion with increasing energy intake, the ratio LD/PD remains constant until a plateau in protein deposition is reached. This assumption is included in several pig growth models (e.g. Moughan et al., 1987; Pomar et al., 1991; Werkgroep TMV, 1991). However, the results of Close et al. (1983) and Fuller et al. (1976) indicated a positive nitrogen balance at the expense of lipid loss at maintenance energy intake. As a result, LD/PD increased with increasing energy intake. This was confirmed by the results of Campbell et al. (1983), De Greef et al. (1994) and others. The response of LD/PD to energy intake was also examined in this study.

The relationship between energy intake and tissue deposition may depend on the body composition of the pig at the start of the treatment period (Kyriazakis et al., 1991). A period of protein or energy restriction can result in relatively fat or lean pigs, respectively, which may affect the accretion of protein and lipid in a later stage. Indeed several authors have reported an increased rate and efficiency of growth after a previous restriction. Most of these studies, however, do not allow an assessment of which body components gained faster during rehabilitation. In addition, it is often not clear at which stage differences, detected after slaughter, had developed. Results of De Greef et al. (1992) and Kyriazakis et al. (1991) indicate that protein accretion can be increased and lipid accretion decreased in pigs which were previously fed a low protein diet. It is not clear what effects an energy or feed restriction may have on subsequent protein or lipid accretion, nor whether a possible effect depends on the feed intake during rehabilitation. These effects have been studied in this project.

THIS THESIS

At an adequate protein intake, the partition of dietary energy between protein and lipid accretion is determined by the relationship between energy intake and protein deposition (Whittemore and Fawcett, 1976). Knowledge of this relationship is essential for the determination of the effect of an increase in energy intake on the rate of gain and body composition. In addition, this relationship determines the possible rate of protein accretion at each level of energy intake and thus the amino acid requirements at tissue level. Therefore, this relationship has a big influence on the amino acid requirements and the optimal amino acid to energy ratio in the diet. However, there is little information about the relationship between energy intake and protein and lipid accretion in pigs of improved genotype for lean tissue gain (Campbell and Taverner, 1988; Rao and McCracken, 1991). Furthermore, as mentioned above, no sound data have been published, which would allow the determination of the effects of body weight and previous nutrition on these relationships. In addition, hardly any information is available about the effect of energy intake on accretion rates of lean tissue and other body tissues, and about the distribution of protein and lipid among body components. Therefore in this study the effect of energy intake on protein and lipid accretion, LD/PD, growth of body components and distribution of protein and lipid among body components were determined in pigs from 20 to 45 kg and from 45 to 85 kg. It was also studied how a previous feed restriction affects the pigs' response to energy intake in the latter weight range.

Both for the definition of efficient feeding strategies and in order to determine the pigs' response to energy intake at adequate protein intake, the protein/energy requirements of genetically improved pigs need to be known. Although many requirement studies have been published, less information is available concerning the requirements of genetically improved animals. In addition the interaction between feeding level and optimal protein/energy ratio in improved pigs is not well known. Since data of ileal digestible amino acid contents of feedstuffs become increasingly available, requirements should also be based on amino acids absorbed in the small intestine. Since lysine is often the first limiting amino acid, we determined the optimal ileal digestible lysine/energy ratio for genetically improved gilts from 20 to 45 kg (Chapter 1). This chapter also shows the differences in estimated requirements owing to different response models.

We realize that the requirement figure determined was related to the sex and specific genotype of the pigs used in this trial. However, from the response relationship between energy intake and protein accretion, the dietary lysine or protein requirements can be estimated when the marginal efficiency of protein utilization for protein retention is known. This marginal efficiency is derived from the relationship between protein intake and protein deposition. As discussed above, this relationship cannot be predicted very well. In addition, in many studies in which protein utilization was estimated, the results were partly determined by the digestibility and amino acid pattern of the dietary protein. Therefore we determined the relationships between ileal digestible protein and lysine intake and protein and lysine retention (Chapter 2). We used a large number of lysine intake levels and a diet in which lysine was the first limiting amino acid. In order to determine the interactions with energy intake, we assessed these relationships at two energy intake levels. Within this study it was not possible to determine the effects of protein and energy intake separately in two weight ranges. This would have required more time and experimental capacity than was available. Since the amino acid requirements are most crucial in young pigs, we conducted this part of the study in growing pigs (20-45 kg) rather than in fattening pigs. We used the results to develop a simple factorial model to estimate the optimal lysine/energy ratio. In the model, a parameter was used which represented the marginal efficiency of amino acid utilization. This model allows simulations of the effects of energy intake, body weight, sex and genotype, on the optimal lysine/energy ratio for protein accretion, based on the effects of these factors on protein and lipid accretion.

OUTLINE OF THIS THESIS

The first three chapters relate to the first series of investigations (Experiment 1) of this project, in which the effects of energy and protein intake were varied independently. In Chapter 1 the optimal ratio between ileal digestible lysine and energy was determined for improved pigs at two levels of energy intake. In addition a simple factorial model was developed to calculate lysine/energy requirements. In Chapter 2 the interrelationships between energy and protein (lysine) intake on protein (lysine) deposition have been further analysed, and different models to describe this relationship have been compared. In Chapter 3 the effects of energy and protein intake on the amino acid composition of the carcass, the organs and the whole body are described. Possible consequences for losses and requirements of amino acids are discussed.

Chapter 4 to 6 relate to the second series of investigations (Experiment 2) to determine the responses of body gain and body composition to energy intake, in pigs of different body weight and with different nutritional histories. In Chapter 4 the response relationships of growth performance and body composition to energy intake were determined in growing pigs from 20 to 45 kg. We measured the rate and efficiency of body gain, the deposition of protein and lipid, and the accretion of organs, lean and fat tissue in relation to the level of energy intake. In Chapter 5 and 6 these response criteria were determined in pigs from 45 to 85 kg. These pigs had received either a low or a high energy level from 20 to 45 kg, to assess the effects of previous nutrition on subsequent performance and body composition. In Chapter 5, the results have been reported for body gain, body composition, and accretion of organs, lean and fat tissue. In Chapter 6 the responses of protein and lipid accretion in body components in relation to energy intake and previous nutrition are discussed.

In the general discussion the results of the six chapters of this thesis are combined. First the interrelationships between protein and energy intake, body weight and previous nutrition on rate and composition of gain are discussed. Thereafter, the consequences for the efficiency of protein and energy utilization are addressed. Finally, some important consequences of the results of this study for the pig husbandry are suggested.

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Paul Bikker
Protein and lipid accretion in body components of growing pigs: effects of body weight and nutrient intake.
Wageningen, 13 september 1994.

STELLINGEN

1 Om de eiwitbenutting van varkens te kunnen verhogen moet meer rekening gehouden worden met de eiwit- en energieafhankelijke fasen in de eiwitaanzet.

Dit proefschrift

2 Zolang de intrinsiek bepaalde maximale dagelijkse eiwitaanzet niet is bereikt, wordt de optimale eiwit/energie verhouding in het voer weinig beïnvloed door het voerniveau.

Dit proefschrift

3 Een lineaire toename in zowel eiwit- als vetaanzet bij een toenemende energieopname impliceert meestal een kromlijnige stijging in de verhouding tussen vet- en eiwitaanzet.

Dit proefschrift

4 Een lineaire relatie tussen energieopname en energieretentie, bij een stijgende verhouding tussen vet- en eiwitaanzet, impliceert nog geen variatie in k_p of k_f.

Dit proefschrift

5 De verhouding tussen vet- en eiwitaanzet stijgt bij een toenemend diergewicht. Deze stijging is groter bij een hogere energiegift.

Dit proefschrift

6 De gunstigere lichaamssamenstelling (meer vlees, minder vet) bij slachten, zoals soms gevonden na een voerbeperking in het eerste deel van het mesttraject, is geen gevolg van compensatoire groei, maar een direct gevolg van de eerdere voerbeperking.

Dit proefschrift

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Chapter 1

DIGESTIBLE LYSINE REQUIREMENT OF GILTS WITH HIGH GENETIC POTENTIAL FOR LEAN GAIN, IN RELATION TO THE LEVEL OF ENERGY INTAKE

P. Bikker, M.W.A. Verstegen, R.G. Campbell[1], and B. Kemp[2]

Department of Animal Nutrition, Wageningen Agricultural University,
Haagsteeg 4, 6708 PM Wageningen, The Netherlands

[1] Bunge Meat Industries, Corowa, Australia

[2] Department of Animal Husbandry, Wageningen Agricultural University

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ABSTRACT

One hundred gilts were used to determine the optimal ratio between ileal digestible lysine and digestible energy in the diet, and the effect of energy intake level on this optimal ratio for gilts with high genetic potential for lean gain, between 20 and 45 kg BW. In a 2 x 15 factorial arrangement the pigs were fed either 2.5 or 3.0 times the energy requirements for maintenance. Average daily lysine intake in the treatment period ranged from 6.4 to 18.2 g/d in 15 graduated steps. The first 12 increments were .74 g/d, and the last two increments were 1.48 g/d. Average daily gain (ADG), gain/feed, and protein deposition increased curvilinearly ($P < .01$) with increasing lysine intake. The ADG was maximized at 606 and 768 g/d, gain/feed was maximized at .564 and .604 kg/kg, and protein deposition was maximized at 108 and 128 g/d at the low- and high-energy levels, respectively. The ratio between lipid and protein deposition decreased curvilinearly with increasing lysine intake ($P < .01$) and reached a minimum of .53 and .75 at the low- and high-energy levels, respectively. The lysine requirements (ileal digestible lysine/DE, grams/megaJoule), determined with a linear-plateau model, were .57 for ADG and gain/feed, and .62 for protein deposition. These estimated requirements were similar for the two energy levels. Consequently, approximately .60 g of ileal digestible lysine/MJ of DE was required to optimize performance in gilts with high genetic potential for lean gain, irrespective of the feed intake level. In addition, a factorial model to estimate the lysine/energy requirements is proposed.

Key words: Pigs, Energy Intake, Lysine, Protein Retention, Nutrient Requirements

INTRODUCTION

For optimum protein utilization, pigs need a diet with an appropriate amino acid/energy ratio. This optimum ratio is likely to depend on the genetic capacity of the animals for protein deposition (Campbell et al., 1985). Due to improvements in genetic potential for lean tissue growth, protein requirements are also expected to increase. However, information concerning the protein deposition capacity or amino acid requirements of improved animals is scarce. Furthermore, lysine requirements have been determined mostly at one energy intake level or with ad libitum intake, whereby intakes of energy at different dietary lysine contents were different. Energy intake level, however, can affect the ratio between lipid and protein deposition (LD/PD ratio) (De Greef et al., 1992). Therefore, the optimum dietary protein/energy ratio may be affected by energy intake level as well, as reported by Campbell et al. (1984) for male pigs from 45 to 90 kg.

The aims of the present study were to determine the optimum ileal digestible lysine/energy ratio for pigs of 20 to 45 kg BW with high capacity for lean tissue growth, and to investigate the effect of energy intake level on the lipid/protein deposition ratio and lysine/energy requirements. In addition, a factorial model to estimate the required dietary lysine/energy ratio for maximum protein deposition is proposed.

EXPERIMENTAL PROCEDURES

Animals and Design

One hundred female pigs of a commercial strain (VOC Nieuw Dalland) were used in the experiment. At the start of the experiment the animals were 65 days old and BW was 20 kg. To determine initial body composition, five pigs were allocated to an initial slaughter group and slaughtered at 20 kg BW. A second group of five pigs was given ad libitum access to feed in order to determine the maximum protein deposition of these pigs. Ninety pigs were allocated equally among 30 treatments in a 2 x 15 factorial arrangement. The respective factors were level of feeding, equivalent to 2.5 and 3.0 times energy requirements for maintenance, and protein intake, ranging from an average of 127 to 350 g/d during the treatment period in 15 graduated steps. Intake of lysine, being the first-limiting amino acid, ranged concurrently from an average of 6.4 to 18.2 g/d in the treatment period. The first 12 increments in lysine intake were .74 g/d and the last two increments were 1.48 g/d. The 90 pigs were grouped in three blocks on the basis of initial BW, and the 30 dietary treatments were randomly allocated among the pigs in each block.

Diets and Feeding

At each of the 15 levels of lysine (protein) intake, the animals were offered feed at one of two energy intake levels, in order to separate the effects of energy and lysine intake. The animals on the low energy intake level were fed diets with a calculated lysine content ranging from .44 to 1.24 g of lysine/MJ of DE. The first 12 increments were .05 g/MJ, the last two increments were .1 g/MJ. The animals on the high energy intake level received an extra amount of protein-free energy

(Diet 2, Table 1), equivalent to .5 times energy for maintenance. Consequently, the lysine/energy ratios on the high-energy intake were 83% of those for animals on the low-energy intake level and ranged from .37 to 1.03 g/MJ of DE. The pigs offered feed on an ad libitum basis received a diet with 15.3 MJ of DE/kg and .79 g of lysine/MJ of DE. The lysine/energy ratio for each treatment was kept constant throughout the experiment.

To ensure a constant amino acid balance, a protein-rich (Diet 1), and a protein-free diet (Diet 2) were formulated (Table 1). These were fed in different ratios to each of the treatment groups. Consequently, protein and lysine intake varied concurrently. To determine the lysine requirements, lysine had to be the first-limiting amino acid. A mixture of barley and protein-rich feedstuffs was chosen to compose Diet 1 according to this demand. Apart from lysine, the contents (g/16 g of N) of the essential amino acids in Diet 1 were at or above those in ideal protein (Wang and Fuller, 1990). The lysine content (g/16 g of N) of Diet 1 was 80% of that in ideal protein, to ensure that lysine was the first-limiting amino acid. Diet 1 was formulated to contain 1.24 g of lysine/MJ of DE. Diet 2 was formulated to ensure a constant intake of other nutrients (e.g., Na, K, Ca, P, Mg, Cl, and fiber) independent of the ratio between the two diets in the daily ration. Ileal digestibility of crude protein and amino acids was determined in a digestibility experiment involving five entire male pigs averaging 28.6 ± .2 kg BW fitted with Post-Valve T-Caecum (PVTC) cannulas (Van Leeuwen et al., 1991).

The two feeding levels were chosen to provide average DE intakes between 20 and 45 kg BW of 15.8 and 18.8 MJ/d, which was equivalent to 2.5 and 3.0 times energy for maintenance respectively. The pigs' daily feed allowances increased with increasing BW according to a scale based on metabolic BW, with maintenance requirements taken as .475 MJ of DE/kg $BW^{.75}$ (ARC, 1981). The DE concentrations of Diets 1 and 2 were determined using 12 intact male pigs in metabolism cages at two different body weights, averaging 23.2 ± .5 and 41.5 ± .9 kg. Because of a difference in DE content of Diets 1 and 2 (Table 1), the DE concentration of the daily ration increased slightly with an increasing proportion of Diet 2 in the ration. Therefore gain/feed (kilograms/kilogram) was standardized on the basis of a diet with 15 MJ of DE/kg by calculating gain/15 MJ of DE intake for each individual animal.

Diets were analysed for dry matter, nitrogen, and ash according to ISO (International Organization for Standardization) 6496 (1983), ISO 5983 (1979), and

ISO 5984 (1978), respectively. Amino acids were determined at the laboratories of Eurolysine (Paris, France) with an amino acid analyzer (Beckman 6300, Palo Alto, CA) after hydrolysis with 6 N hydrochloric acid under reflux at 110°C for 23 h. The sulphur amino acids were analyzed after oxidation with performic acid and subsequent hydrolysis with HCl as previously described (Mason et al., 1980). Tryptophan was determined by HPLC after alkaline hydrolysis using barium hydroxide at 125°C for 16 h (Landry et al., 1988).

Table 1. Composition of the experimental diets as fed

Ingredient, g/kg	Diet 1	Diet 2	Nutrient, g/kg[b]	Diet 1	Diet 2
Barley	345	-	Dry matter	897.3	890.7
Maize starch	-	726.5	Crude protein[c]	350.4	6.2
Soybean meal (45% CP)	200	-	Ash	55.9	56.0
Maize gluten meal (63.7% CP)	100	-	Digestible energy, MJ	16.00	13.97
Potato protein	50	-	Lysine[c]	18.5	.09
Danish herring meal	100	-			
Skimmed milk powder	130	-			
Dextrose	-	50			
Animal fat	8.0	18.0			
Soybean oil	12.0	27.0			
Cane molasses	20.7	50.0			
Cellulose	5.0	45.0			
$CaCO_3$	5.0	8.5			
Monocalcium phosphate	-	26.0			
NaCl	1.0	6.3			
MgO	-	2.8			
$KHCO_3$	-	20.0			
DL-methionine	1.4	-			
L-threonine	1.2	-			
L-tryptophan	.7	-			
Fumaric acid	10.0	10.0			
Premix[a]	10.0	10.0			

[a] Contributed the following per kilogram of diet: retinol, 9,000 IU; cholecalciferol, 1,800 IU; α-tocopherol, 40 mg; menadione dimethyl-pyrimidinol bisulphite, 3 mg; thiamin, 2 mg; riboflavin, 5 mg; niacin, 30 mg; d-pantothenic acid, 12 mg; vitamin B_6, 3 mg; vitamin B_{12}, 40 μg; ascorbic acid, 50 mg; choline, 1,000 mg; d-(+)biotin, .10 mg; folic acid, 1.0 mg; copper, 168 mg; cobalt, .53 mg; iodine, .38 mg; iron, 80 mg; manganese, 44 mg; selenium, .060 mg; zinc, 109 mg. This mixture also supplied 40 mg of tylosin per kilogram of diet.

[b] Analysed content.

[c] Determined ileal digestibility coefficients: crude protein .81, lysine .83.

Housing and Management

The pigs were housed individually in pens with half-slatted floors in an insulated building, from June to September. They were fed equal portions twice daily at 0800 and 1600. Water was available ad libitum. The animals were weighed twice a week, on Monday and Thursday, before feeding and feed allowances were adjusted to expected gain for the following period of 3 or 4 d, respectively. Pigs reaching 45 kg were killed on Tuesday or Friday, on the date that their BW was closest to 45 kg. If after weighing, it was decided that the animal was to be slaughtered the next day, the pig was given its normal feed allowance for that day and was killed the following morning.

Slaughter Procedure and Carcass Analysis

The gilts were killed by electrical stunning and exsanguination and the blood and organs were collected separately. After emptying the gastrointestinal tract, blood and individual organs were weighed, stored together per pig in a plastic bag, and frozen at -20°C. The scalded, scraped, and eviscerated carcass, including head and feet (carcass), was split longitudinally and the two halves were weighed. The right half was sealed in a plastic bag and stored at -20°C. The frozen carcass and organ fractions (referred to together as empty body) were cut into small pieces and homogenized separately in a commercial butcher's mincer. Each fraction was subsampled for proximate analysis.

Dry matter content was determined after drying samples in a vacuum oven at 50°C and a vacuum of 100 torr, using anhydrous calcium chloride as the drying agent. After 16 h, the vacuum was changed to 15 torr and the samples were weighed every 4 h until they obtained constant weight. Nitrogen content was determined in the fresh samples by Kjeldahl analysis according to ISO 5983 (1979). Lipid content was assessed by extraction of freeze-dried samples with petroleum-ether and drying the extract at 103°C to a constant weight according to ISO 6492. Ash was analysed by burning oven-dried samples in a muffle furnace at 550°C according to ISO 5984 (1978).

Statistical Analysis

From the 90 animals used in the factorial arrangement, four pigs (treatments 2.5 x M .94 g of lysine/MJ of DE; 3.0 x M .41, .53, and 1.03 g of lysine/MJ of DE) were excluded from the statistical analysis, due to ill health. For the remaining 44 animals on the low and 42 animals on the high-energy intake treatments, the effect of lysine (protein) intake on criteria of performance and body composition was determined by regression analysis estimating a linear and curvilinear effect of average daily lysine intake in the treatment period. The curvilinear effect was determined using a two-phase linear model based on Koops and Grossman (1993):

$$y = A - b * s * \ln (1 + e^{(c - x) / s}) \qquad [1]$$

in which: y = dependent variable, x = independent variable, A = plateau for the dependent variable (second phase), b = slope of the linear (first) phase, c = point of transition for the independent variable, and s = parameter regulating the smoothness of transition. This model was chosen because it can describe both linear-plateau and curvilinear relationships. A small smoothness parameter (s) results in an abrupt change from linear to plateau, whereas a large value of s results in a smooth transition. When the data did not enable a proper estimation of the smoothness of transition, parameter s was fixed to a value of .05, which guaranteed a sharp change from linear to plateau.

If only the linear effect of lysine intake was significant ($P < .05$), the effect of energy intake on the intercept and slope of this linear relationship was determined using dummy variables and the backward elimination procedure (Draper and Smith, 1981). The F-value 3.96 ($P = .05$, error df = 80) was used as the criterion. When a curvilinear effect was present ($P < .05$), the effect of energy intake on each of the three parameters A (plateau), b (slope), and c (inflection point) in Model [1] was determined using the same procedure.

Data were analysed by linear (GLM) and derivative-free nonlinear (NLIN, method DUD) regression procedures (SAS, 1989).

RESULTS

Performance Criteria

Both BW at slaughter and empty body weight (weight of carcass plus organs and blood) as a fraction of BW were not affected by energy or lysine intake ($P > .1$). The average slaughter weight was 45.5 kg (SEM .58) and empty body weight as a fraction of slaughter weight was .92 (SEM .009). Average daily gain and gain/feed increased curvilinearly with increasing lysine intake ($P < .01$; Table 2).

Table 2. Effect of daily lysine intake on the growth rate and gain/feed of gilts from 20 to 45 kg, fed at 2.5xM or 3.0xM (M = energy for maintenance)

Mean lysine intake, g/d[a]		ADG, g/d		Gain/feed, kg/kg	
		2.5xM	3.0xM	2.5xM	3.0xM
6.38	(127)	425	477	.403	.390
6.98	(139)	462	505	.443	.418
7.87	(155)	468	563	.445	.452
8.55	(168)	527	609	.507	.490
9.24	(181)	511	608	.496	.484
10.1	(197)	558	643	.531	.510
10.9	(212)	611	737	.582	.577
11.4	(222)	569	708	.547	.567
12.3	(238)	610	684	.570	.554
12.9	(251)	588	736	.557	.593
13.7	(265)	578	724	.545	.584
14.5	(279)	581	796	.547	.642
15.4	(297)	602	762	.560	.602
16.9	(325)	623	739	.582	.581
18.2	(350)	614	784	.577	.616
Mean		555	672	.526	.537
SEM[b]		23.0		.0187	
Regression[c]					
Intercept (a)		-	-	-	-
Slope (b)		48.7		.0332	
Transition point (c)		10.2	12.1**	11.0	12.6**
Plateau (A)		607	768**	.565	.604**
Smoothness parameter (s)		1.36		.503	
RSD[d]		40.2		.031	

[a] Mean daily protein intake (g/d) in parentheses.

[b] Pooled standard error for 30 treatment groups.

[c] Regression analysis using Model [1] $y = A - b * s * \ln(1 + e^{(c - x)/s})$ in which: y = dependent variable, x = independent variable, A = plateau for the dependent variable, b = slope of the linear phase, c = point of transition for the independent variable, and s = parameter regulating the smoothness of transition. When the curvilinear effect was not significant ($P > .05$), the model was reduced to a linear model: $y = a + b * x$.

* $P < .05$ and ** $P < .01$ for differences in estimates of parameters A, a, b, and c between the two energy levels. When parameter estimates for the two energy levels were not different, one estimate is given. Also one estimate is given for smoothness parameter s.

[d] RSD, Residual standard deviation of the model including only significant ($P < .05$) parameters.

The ADG increased with increasing lysine intake to a level of 607 and 768 g/d at the low- and high-energy levels, respectively. The rate of increase (slope) was similar for the two energy levels ($P > .1$), but at the lower energy level the plateau was reached at a lower lysine intake ($P < .01$). The same effects were found for gain/feed, which increased to .565 and .604 kg/kg at the low- and high-energy levels, respectively. The ADG and gain/feed for the animals with ad libitum access to feed were 1,097 ± 41 g/d and .594 ± .014 kg/kg, respectively.

Empty Body Characteristics

The mean empty body composition (grams/kilogram) of the five pigs killed at 20 kg was water 690 ± 1.9, protein 164 ± 2.0, lipid 105 ± 3.2, and ash 30.9 ± .73.

Water and protein content at 45 kg increased while lipid content decreased, both curvilinearly ($P < .05$) with increasing lysine intake; whereas ash content decreased linearly ($P < .01$; Table 3). The slopes of these relationships were not affected by energy intake ($P > .05$), which implies that the respective rates of increase and decrease in content with increasing lysine intake were similar at the two energy intake levels. Water content increased with increasing lysine intake to a maximum of 682 and 664 g/kg on the low- and high-energy levels, respectively. Protein content reached maxima of 182 and 176 g/kg and lipid content decreased to 104 and 124 g/kg on the low- and high-energy levels, respectively. At each level of lysine intake, lipid content was higher and water, protein and ash contents were lower at the high-energy intake level.

Rates of Deposition

The mean empty body composition of the animals slaughtered at 20 kg BW, was used to calculate the deposition rates of body components between 20 and 45 kg (Table 4). Water, protein, and ash deposition rates increased curvilinearly with increasing lysine intake ($P < .01$). Lipid deposition decreased curvilinearly with increasing lysine intake ($P < .05$). The respective rates of increase (slopes) in water, protein and ash deposition rates and the decrease in lipid deposition rate were not affected by energy intake ($P > .1$). At each level of lysine intake, lipid deposition was on average 47 g/d higher for pigs on the high-energy level than for pigs on the low-energy level. Water, protein, and ash deposition rates were similar for the two energy intake levels, at each level of lysine intake below the intake point at which the plateau started. However, at lysine intakes beyond the point of inflection, for gilts fed the low-energy diet, extra energy intake enhanced the plateau in water deposition from 367 to 441 g/d, in protein deposition from 108 to 128, g/d and in ash deposition from 17.6 to 19.3 g/d. Deposition rates in the empty body (grams/day) for the animals having ad libitum access to feed were 571 ± 17.9 for water, 166 ± 5.2 for protein, 217 ± 15.0 for lipid, and 26.1 ± 1.8 for ash.

Table 3. Effect of daily lysine intake on the composition of the empty body of gilts at 45 kg, fed 2.5xM or 3.0xM (M = energy for maintenance) between 20 and 45 kg

	Empty body composition, g/kg							
	Water		Protein		Lipid		Ash	
Mean lysine intake, g/d[a]	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM
6.38	618	581	161	143	177	231	35.3	36.0
6.98	618	605	163	150	179	204	35.7	34.1
7.87	641	613	169	154	150	190	33.4	31.5
8.55	638	613	167	155	153	196	33.9	30.6
9.24	655	630	172	159	132	173	32.7	31.2
10.1	660	637	175	162	121	159	32.8	32.6
10.9	663	640	173	165	124	154	33.2	31.9
11.4	666	647	181	169	116	147	32.1	30.2
12.3	665	652	181	168	115	140	31.9	29.3
12.9	670	663	183	171	111	130	31.7	30.9
13.7	673	659	181	174	106	131	32.5	31.2
14.5	660	669	181	176	118	119	32.8	30.1
15.4	679	654	180	176	101	130	31.7	30.0
16.9	684	653	182	175	97	138	29.8	29.6
18.2	683	671	184	176	99	116	29.9	28.4
Mean	658	639	176	165	127	157	32.6	31.2
SEM[b]	6.79		2.45		7.52		.984	
Regression[c]								
Intercept (a)	-	-	-	-	-	-	37.5	36.0**
Slope (b)	38.1		4.44		-19.2		-.42	
Transition point (c)	6.25		11.3	13.2**	10.4	11.5**	-	-
Plateau (A)	682	664**	182	176**	104	124**	-	-
Smoothness parameter (s)	2.87		.98		1.53		-	
RSD[d]	11.7		3.75		12.7		1.67	

[a,b,c,d] See Table 2.

Ratio between Lipid and Protein Deposition

The ratio between lipid and protein deposition (LD/PD) decreased curvilinearly ($P < .01$) with increasing lysine intake both in the carcass and organ fraction and in the empty body (Table 5). For all three fractions the rates of decrease (slopes)

Table 4. Effect of daily lysine intake on the deposition rates of water, protein, lipid, and ash in the empty body of gilts between 20 and 45 kg, fed at 2.5xM or 3.0xM (M = energy for maintenance)

	Deposition rates, g/d							
Mean lysine intake, g/d[a]	Water		Protein		Lipid		Ash	
	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM
6.38	213	214	61	55	94	145	15.3	17.5
6.98	229	242	67	63	99	140	16.5	17.2
7.87	258	277	74	73	80	133	15.2	16.1
8.55	286	298	82	80	94	152	17.6	16.6
9.24	288	318	82	86	71	133	15.5	17.5
10.1	321	336	94	91	68	114	17.4	19.3
10.9	341	393	97	111	76	133	18.9	21.8
11.4	344	397	104	112	65	118	17.5	19.2
12.3	347	385	107	107	68	106	17.9	17.4
12.9	351	423	107	117	61	101	17.4	20.3
13.7	347	404	102	118	56	99	17.8	20.0
14.5	326	436	100	126	68	88	18.0	19.8
15.4	354	419	103	126	51	104	17.2	19.7
16.9	387	419	112	124	51	111	16.5	19.2
18.2	382	457	113	129	53	86	16.4	18.3
Mean	318	361	94	101	70	117	17.0	18.7
SEM[b]	14.5		3.81		7.99		.994	
Regression[c]								
Intercept (a)	-	-	-	-	-	-	-	-
Slope (b)	43.0		10.8		-5.78		.57	
Transition point (c)	9.79	11.4^{**}	10.9	13.0^{**}	14.0		10.9	
Plateau (A)	367	441^{**}	108	128^{**}	54	101	17.6	19.3^{**}
Smoothness parameter (s)	1.89		24.4		.05[e]		.05[e]	
RSD[d]	24.2		6.3		14.9		1.74	

[a,b,c,d] See Table 2.

[e] Smoothness parameter (s) could not be estimated and was fixed to the value of .05 in Model [1].

were similar for the two energy levels (P > .1). However, both in the carcass and empty body, at each level of lysine intake, LD/PD ratios were higher at the high-energy level than at the low-energy level. At levels of lysine intake beyond which maximum protein deposition was reached, LD/PD in the carcass was .57 and .81, and in the empty body .53 and .74, at the low- and high-energy intake levels,

Table 5. Effect of daily lysine intake on the ratio between lipid and protein deposition in body components of gilts between 20 and 45 kg live weight, fed at 2.5xM or 3.0xM (M = energy for maintenance)

Mean lysine intake, g/d[a]	Lipid deposition/protein deposition					
	Carcass		Organs		Empty body	
	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM
6.38	1.64	3.00	.79	.90	1.54	2.66
6.98	1.62	2.42	.60	.94	1.49	2.22
7.87	1.17	2.01	.41	.64	1.08	1.81
8.55	1.23	2.13	.54	.64	1.15	1.91
9.24	.95	1.69	.28	.63	.87	1.55
10.1	.79	1.39	.29	.48	.72	1.25
10.9	.85	1.30	.30	.50	.78	1.20
11.4	.69	1.14	.22	.47	.64	1.06
12.3	.69	1.10	.22	.32	.63	.99
12.9	.62	.96	.27	.30	.58	.86
13.7	.60	.94	.19	.25	.55	.84
14.5	.73	.77	.31	.24	.68	.70
15.4	.56	.91	.20	.33	.51	.83
16.9	.51	.98	.17	.40	.46	.90
18.2	.52	.75	.17	.21	.47	.67
Mean	.88	1.43	.33	.48	.81	1.30
SEM[b]	0.103		0.062		0.092	
Regression[c]						
Intercept (a)	-	-	-	-	-	-
Slope (b)	-.57		-.096		-.45	
Transition point (c)	7.61	9.55^{**}	10.7	13.1^{**}	8.25	10.1^{**}
Plateau (A)	.57	$.81^{**}$	.25		.53	$.74^{**}$
Smoothness parameter (s)	1.97		.29		1.82	
RSD[d]	.180		.115		.162	

[a,b,c,d] See Table 2.

respectively. In the organs LD/PD ratio was on average .15 higher at the high-energy intake level than the low intake level: .33 vs .48. The plateau in LD/PD ratio, however, estimated as .25, was similar (P > .05) for the two energy intake levels.

Required Lysine/Energy Ratios

The lysine/energy ratios required to maximize ADG, gain/feed, and protein deposition were calculated using quadratic and linear-plateau models. The linear-plateau model was based on Model [1] with parameter s fixed at .005 and ileal digestible lysine/digestible energy (grams/megaJoule of DE) as the independent variable. The results from these calculations are presented in Table 6. Energy intake level did not affect the optimum lysine/energy ratio (P > .05). Furthermore, the lysine/energy ratio required to support maximum protein deposition was higher than the corresponding ratios required to support maximum gain and gain/feed. Estimates of requirements based on the quadratic model were considerably higher than those using the linear-plateau model.

Table 6. Ileal digestible lysine requirements (g/MJ of DE) for live weight gain, gain/feed, and protein deposition based on linear-plateau and quadratic regression models for gilts between 20 and 45 kg live weight, fed at 2.5 or 3.0 times energy for maintenance

	Linear-plateau		Quadratic	
Criterion	Requirement[a]	F-value[b]	Requirement[a]	F-value[b]
Live wt gain	.57 ± .019	.18	.79 ± .037	2.42
Gain/feed	.57 ± .017	.01	.78 ± .029	2.01
Protein deposition	.62 ± .013	1.1	.82 ± .027	3.15

[a] Lysine/energy ratio (mean ± SE) required for maximum performance of pigs at the two energy intake levels.

[b] F-value for an effect of energy intake level on lysine requirements. Critical value of F(1,80): P = .05, F = 3.96.

DISCUSSION

Deposition Rates

Gilts that had ad libitum access to feed gained 1,097 g/d, of which they deposited 166 g of protein and 217 g of lipid. Thus, the gilts used in this experiment had a high potential for lean tissue growth. On the basis of genetic capacity for protein deposition, these animals were comparable with those used by Rao and McCracken (1990, 1992) and in general were better than pigs used in other requirement studies reported in the literature. Compared with animals with ad libitum access to feed, protein and lipid deposition and LD/PD were much lower for the pigs on the 2.5 and 3.0 times energy for maintenance treatments. At each of the latter two energy intake levels, protein deposition increased, and lipid deposition and LD/PD decreased with increasing lysine (protein) intake in agreement with the results of Campbell et al. (1985).

At levels of lysine intake beyond those required to maximize protein deposition, protein deposition remained constant and independent of lysine intake. Lipid deposition also reached a plateau but only at very high levels of lysine intake (Table 4). This plateau could only be estimated with a fixed smoothness parameter (s). The latter was mainly caused by the relatively large variation in lipid deposition between animals, and the smaller range of lysine intake levels over which the plateau was valid. At similar protein gain and rising protein intake, increasing amounts of amino acids have to be deaminated. Therefore, the energy available for deposition of protein and lipid will decrease. The plateau in protein deposition and the continued decrease in lipid deposition, suggest that at high levels of lysine and protein intake excess dietary protein was deaminated and excreted mainly at the expense of lipid deposition. This is somewhat different from the results of Campbell et al. (1984, 1985), who found a decreased protein deposition at high levels of protein intake, and probably reflects differences in genotypes and in protein deposition capacity between the experiments.

At levels of lysine and protein intake beyond those required to maximize protein deposition, protein and lipid deposition in the body increased with increasing energy intake (Tables 4 and 5). These results are in agreement with Ellis et al. (1983), Campbell et al. (1984, 1985), and Rao and McCracken (1992) for animals of similar or higher body weights. Apart from the latter, these authors also reported an increased LD/PD ratio at higher energy or feed intake levels, as in the present experiment. However, the carcass LD/PD ratios of .57 and .81 for pigs on the low- and high-energy intake levels in the present experiment were lower than most values from the literature, which range from .7 to 1.2.

Lysine Requirements

Lysine requirements are defined here as the required ratio between ileal digestible lysine and digestible energy (grams/megaJoule), which supports maximum ADG, gain/feed, or protein deposition. These requirements were estimated with a linear-plateau and a quadratic model. According to Baker (1986) the curvilinear method indicates the requirements for maximal response of all animals in a population, whereas a broken-line response predicts requirements for the average animal in the population. Furthermore, the quadratic method tends to overestimate the requirement of a nutrient, if the dependent variable (e.g., ADG) remains constant after the requirement for that nutrient has been met (Williams et al., 1984). Presumably this overestimation increases if the range of intake levels of that nutrient increases above the requirement. In our experiment, the linear-plateau model gave a good estimate of the optimum lysine/energy ratios for the average animal, because ADG, gain/feed, and protein deposition remained constant after the inflection point. The quadratic model gave a large overestimation as illustrated for the rate of protein deposition in Figure 1. The plateau model used in this experiment

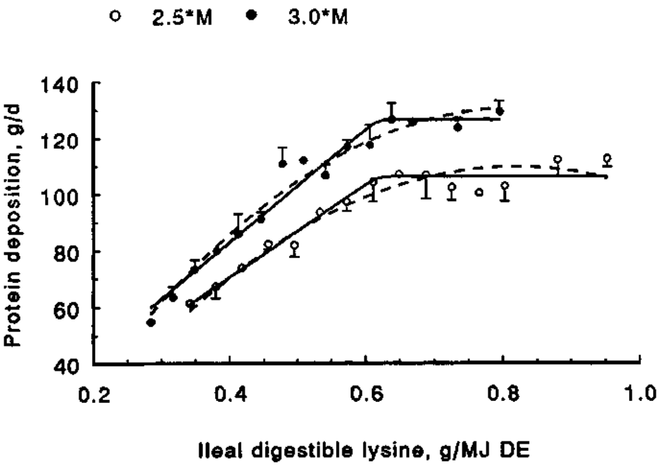

Figure 1. Effect of dietary lysine/energy on protein deposition (mean + SE, n = 3) in gilts from 20 to 45 kg body weight, fed at 2.5 or 3.0xM (M = energy for maintenance) described with a linear-plateau (——) and a quadratic regression model (- -). Maximum protein deposition was reached at .62 and .82 g of ileal digestible lysine/MJ of DE, calculated with the linear-plateau and the quadratic model, respectively. These lysine/energy requirements were not affected by the level of energy intake (P > .05).

has the ability to interpolate between tested levels of a nutrient and describes an objective breakpoint. This represents a large benefit compared with the plateau model described by Martinez and Knabe (1990) and the method of using two intersecting straight lines.

In this experiment, the optimum lysine to energy ratios for ADG and gain/feed were somewhat lower than the optimum for protein deposition (Table 6). Similar results were reported by Campbell et al. (1985) and Batterham et al. (1990) for pigs of similar body weight. Requirements in our experiment based on the linear-plateau relationship were .57 g of ileal digestible lysine/MJ of DE for ADG and gain/feed and .62 g for protein deposition. The corresponding total lysine/energy values were .69 and .75 g of lysine/MJ of DE, respectively. Published results of experiments in which lysine requirements were determined on ileal digestible bases are scarce. Batterham et al. (1990) using quadratic regression estimated ileal digestible lysine/digestible energy requirements of restrictedly fed females of .59, .60, and .66 g/MJ for ADG, gain/feed, and protein deposition, respectively. In contrast Martinez and Knabe (1990) reported ileal digestible lysine requirements for ADG and gain/feed ratio for female and castrated male pigs with ad libitum access to feed as .50 g/MJ of DE. Differences between the three experiments presumably reflect differences in genetic capacity for protein deposition between the pigs and possibly also differences in feed intake.

A number of experiments have been published in which lysine requirements were estimated on the basis of total lysine. These were reviewed by the ARC (1981) and NRC (1988). The ARC (1981) and NRC (1988) propose total lysine requirements for pigs of approximately 20 to 45 kg as .84 and .53 g/MJ of DE, respectively. Recent experiments with animals in the same live weight range suggest requirements of .80 (Yen et al., 1986) and .71 g of lysine/MJ of DE (Campbell et al., 1988) for female pigs; and .72 g/MJ of DE for females and barrows (Chiba et al., 1991). For entire males requirements were determined as .80 g of total lysine/MJ of DE (Rao and McCracken, 1990). Large differences between proposed requirements for animals within a certain weight range are due to variations in energy intake level (Campbell et al., 1984), sex (Williams et al., 1984), genetic capacity (Campbell et al., 1985), measuring technique (Rao and McCracken, 1990), method of analysis (Baker, 1986), pattern, digestibility and availability of dietary amino acids, and environmental conditions (ARC, 1981). These discrepancies can be reduced to some extent, if protein requirements are based on ileal digestible amino acids. This can be done because a considerable amount of data on ileal digestible amino acid contents of feedstuffs has become available in the last few years (Lenis, 1992).

Effect of Energy Level on Lysine/Energy Requirements

In this experiment, the optimum lysine/energy ratios were not affected by energy intake level. The ad libitum feed intake was considerably higher than feed intake on the energy level of 3.0 times maintenance. Therefore, no firm conclusions can be drawn for feeding levels that approach ad libitum intake. However, as long as the intrinsic capacity for protein deposition has not been fully utilized, protein deposition reaches a maximum at each energy level, determined by minimum lipid deposition. Thus, the reason why protein deposition reaches a plateau is similar at each energy level, namely the distribution of energy between protein and lipid deposition. Therefore, also at high-energy levels, protein deposition may approach the plateau with similar protein utilization.

A constant optimum protein/energy ratio was also determined by Campbell et al. (1985) and Fuller et al. (1986) for restrictedly fed animals. Giles et al. (1987), however, reported higher lysine/energy requirements for restrictedly fed female pigs between 20 and 45 kg than for animals offered feed on an ad libitum basis. Similarly, Campbell et al. (1984) found that the dietary protein/energy requirement of male pigs from 45 to 90 kg, fed 3.2 times energy for maintenance, was lower than that of pigs fed 2.5 times maintenance energy. In the latter two experiments, the higher energy intake levels probably exceeded those required to support maximum protein deposition. The excess energy allowance, without increase in PD, would result in a reduced estimate of the optimum lysine/energy. This interaction between energy intake and protein requirements is most likely to occur at live weights above rather than below 50 kg, in females and barrows rather than in males, and also in pigs of low rather than of high genetic potential for lean gain (SCA, 1987).

Below maximum protein deposition, LD/PD increased with increasing energy intake. However, in the present and afore mentioned experiments this increasing LD/PD did not result in a noticeable reduction of lysine/energy requirement. This may be because as energy intake level increases, the proportion of consumed nutrients used for maintenance processes decreases. Protein/energy required for maintenance is lower than protein/energy required for growth, because maintenance requirements are mainly energy requirements. Consequently, an increase in energy level, with a concomitant increase in growth, results in a dilution of these maintenance requirements and therefore an increased total protein/energy requirement. As a result, an increasing energy level can have two antagonistic effects on the optimum protein/energy ratio, by a dilution of maintenance requirements and an increase in LD/PD. The net effect depends on the relationship between energy intake and protein deposition and probably will be small below the maximum protein deposition. In the present experiment, these effects presumably compensated each other.

As discussed above, the effect of energy intake on lysine/energy requirements is likely to be mediated by an effect on the partitioning of consumed energy between maintenance, protein deposition, and lipid deposition. Presumably the same is true for the effects of body weight, sex, and genotype on the optimum lysine/energy. Consequently, the effect of these factors on lysine/energy requirements can be estimated without conducting experiments, if a factorial model is used in which both lysine and energy requirements for maintenance, protein and lipid deposition have been included.

Factorial Approach

Based on ARC (1981) and Fuller and Wang (1987) ileal digestible lysine requirements (Lys_i) can be estimated as follows:

$$Lys_i = Lys_m + (PD * Lys_{pr}) / e \qquad [2]$$

where Lys_m = lysine for maintenance, PD = protein deposition (grams/day), Lys_{pr} = lysine content of deposited body protein (grams/gram), and e = efficiency with which ileal digestible lysine is retained.

Based on the ARC (1981), energy requirements (ME_i) can be calculated as follows:

$$ME_i = ME_m + 1/k_p*P + 1/k_f*F \qquad [3]$$

where ME_i = metabolizable energy intake (megaJoules/day), ME_m = ME required for maintenance (megaJoules/kilogram $BW^{.75}$), P and F are energy retained as protein and fat and k_p and k_f are efficiencies of utilization of ME for protein and fat accretion.

The combination of Models [2] and [3] allows the calculation of the required lysine/energy ratio (Q) in grams/megaJoules.

$$Q = \frac{[Lys_m + (PD * Lys_{pr}) / e] * (1000 * .96)}{ME_m + 1/k_p * PD * 23.7 + 1/k_f * LD * 39.6} \qquad [4]$$

PD and LD are protein and lipid deposition, respectively, 23.7 and 39.6 are energy contents of body protein and fat, respectively, (kiloJoules/gram) 1,000 is a factor to calculate megaJoules from kiloJoules and .96 is a factor to calculate DE from ME (ARC, 1981).

To test the validity of Equation [4], the value of Q was calculated for the present experiment. Protein and lipid deposition at adequate levels of lysine intake (Table 6), were 106 and 57 g/d at the low-intake level and 126 and 101 at the high-intake level. In addition the following values were adopted: Lys_m = .036 g/kg $LW^{.75}$ (Fuller et al., 1989), Lys_{pr} = .066 g/g, e = .74 and ME_m = 550 kJ/kg $LW^{.75}$, (Bikker et al., 1993), k_p = .54 and k_f = .74 (ARC, 1981).

Based on these values, the required lysine/DE ratios (Q) for the pigs at the low- and high-energy intake levels were calculated as .63 and .61 g of ileal digestible lysine/MJ of DE, respectively. These values agree with the determined optimum of .62 g of lysine/MJ of DE. This result implies that Equation [4] can be useful to estimate the optimal dietary lysine/energy. The correctness of the results, however, depends on the precision with which the input factors are known. Furthermore, it should be stressed that when a constant efficiency of lysine utilization (e) is assumed as in the present experiment, Equation [4] gives the optimum lysine/energy ratio according to the linear-plateau method.

IMPLICATIONS

An exact quantification of the optimum ratio between ileal digestible amino acids and energy in the diet for genetically improved pigs is necessary for efficient nitrogen utilization and minimal nitrogen excretion. The present results showed that the optimum lysine/energy ratio for growing gilts (20 to 45 kg) with a high potential for lean tissue growth was .60 g of ileal digestible lysine/MJ of digestible energy.

There was only a small difference between optima for daily gain, gain/feed, and protein deposition. The optimum lysine to energy ratio was not affected by feed intake level. Extrapolation of these results using a factorial model indicated that as long as an intrinsically determined maximum protein deposition has not been reached, the optimum lysine to energy ratio is largely unaffected by feed intake level.

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Chapter 2

INDEPENDENT EFFECTS OF ENERGY AND PROTEIN INTAKE ON PROTEIN DEPOSITION AND UTILIZATION IN GROWING PIGS

P. Bikker, M.W.A. Verstegen, B. Kemp[1], and R.G. Campbell[2]

Department of Animal Nutrition, Wageningen Agricultural University,
Haagsteeg 4, 6708 PM Wageningen, The Netherlands

[1] Department of Animal Husbandry, Wageningen Agricultural University

[2] Bunge Meat Industries, Corowa, Australia

Submitted

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P. Bikker, M.W.A. Verstegen, B. Kemp, and R.G. Campbell

ABSTRACT

One hundred gilts of a commercial strain were used to determine independently the effects of protein and energy intake, on protein and lysine deposition and utilization in gilts with high genetic potential for lean gain, from 20 to 45 kg. In a 2 x 15 factorial arrangement, protein intake ranged from 127 to 350 g/d in 15 graduated steps. The first 12 increments were 14 g/d, the last two increments were 28 g/d. Lysine was the first limiting amino acid in the diet. At each of the 15 levels of protein intake, the animals were offered energy at one of two levels (2.5 and 3.0 times energy for maintenance, on average 15.8 and 18.8 MJ of DE/d). Protein and lysine deposition, increased with increasing protein intake to a maximum rate of 108 and 8.0 g/d respectively, at the low energy level. The extra protein-free energy allowance of 3.0 MJ of DE/d for pigs fed 3.0 times maintenance did not affect these deposition rates at low levels of protein intake, but improved protein and lysine deposition to approximately 128 and 9.5 g/d respectively, at high levels of protein intake. These results support the concept of protein and energy dependent phases in protein deposition. Gross efficiencies of utilization of ileal digestible protein and lysine were .58 and .77, respectively, in the protein dependent phase, at both energy levels. The relationships between protein intake and deposition and between lysine intake and deposition were best described by a linear-plateau model. However, no firm conclusion was drawn about the smoothness of transition between the linear and plateau phase.

Keywords: Pigs, Energy Intake, Protein Intake, Protein Utilization, Lysine Utilization

INTRODUCTION

Utilization of dietary protein depends both on the composition of the diet (i.e., amino acid pattern and protein to energy ratio), and the efficiency with which body protein is being deposited. Knowledge of the efficiency of body protein deposition is essential for a factorial calculation of requirements of pigs and also to accurately predict the growth response of the animals to a change in nutrient input (Whittemore, 1983).

According to the ARC (1981) and Fuller and Crofts (1977) the efficiency of protein utilization decreased gradually with increasing protein intake and with increasing protein/energy ratio. Campbell et al. (1984, 1985), however, reported a constant marginal efficiency of protein utilization, independent of protein or energy intake, at levels of protein intake below the requirements. Furthermore, efficiency of protein utilization has often been calculated using a reference value for ideal protein and faecal rather than ileal digestibilities, both of which are a possible source of error. In addition the amino acid pattern of body protein can be affected by protein and energy intake (Batterham et al., 1990; Bikker et al., 1994a)

The present study was therefore undertaken to determine: (1) the relationships between ileal digestible protein intake and deposition, and lysine intake and deposition, (2) the efficiencies of utilization of ileal digestible protein and lysine, and (3) the interrelationships between protein and energy intake, on protein and lysine deposition and utilization.

EXPERIMENTAL PROCEDURES

Animals and Experimental Design

One hundred female pigs of a commercial strain (VOC Nieuw Dalland, Venray, The Netherlands) were used in this study. At an average BW of 20 kg, 90 animals were allocated on the basis of BW among 30 treatment combinations in a 2 x 15 factorial arrangement with three pigs per treatment combination. The respective treatments were energy intake level, equivalent to 2.5 and 3.0 times energy required for maintenance, and protein intake, in 15 graduated steps ranging from an average of 127 to 350 g/d during the treatment period. To allow calculation of nutrient retention, five animals were killed at commencement of the experiment for determination of initial body composition, at 20 kg BW. In addition, five animals received feed ad libitum, to determine maximum protein deposition.

Diets and Feeding

At each of the 15 levels of protein intake, the animals were offered feed at one of the two energy intake levels in order to separate the effects of energy and protein intake. On the low energy intake level, the animals were fed diets with a calculated total lysine content ranging from .44 to 1.24 g/MJ DE. The ileal digestible lysine/DE ratio for these 15 groups were as follows: .34, .38, .42, .46, .50, .53, .57, .61, .65, .69, .73, .77, .80, .88, and .95 g/MJ. The animals on the high energy level received an extra amount of protein-free energy of 3.0 MJ per day. Consequently lysine/energy ratios at this intake level were 83% of those for the animals on the lower energy level. The ratios determined ileal digestible lysine/DE for these 15 groups were: .28, .32, .35, .38, .41, .45, .48, .51, .54, .57, .61, .64, .67, .73, and .80 g/MJ of DE. The two energy intake levels, averaging 15.8 and 18.8 MJ of DE/d, were equivalent to 2.5 and 3.0 times energy for maintenance respectively. The animals were fed according to a scale based on metabolic BW ($kg^{.75}$), with maintenance requirements taken as .475 MJ of DE/$kg^{.75}$ (ARC, 1981). The pigs provided feed on an ad libitum basis received a diet with 15.3 MJ of DE/kg and .61 g of ileal digestible lysine/MJ of DE.

A protein-rich (Diet 1) and a protein-free diet (Diet 2) were formulated to ensure a constant dietary amino acid balance. Diet 1 consisted mainly of barley, soybean meal, maize gluten meal, herring meal, skimmed milk powder, and potato protein. The main ingredients of Diet 2 were maize starch, dextrose, animal fat, and soybean oil. The composition of the diets has been previously published by Bikker et al. (1994b). The chemical composition of the diets, including amino acids, is presented in Table 1. These two diets were fed in different ratios to each of the treatment groups. Diet 1 was formulated to contain 1.24 g lysine/MJ of DE.

A more detailed description of procedures, including proximate analysis of the diets and determination of digestible energy and ileal digestible amino acids, has been given elsewhere (Bikker et al., 1994b).

Management and Carcass Analyses

The gilts were housed individually in pens with half slatted floors in an insulated building. They were fed equal rations twice daily at 800 and 1600. Water was available ad libitum. The animals were weighed twice a week and feed allowances adjusted accordingly. At 45 kg the gilts were killed by electrical stunning and exsanguination. The blood and organs were collected and the contents of the gastro-intestinal tract were removed. The blood and individual organs (together referred to as organ fraction) were weighed, stored together per pig in a plastic bag and frozen at -20°C. The scalded, scraped and eviscerated carcass, including head and feet (carcass), was split longitudinally and the two halves were weighed. The right half was sealed in a plastic bag and stored at -20°C. The frozen carcass and organ fractions (together referred to as empty body) were homogenized separately in a commercial butcher's mincer. Each fraction was subsampled for proximate analysis as described by Bikker et al. (1994b). In addition, the ether extracted carcass and organ samples were ground with a centrifugal mill (Retsch ZM-1), and amino acid contents subsequently determined at the laboratories of Eurolysine

Table 1. Analysed chemical composition and determined ileal digestibility of crude protein and amino acids of the experimental diets as fed

Nutrient, g/kg	Diet 1	Diet 2	Ileal digestibility
Dry matter	897.3	890.7	-
Crude protein	350.4	6.2	.81
Ash	55.9	56.0	-
Digestible energy (MJ/kg)	16.00	13.97	-
Essential amino acids			-
Lysine	18.5	.09	.83
Methionine	9.6	ND[a]	.91
Methionine + Cystine	13.8	.07	.84
Threonine	14.6	.09	.81
Tryptophan	4.1	.04	.82
Arginine	18.4	ND	.90
Histidine	8.0	ND	.86
Isoleucine	15.5	.09	.86
Leucine	31.3	.33	.90
Phenylalanine	16.6	ND	.89
Phenylalanine + Tyrosine	27.7	ND	.90
Valine	17.3	.19	.84
Nonessential amino acids			
Alanine	18.5	.19	.85
Aspartic acid	29.7	.61	.78
Cystine	4.2	.07	.67
Glutamic acid	59.6	.61	.89
Glycine	13.2	.09	.76
Serine	16.7	.12	.83
Tyrosine	11.1	ND	.91

[a] ND not detectable

(Paris). Amino acids were determined with an amino acid analyzer (Beckman 6300, Palo Alto, California) after hydrolysis with 6 N hydrochloric acid under reflux at 110°C for 23 h. The sulphur-containing amino acids were analysed after oxidation with performic acid and subsequent hydrolysis with HCl as previously described (Mason et al., 1980).

Statistical Analysis

Four animals had to be excluded from the experiment due to bad health. For the remaining animals, 44 and 42 at the low and high energy intake level, respectively, the effect of protein and lysine intake on protein and lysine deposition was determined with regression analysis, using a two-phase linear model, based on Koops and Grossman (1993):

$$y = a + b_1 * x - (b_1 - b_2) * s * \ln (1 + e^{(x - c) / s})$$

in which y = dependent variable, x = independent variable, a = intercept, b_1 = slope of the first phase, b_2 = slope of the second phase, c = point of transition between the first and the second phase, and s = parameter regulating the smoothness of transition.

This model was used to determine whether protein and lysine deposition reached a maximum, or continued to increase at high levels of protein intake. Subsequently, four different models were used to describe the relationship between intake and deposition of ileal digestible protein and lysine. These four models were: a linear-plateau model with smooth transition (Koops and Grossman, 1993), a linear-plateau model with abrupt transition, similar to a bent-stick model (Campbell et al., 1984, 1985), a monomolecular model (ARC, 1981), and a Michaelis-Menten model (Phillips, 1981, Fuller and Garthwaite, 1993). The respective equations of these models are given in Table 3.

The effect of energy intake on regression parameters was determined using dummy variables and the backward elimination procedure (Draper and Smith, 1981). Data were analysed by linear (GLM, SAS, 1989) and nonlinear (NONLIN package, Dennis et al., 1981) regression procedures.

RESULTS

Protein and Lysine Deposition

The results of protein and lysine deposition and utilization are presented in Table 2. In addition, animals receiving feed on an ad libitum basis deposited 166 ± 5.2 g of protein and 10.9 ± .56 g of lysine per day. Deposition of protein and lysine increased curvilinearly ($P < .001$) with increasing protein intake. The results of calculations with the two-phase linear model showed that the slopes, representing the marginal efficiencies of protein and lysine utilization, were not affected by energy intake ($P > .1$). In addition, the slope of the second phase (b_2) for protein and lysine deposition was not different from zero ($P > .1$). Thus at high levels of protein intake, protein and lysine deposition had reached a maximum,

Table 2. Effect of daily protein and lysine intake on deposition rates of protein and lysine in the empty body of gilts between 20 and 45 kg, fed 2.5xM or 3.0xM (M = energy for maintenance)

Protein intake[a], g/d	Protein deposition, g/d		Protein deposition: ileal digestible protein intake, g/g		Lysine deposition, g/d		Lysine deposition: ileal digestible lysine intake, g/g	
	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM	2.5xM	3.0xM
127 (6.37)	61	55	.58	.53	4.3	3.6	.79	.69
138 (6.98)	67	62	.58	.56	4.6	4.6	.78	.80
155 (7.86)	74	73	.58	.58	5.5	5.1	.84	.78
168 (8.55)	82	80	.60	.58	5.3	5.9	.74	.82
181 (9.25)	82	85	.56	.56	5.6	5.5	.73	.71
197 (10.1)	94	91	.58	.56	6.7	6.4	.80	.76
212 (10.9)	97	111	.57	.63	6.5	7.5	.72	.82
222 (11.4)	104	112	.58	.62	7.3	6.9	.76	.72
238 (12.3)	107	107	.54	.56	7.9	8.2	.75	.82
251 (12.9)	107	117	.52	.58	7.8	8.3	.71	.77
265 (13.7)	102	118	.47	.55	7.2	8.3	.62	.73
279 (14.5)	100	126	.44	.56	7.2	9.1	.59	.76
297 (15.4)	103	126	.42	.52	7.6	9.3	.59	.73
325 (16.9)	112	124	.42	.47	8.4	8.9	.59	.63
350 (18.2)	113	131	.40	.46	8.2	9.6	.54	.64
Mean	94	101	.52	.55	6.7	7.1	.69	.73
SEM[b]	3.8		.0189		.44		.041	
Regression[c]								
Intercept (a)	-7.3				-.010			
Slope 1 (b_1)	.64				.77			
Slope 2 (b_2)	.067[d]				.12[d]			
Transition point (c)	173**	204**			9.61**	11.7**		
Smoothness parameter (s)	10.7				.52			
RSD[e]	6.29				.7123			

[a] In parentheses the daily lysine intake is given. Ileal digestibility for protein and lysine was .815 and .834, respectively.

[b] Pooled standard error for 30 treatment groups.

[c] Analysis using a two-phase linear model $y = a + b_1 * x - (b_1 - b_2) * s * \ln(1 + e^{(x - c)/s})$ in which: y = dependent variable, x = independent variable, a = intercept, b_1 and b_2 = slope of the first and second phase respectively, c = transition point between the two phases, and s = parameter regulating the smoothness of transition. $^{**}P < .01$ for differences in estimates of parameter a, b_1, b_2, and c between the two energy levels. When parameter estimates for the two energy levels were not different, one estimate is given. Also one estimate is given for smoothness parameter s.

[d] b_2 estimates for protein and lysine deposition were not different from zero ($P > .1$)

[e] RSD Residual standard deviation of the model including only significant ($p < .05$) parameters.

which had been determined by energy intake. Consequently, the relationships between protein and lysine intake, and protein and lysine deposition were further analysed with the four models that contained a maximum or an asymptote. The results of these analyses are presented in Table 3 for protein deposition and in Table 4 for lysine deposition. One parameter estimate is given when differences in the estimate between the two energy levels were not significant (P > .05). In Figure 1 the respective relationships for protein deposition, using parameter estimates from Table 3, are presented graphically.

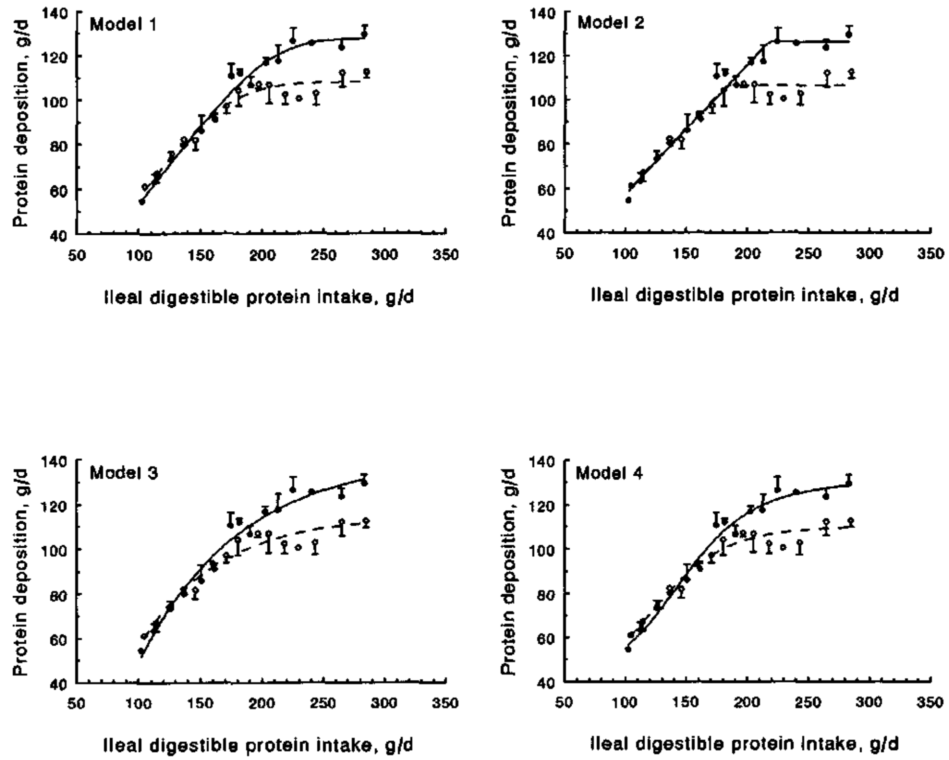

Figure 1. *Effect of daily ileal digestible protein intake on protein deposition (mean ± se, n = 3) in gilts from 20 to 45 kg BW, fed 2.5xM (-o-) or 3.0xM (-●-) (M = energy for maintenance), described with four models: linear-plateau with smooth transition (Model 1), linear-plateau with sharp transition (Model 2), monomolecular (Model 3), and Michaelis-Menten (Model 4). The parameter estimates are presented in Table 3).*

Table 3. Parameter estimates of four different models to describe the relationship between ileal digestible protein intake (g/d) and protein deposition in the empty body of gilts between 20 and 45 kg, fed at energy levels (EL) of 2.5 or 3.0 times energy for maintenance

		Parameter estimates[a]						
Model	EL	a[b]	b	c	s	int.[b]	R^2	RSD[c]
[1] $a-b*s*\ln(1+e^{(c-x)/s})$	2.5	108	.70	173	19.9	-8.1	.9174	6.30
	3.0	128		206				
[2] $a-b*s*\ln(1+e^{(c-x)/s})$	2.5	107	.58	183	1[d]	-.48	.9121	6.46
	3.0	126		218				
[3] $a-(a-b)*e^{-cx}$	2.5	115	-170	.0158	-	-170	.9089	6.58
	3.0	141		.0122				
[4] $b+(a-b)/(1+(c/x)^s)$	2.5	111	47.6	134	5.35	47.6	.9168	6.32
	3.0	131		152				

[a] One parameter estimate is given when estimates for the two energy levels were not different ($P > .05$). Two estimates are given when estimates for the two energy levels were different ($P < .01$)

[b] Parameter a represents the maximum protein deposition. Int. is the intercept, representing the protein deposition at zero protein intake.

[c] RSD Residual Standard Deviation of the model, including only significant ($P < .05$) parameters.

[d] Parameter s fixed to a value of 1 in order to describe a linear-plateau relationship, with sharp transition.

Table 4. Parameter estimates of four different models to describe the relationship between ileal digestible lysine intake (g/d) and lysine deposition in the empty body of gilts between 20 and 45 kg, fed at energy levels (EL) of 2.5 or 3.0 times energy for maintenance

		Parameter estimates[a]						
Model	EL	a[b]	b	c	s	int.[b]	R^2	RSD[c]
[1] $a-b*s*\ln(1+e^{(c-x)/s})$	2.5	8.00	.85	9.85	1.28	-.20	.8314	.7159
	3.0	9.52		11.79				
[2] $a-b*s*\ln(1+e^{(c-x)/s})$	2.5	7.80	.74	10.26	.01[d]	.27	.8288	.7170
	3.0	9.30		12.26				
[3] $a-(a-b)*e^{-cx}$	2.5	8.76	-6.82	.226	-	-6.82	.8269	.7210
	3.0	11.0		.169				
[4] $b+(a-b)/(1+(c/x)^s)$	2.5	8.62	3.46	8.12	4.49	3.46	.8195	.7362
	3.0	9.61						

[a,c] See footnotes Table 3.

[b] Parameter a represents the maximum lysine deposition. Int. is the intercept, representing the lysine deposition at zero lysine intake.

[d] Parameter s fixed to a value of .01 in order to describe a linear-plateau relationship, with sharp transition.

Utilization of Dietary Protein and Lysine

The gross efficiencies of protein and lysine utilization are also presented in Table 2. These efficiencies are calculated as the ratio of protein deposition to ileal digestible protein intake and lysine deposition to ileal digestible lysine intake. The efficiencies of protein and lysine utilization decreased curvilinearly with increasing protein and lysine intake. The relationship between protein (lysine) intake and gross efficiency of protein (lysine) utilization is implicitly determined by the model chosen to describe the relationship between protein intake and protein deposition. This is illustrated in Figure 2, in which the efficiency of protein utilization is described on the basis of Model [1], using the parameter estimates from Table 3. Therefore, no separate analysis was conducted to describe the relationship between protein intake and the gross efficiencies of protein and lysine utilization.

The response curve for protein and lysine deposition described by Model [2], can be divided into a protein dependent phase, in which protein deposition is limited by protein intake, and an energy dependent phase (the plateau), in which protein deposition is determined by energy intake. The gross efficiencies of protein and lysine utilization of animals in the protein dependent phase were .581 ± .0064

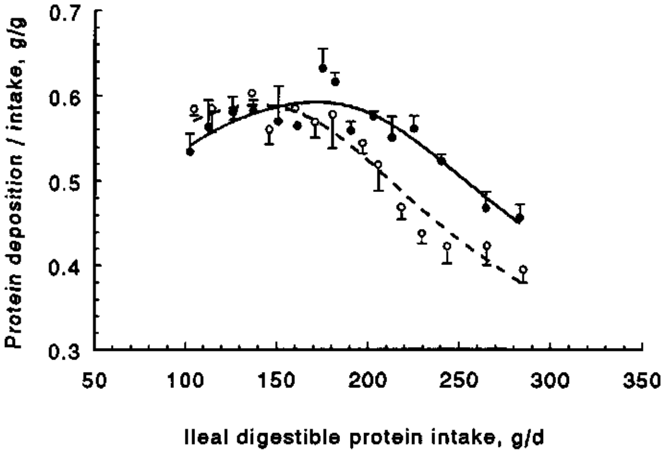

Figure 2. Effect of daily ileal digestible protein intake on gross efficiency of protein utilization (mean ± se, n = 3) in gilts from 20 to 45 kg BW, fed 2.5xM (-o-) or 3.0xM (-●-) (M = energy for maintenance), described on the basis of Model 1, linear-plateau with smooth transition, using the parameter estimates from Table 3.

(n = 24) and .576 ± .0068 (n = 31) for protein and .770 ± .016 and .769 ± .012 for lysine at the low and high energy level respectively. These gross efficiencies were not significantly affected by protein intake ($P > .05$), nor by energy intake ($P > .1$). However, protein and lysine utilization decreased rapidly with increasing protein intake when deposition rates had reached a maximum (Table 2).

DISCUSSION

Protein and Lysine Deposition

The relationship between protein intake and protein deposition at constant energy intake has been described as linear (Zhang et al., 1984), two-phase linear (Batterham et al., 1990), curvilinear (ARC, 1981; Fuller and Garthwaite, 1993) and linear-plateau (Campbell et al., 1984, 1985). Different models often accounted efficiently for the measured variation in the response parameter. Frequently, however, only a small number of protein intake levels was used to derive a model. Therefore, protein and lysine intake were varied over a wide intake range in 15 graduated steps in the present study. Four models that mathematically represent the biological response of the animal were used to describe the relationship between protein and lysine intake and protein and lysine deposition. The slope of each model represents the marginal efficiency of protein or lysine utilization. This marginal efficiency is defined as the increase in protein or lysine deposition per unit increase in protein or lysine intake, and is calculated as the first derivative of the model.

In order to select the most suitable model to describe the response relationships, physiological criteria should be taken into account. A model which relates to physiological mechanisms is to be preferred. There is little sense in selecting the model with the best fit, if it is not in line with physiological processes. In addition, statistical criteria can be used to evaluate the models. Since protein accretion is determined by protein synthesis and degradation, ideally the description should take into account how amino acid intake affects these two processes. However, this was not possible because in our study only the changes in protein accretion, being the net result of protein synthesis and degradation, in response to protein and energy intake were measured. Therefore, the description of the response of protein deposition should meet present knowledge of protein utilization at different levels of protein intake.

It seems unlikely that animals continue to increase protein deposition at extremely high levels of protein intake, at a constant digestible energy intake level (Harper, 1983). This was confirmed by results of the two-phase linear model (Table 2). These results showed that the marginal efficiencies of protein and lysine utilization reached zero in the second phase. The linear relationship between protein intake and protein deposition as determined by Zhang et al. (1984), and Fuller et al. (1989) presumably implies that protein requirements were not met in these studies. The two-phase linear relationship reported by Batterham et al. (1990) could be the result of combining data of male and female pigs in the analysis, whereas the two sexes presumably differed in maximum protein deposition at the supplied energy level. Consequently, models with a maximum or asymptote were chosen in the present study.

At amino acid intakes below maintenance requirements, dietary amino acids are used to replace obligatory losses. The efficiency of utilization of limiting amino acids for this aim seems constant (ARC, 1981; Fuller et al., 1989). At low and moderate protein intake levels above maintenance, the marginal efficiency of amino acid utilization for protein accretion seems largely constant and independent of the level of protein intake as reported by Batterham et al. (1990) and Fuller et al. (1989) in pigs, and Bolton and Miller (1985) in rats. At high levels of protein intake the pigs presumably will reach a maximum rate of protein accretion, determined by the daily energy intake. Whether the marginal efficiency diminishes gradually at high protein levels (curvilinear) or drops abruptly when a plateau is reached (rectilinear) is a matter of debate. Fisher et al. (1973) have shown that a linear-plateau relationship between amino acid intake and egg output in individual chicks, resulted in a smooth population response curve, due to variation in body weight and maximum egg production between birds. The transition was more gradual with increasing variation in the maximum egg output. A similar difference between the response of individual animals and the response of a group of animals may exist for protein and lysine deposition. Therefore, a curvilinear decrease was to be expected in this study.

The results in Table 3 and 4 indicated that the goodness of fit of the four models was quite similar. However, differences between the models were present in their estimates of maximum protein (lysine) deposition at the two energy levels and of protein (lysine) gain or loss at zero protein intake. Although care has to be taken when judging the response of a model outside the data range, a model which describes a biologically acceptable response over a large intake range is to be preferred. In Model [3] estimates for maximum protein and lysine deposition were somewhat higher than in the other models. Furthermore, Model [3] gave very large negative estimates, whereas Model [4] gave positive estimates for protein accretion at zero protein intake. No measurements were taken at low intake levels in this study. These would be needed in order to accurately determine and interpret estimates at zero protein intake. Nevertheless, these results suggest that the Models [3] and [4] are not suitable to describe the response relationships.

Model [3] represents a diminishing decrease in marginal efficiency of protein utilization with increasing protein intake. The largest decrease is found at low levels of protein intake (Figure 3). Model [4] describes a sigmoid relationship with an inflection point between 130 and 150 g protein intake per day, resulting in an increasing marginal efficiency until the inflection point, and a decrease thereafter (Figure 3). These responses are not in harmony with the criteria discussed above. Therefore, the monomolecular model and the Michaelis-Menten equation were considered less suitable to describe the response relationship between protein (lysine) intake and protein (lysine) retention.

Models [1] and [2] describe a linear response in protein deposition at low levels of protein intake. In Model [1], the marginal efficiency decreases gradually with increasing protein intake, whereas in Model [2], the marginal efficiency is constant until a plateau is reached, whereby it drops to zero (Figure 3). The intercept of Model [1], representing the obligatory protein losses, results in a maintenance requirement of 11.6 g/d (8.1 / .70), which is in good agreement with ARC (1981).

The intercept of Model [2] suggests a small overestimation of protein gain at zero protein intake. Furthermore, as discussed above, a curvilinear response curve for a population of animals is to be expected. These results and considerations suggest that of the four models used in this study, Model [1] is the most appropriate to describe the relationship between protein intake and protein deposition for a group of animals. Firm conclusions about the smoothness of the transition between the increasing phase and the plateau phase for an individual animal could not be drawn because of variation in the data between animals.

In order to exclude the effect of variation between animals, Fuller and Garthwaite (1993) measured the response in nitrogen retention of individual animals between

35 and 73 kg, in six sequential balance periods. Because of the better fit of the curvilinear models compared with a rectilinear model, they concluded that the rectilinear model is presumably not the most appropriate model for a description of the response of individual animals. In their design however, the effect of body weight on protein deposition and on protein/energy requirements presumably led to variation between measurements on the same animal, contributing to the better fit of the curvilinear functions. These considerations imply that it is unclear whether the linear-plateau Model [2] is a good approximation of the response of an individual animal. In our opinion their is no published evidence which confirms or invalidates the suitability of this model.

It is clear from Figure 1 and Tables 3 and 4, that at low levels of protein and lysine intake, the extra energy allowance had no beneficial effect on the rate of protein or lysine deposition. Protein and lysine deposition were similar regardless the level of energy intake. With extra energy intake only lipid deposition increased at these low protein (lysine) levels (Bikker et al., 1994b). However, at high levels of protein intake, protein and lysine deposition increased by 20 and 1.5 g/d respectively, with an extra energy allowance of 3.0 MJ DE per day. This means that at high protein intake levels energy intake limits protein accretion. These

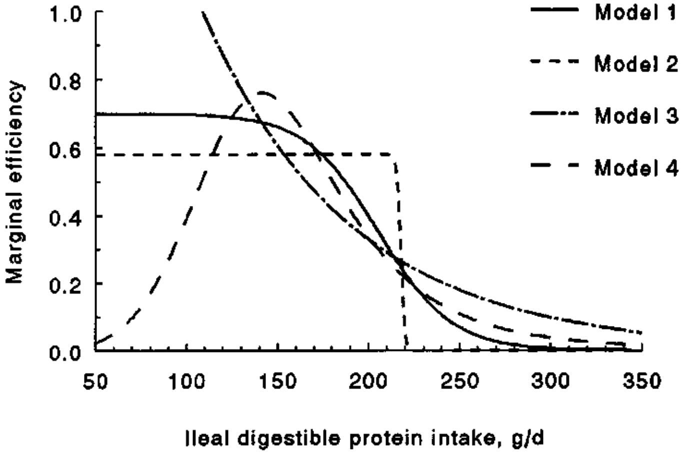

Figure 3. The marginal efficiency of ileal digestible protein utilization in gilts from 20 to 45 kg fed 3.0 times energy for maintenance. The lines were calculated as the first derivative of the four models from Table 3: linear-plateau with smooth transition (M1), linear-plateau with sharp transition (M2), monomolecular (M3), and Michaelis-Menten (M4).

results are in agreement with Campbell et al. (1984, 1985) and support the concept of energy and protein dependent phases in protein deposition as discussed by Campbell (1988). Around the transition point, the protein dependent phase may gradually change into the energy dependent phase (see discussion above).

Protein and Lysine Utilization

The gross efficiencies of ileal digestible protein and lysine utilization were determined as .58 and .77, respectively, in the protein dependent phase. In this phase, these efficiencies were not significantly affected by protein or energy intake. The lower value for protein is a reflection of the dietary amino acid composition, which was designed to be lysine-deficient. The almost constant gross efficiencies of protein and lysine utilization in the protein dependent phase, suggest that protein and lysine requirements for zero nitrogen balance were only a small part of the ileal digestible protein and lysine intake. This is partially due to the use of apparent rather than true ileal digestibility coefficients. Ileal losses account for a large part of the maintenance requirements for protein and lysine (Fuller, 1991), and these losses are already accounted for in the use of apparent digestibility values. Protein and lysine utilization decreased rapidly when protein deposition reached a plateau, as a result of an over-supply of dietary protein relative to dietary energy. Under these conditions, an extra energy allowance improved protein and lysine utilization (Table 2, Figure 2). The maximal gross efficiency of lysine utilization of .77 is in good agreement with the maximum of about .73 in pigs calculated by Batterham et al. (1990) and of .75 in rats by Bolton and Miller (1985).

Marginal efficiency of lysine utilization is represented by the parameter b in Models [1] and [2]. In Model [1] the estimate of .85 ± .16 is valid at low levels of lysine intake, and decreases gradually with increasing lysine intake (Figure 3). In Model [2], the estimate of .74 ± .05 is the average marginal efficiency for the protein dependent phase (Figure 3). Batterham et al. (1990), determined a marginal efficiency of ileal digestible lysine utilization of .85 using a bent-stick model, and Bolton and Miller (1985) determined a value of .83 using a linear model. Differences between the latter two values and the average of .74 in the linear phase of this study may have been due to the fact that the lowest levels of lysine intake in the studies of Batterham et al. (1990) and Bolton and Miller (1985) were much lower than in this study: approximately 10% versus 45% of requirements. The use of different regression models may also have affected the calculated marginal efficiencies. Furthermore, variability in amino acid analyses and feed characteristics, and the use of different methods to estimate ileal digestibility may have contributed to the reported differences.

The inefficiency of approximately 15% of ileal digestible lysine in these three studies may be due to part of the lysine being absorbed in a form unavailable for protein synthesis, or to losses in physiological processes. Taking into account the composition of the diets used in these studies, a reduced availability of lysine is not likely to be the main source of loss. However, several pathways in the intermediate metabolism can be distinguished, by which absorbed amino acids can be lost or used for purposes other than protein synthesis. Of these, losses due particularly to the inefficiency of protein turnover and(or) inevitable amino acid catabolism may be considerable (Moughan, 1991). It has been reported that oxidation of a limiting amino acid can be reduced to less than 5% of the amino acid flux (Simon, 1989). However, because the flux rate can amount five to eight times the deposition rate (Simon, 1989, Rao and McCracken, 1992), this oxidation can be a considerable proportion of the digested amino acids. In conclusion, for practical purposes it is advisable to adopt a maximum efficiency of lysine utilization for protein deposition considerably less than 100%. On the basis of the discussed results, a maximum of 80% seems preferable.

IMPLICATIONS

An optimum in efficiency of utilization of dietary protein is required, if sustainable animal production is to be achieved. For the gilts in this study, the maximum efficiencies of utilization of ileal digestible protein and lysine, being the first limiting amino acid, were .58 and .77 respectively. This indicates possibilities to improve protein utilization in practice by using an amino acid profile attuned to the requirements of the animals. This study indicates a maximum marginal efficiency of lysine utilization of approximately .80. In order to improve protein deposition and(or) utilization effectively, it is crucial to know whether protein deposition is limited by protein or by energy intake. Supplying dietary protein above the requirement results in a drastic decrease in protein utilization. Consequently possibilities to improve protein utilization should be studied under conditions whereby protein intake limits protein deposition.

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Chapter 3

AMINO ACID COMPOSITION OF GROWING PIGS IS AFFECTED BY PROTEIN AND ENERGY INTAKE

P. Bikker, M.W.A. Verstegen, and M.W. Bosch

Department of Animal Nutrition, Wageningen Agricultural University,
Haagsteeg 4, 6708 PM Wageningen, The Netherlands

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AMINO ACID COMPOSITION OF GROWING PIGS IS AFFECTED BY PROTEIN AND ENERGY INTAKE

P. Bikker, M.W.A. Verstegen, and M.W. Bosch

ABSTRACT

Ninety five female pigs from 20 to 45 kg body weight were used to elucidate the effects of energy and protein intake on the amino acid composition of the protein in the carcass, organs and empty body of growing pigs. In a 2 x 15 factorial arrangement, protein intake ranged from 127 to 350 g/d in 15 graduated steps. The respective digestible energy allowances were 15.8 and 18.8 MJ/d. Whole body amino acid contents (g/16 g nitrogen) were (mean ± SEM) lysine 6.64 ± .028, methionine 2.11 ± .012, threonine 3.62 ± .016 and total essential amino acids 42.8 ± .16. The organ fraction contained 14.8 and 15.8% (SEM .13) of whole body protein at the low and high energy levels, respectively. The concentrations of essential amino acids were 41.8 ± .19 and 48.4 ± .13 g/16 g nitrogen in the carcass and organs, respectively. Concentrations of a number of amino acids, both in carcass, organ and whole body protein, and protein deposited between 20 and 45 kg, were affected by protein and(or) energy intake. The amino acid pattern of the newly deposited protein was slightly different from that of the empty body protein. The changes in amino acid contents were presumably the result of effects of protein and energy intake on the proportions of muscle and non-muscle carcass tissues, and on relative weights of blood and viscera. Consequences of these changes for the amino acid requirements are discussed.

Keywords: pigs, amino acid composition, protein intake, energy intake, body protein

INTRODUCTION

The amino acid requirements of growing pigs depend upon the relative proportions of dietary amino acids utilized for maintenance and for body gain, and upon the amino acid composition of protein being deposited. The ratio between amino acids used for maintenance and those used for growth, can be affected by animal factors such as body weight, sex, and genotype, and nutritional factors such as feeding level and dietary composition. Considerable differences exist between the optimal amino acid composition for maintenance, including endogenous losses, and for growth (Fuller et al. 1989). Therefore, differences in the above mentioned ratio between maintenance and growth may influence the ideal amino acid composition of the diet.

The amino acid requirements for growth are often assumed to be constant, but Batterham et al. (1990) and Campbell et al. (1988) showed an effect of dietary protein content on whole body amino acid composition. However, it was not clear which changes in the body led to this effect on composition. Bikker et al. (unpublished data) determined an increase in the relative organ mass and a decrease in relative lean tissue mass with increasing energy intake, which may also have an effect on whole body amino acid composition. Therefore in this study the effect of protein and energy intake on the amino acid composition of carcass, organ and whole body protein in growing pigs was determined, and the consequences for the ideal dietary amino acid composition are discussed.

The present study is part of a project to determine the interrelationships between dietary protein and energy on protein and lipid deposition, and the amino acid composition of growing pigs with a high genetic potential for lean gain, in order to derive an efficient feeding strategy for these animals. The effects of protein and energy intake on performance criteria, and deposition rates of protein and lipid of pigs in the present experiment has been reported previously (Bikker et al. 1994a).

EXPERIMENTAL PROCEDURES

Animals and Design

The amino acid composition of carcass and organ protein was determined in pigs of 20 ($n=5$) and 45 kg ($n=90$) body weight. Five animals from a group of 95 female pigs of a commercial strain (VOC Nieuw Dalland, Venray, The Netherlands), were allocated on the basis of body weight to an initial slaughter group. These pigs were killed at 20 kg to determine the body composition at the start of the experiment. The remaining 90 pigs were allocated among 30 treatment combinations in a 2 x 15 factorial arrangement, with three pigs per treatment combination. The respective treatments were energy intake level, equivalent to 2.5 and 3.0 times the energy required for maintenance, and protein intake, ranging from an average of 127 to 350 g/day during the treatment period in 15 graduated steps. The first 12 increments were 14 g/d, the last 2 increments were 28 g/d.

Diets and Feeding

A protein-rich (Diet 1, Table 1 in Chapter 1) and a virtually protein-free diet (Diet 2, Table 1 in Chapter 1) were formulated and combined in different ratios, and were fed to each of the 30 treatment groups in order to supply the appropriate daily amounts of protein and energy. The contents of dry matter, crude protein, inorganic matter, digestible energy, and amino acids of Diet 1 and Diet 2 were analysed as described by Bikker et al. (1994a). The use of these two diets ensured a constant amino acid balance in the daily ration and allowed for the separation of the effects of energy and protein intake. Lysine was the first limiting amino acid in Diet 1, which was formulated to contain 1.24 g lysine per MJ digestible energy (DE). On the low energy level (2.5 times maintenance) the animals received diets with calculated lysine contents of .44, .49, .54, .59, .64, .69, .74, .79, .84, .89, .94, .99, 1.04, 1.14, and 1.24 g/MJ DE. At the high energy level (3.0 times maintenance), the animals had similar levels of daily protein intake, but received extra non-protein energy (Diet 2) of 3.0 MJ DE/d, equivalent to .5 times energy for maintenance. Consequently, the lysine/energy ratios at this energy intake level were 83% of those at the low energy level, and ranged from .37 to 1.03 g/MJ DE. The daily energy allowances were calculated on the basis of metabolic body weight ($kg^{.75}$) with energy requirements for maintenance taken as .475 MJ DE/$kg^{.75}$ (ARC 1981). The daily energy intakes on the low and the high energy levels were an average of 15.8 and 18.8 MJ DE respectively, during the treatment period. The pigs received their daily allowances in two equal rations at 800 and 1600 h. They had free access to drinking water.

Carcass Analyses

At 45 kg the animals were killed by electrical stunning and exsanguination. Blood and organs were collected and the contents of the gastro-intestinal tract removed. Blood and individual organs, including mesenteric fat (together referred to as the organ fraction), were weighed, stored together per pig in a plastic bag and frozen at -20°C. The scalded, scraped and eviscerated carcass, including head and feet (carcass), was split longitudinally and the two halves weighed. The right half was sealed in a plastic bag and stored at -20°C. The frozen carcass and organ fractions were cut into small pieces and homogenized separately in a commercial butchers' mincer. Each fraction was subsampled for proximate analysis. Dry matter content was determined after drying samples in a vacuum oven at 50°C and a vacuum of 100 torr, using anhydrous calcium chloride as the drying agent. After 16 h, the vacuum was changed to 15 torr and the samples were weighed every four h until they obtained constant weight. Nitrogen content was determined in the fresh samples by Kjeldahl analysis according to ISO 5983 (1979). Lipid content was assessed by extraction of freeze-dried samples with petroleum-ether, and drying the extract at 103°C to a constant weight according to ISO 6492. Ash was analysed by burning oven-dried samples in a muffle furnace at 550°C according to ISO 5984 (1978).

In addition, the ether extracted carcass and organ samples were ground with a centrifugal mill, and the amino acid contents determined subsequently at the laboratories of Eurolysine (Paris). A representative sample containing about 10 mg of nitrogen was hydrolysed with 25 ml hydrochloric acid (6 mol/l) under reflux at 110°C for 23 hours (Mason et al. 1980). To determine the sulphur-containing amino acids a similar amount of sample was oxidized for 16 hours at 0°C with 5 ml of an oxidation mixture (.5 ml 30% H_2O_2 and 4.5 ml 80% formic acid solution, also containing 4.73 g phenol per kg). Excess reagent was degraded on completion of the oxidation by adding .84 g sodium disulphite (Mason et al. 1980). The samples were subsequently hydrolysed as described above. On completion of the hydrolysis the pH of the mixture was adjusted to 2.2 by carefully adding NaOH (7.5 mol/l), and then filtered through a .2 μm filter. Subsequently 200 μL of hydrolysate and 50 μL of a norleucine solution as internal standard were supplemented with a buffer solution to 1 ml. Amino acids were determined with an amino acid analyzer (Beckman 6300, Palo Alto, CA), with a Sodium High Performance Column (Beckman 338052) with ion exchange resin. The elution started with a pH 3.7 buffer (Beckman 338057) operating at 50°C, which was changed to a pH 4.0 buffer (Beckman 338058) at 77°C, 15.7 min after injection of the sample. The third buffer with pH 3.0 (Beckman 338056) was used at 77°C from 26.6 to 50.0 min after injection of the sample. Amino acids were determined using ninhydrine as a colouring reagent at 140°C in a spectrophotometer at a wavelength of 570 nm. Amino acids were quantified using an amino acid standard solution containing 18 amino acids (Sigma AA-S-18), L-methionine sulfone (Sigma M 0876), L-cysteic acid (Sigma C 7630), and norleucine. Concentrations of proline, hydroxyproline and tryptophan were not determined.

The protein and amino acid retention between 20 and 45 kg for each individual animal was calculated as the difference of its composition at 45 kg, and the assumed body composition at 20 kg. The latter was derived from the pigs slaughtered at 20 kg.

The protocol of this experiment was approved by the ethical committee of the Wageningen Agricultural University.

Statistical Analysis

Four animals had to be excluded from the experiment, two animals died, and two had large feed refusals. For the remaining animals, 44 and 42 at the low and high energy intake level respectively, the effect of protein intake on amino acid composition of carcass, organ and empty body protein was analysed by linear regression analysis, using the GLM-procedure of SAS (SAS 1989). The effect of energy intake on regression parameters was determined using dummy variables and the backward elimination procedure (Draper and Smith 1981). Probability levels less then .05 were considered statistically significant.

RESULTS

Distribution of Protein and Amino Acids

The protein content of the empty body (g/kg fresh material) increased with increasing protein intake from 161 to 182 at the low energy level and from 143 to 176 at the high energy level (Bikker et al. 1994a). The distribution of this protein between the carcass and organ fraction was affected by energy intake ($P < .001$). At the low energy level, 14.8% of total body protein was in the organs, compared to 15.8% at the high energy level (Table 1). Large differences were present in the distribution of individual amino acids between the carcass and organs. Amino acids in the organs, as a proportion of the whole body amino acid content, varied from 12% (methionine, glycine, arginine) to 20% (cystine, leucine, valine, phenylalanine). At the high energy level, these proportions of individual amino acids in the organs were between 1.01 (glycine) and 1.12 (tyrosine) of those at the low energy level.

Amino Acid Composition

In Tables 2, 3, and 4 the average amino acid patterns in the carcass, organs and total empty body are presented for the low and high energy level. Comparison of Tables 2 and 3, showed marked differences in the amino acid composition between the carcass and organ protein. The contents (g/16 nitrogen (N)) of lysine, threonine, histidine, tyrosine, aspartic acid, and serine were 10 to 30% higher, and the contents of cystine, leucine, phenylalanine, and valine were 40 to 50% higher in the organ fraction than in the carcass. Contents of methionine, arginine, isoleucine,

Table 1. Distribution of whole body protein and amino acids in female pigs at 45 kg as affected by protein and energy intake

	Relative amount in organs, %[a]			Effects[b]		
Amino acid	2.5 x M	3.0 x M	SEM	Energy	Protein	Slope (b)
Crude protein	14.83	15.78	.13	***	NS	-
Lysine	17.07	17.45	.21	NS	**	.00695
Methionine	11.70	13.14	.17	***	NS	-
Cystine	20.70	22.28	.28	***	NS	-
Threonine	16.02	17.08	.21	***	NS	-
Histidine	18.49	19.98	.26	***	NS	-
Isoleucine	12.95	13.65	.17	**	NS	-
Leucine	20.17	20.76	.22	NS	NS	-
Phenylalanine	20.24	21.96	.25	***	NS	-
Tyrosine	16.77	18.76	.31	***	NS	-
Arginine	11.96	12.79	.21	**	NS	-
Valine	20.66	21.53	.22	**	NS	-
EAA[c]	16.85	17.81	.20	***	NS	-
Alanine	15.36	15.80	.16	*	*	.00429
Aspartic acid	16.96	17.63	.19	*	NS	-
Glutamic acid	13.51	14.10	.16	**	NS	-
Glycine	11.15	11.31	.17	NS	*	.00359
Serine	17.46	18.32	.20	**	NS	-

[a] Protein and amino acids in the organs as a percentage of the whole body protein and amino acid content. Values are means for gilts fed 2.5 times maintenance (2.5 x M, n = 44) and 3.0 times maintenance (3.0 x M, n = 42). At each of the two energy levels, the pigs received 15 graded levels of protein. SEM pooled standard error for the two energy intake levels.

[b] Linear regression ($y = a + bx$) was used to determine effects of protein and energy intake. NS not significant ($P > .05$), * $P < .05$, ** $P < .01$, *** $P < .001$. The regression coefficient (b) for the effect of protein intake, if $P < .05$, represents the change in amount of an amino acid in the organs, as a percentage of whole body amino acids, per g increase in daily protein intake.

[c] Essential amino acids, tryptophan not included.

glutamic acid and glycine were 10 to 30% lower in the organ fraction. As a result, the total content of essential amino acids (excluding tryptophan) was considerably higher in the organ protein than in the carcass protein, 48.40 ± .13 and 41.78 ± .19 g/16 g N (mean ± SEM) respectively.

The amino acid composition of the empty body protein (Table 4) is the result of the amino acid patterns of both carcass (about 85%) and organ protein (about 15%). Consequently, the amino acid composition of the empty body protein was to a large extent similar to that of the carcass protein. In Table 5, the amino acid composition of the protein deposited in the treatment period from 20 to 45 kg live

Table 2. *Amino acid composition of the carcass protein of female pigs at 45 kg as affected by* protein and energy intake

	Content, g/16 g nitrogen[a]			Effects[b]		
Amino acid	2.5 x M	3.0 x M	SEM	Energy	Protein	Slope (b)
Lysine	6.49	6.48	.045	NS	NS	-
Methionine	2.17	2.20	.020	NS	NS	-
Cystine	.82	.82	.008	NS	NS	-
Threonine	3.55	3.57	.026	NS	NS	-
Histidine	2.70	2.64	.027	NS	**	.00080
Isoleucine	3.50	3.56	.028	NS	NS	-
Leucine	6.07	6.18	.043	NS	NS	-
Phenylalanine	3.23	3.17	.026	NS	NS	-
Tyrosine	2.43	2.38	.027	NS	NS	-
Arginine	6.70	6.75	.039	NS	NS	-
Valine	4.03	4.12	.029	*	NS	-
EAA[c]	41.68	41.87	.27	NS	NS	-
Alanine	6.20	6.36	.029	***	***	-.00116
Aspartic acid	7.67	7.80	.047	NS	NS	-
Glutamic acid	12.38	12.57	.070	NS	NS	-
Glycine	9.27	9.55	.077	*	***	-.00313
Serine	3.73	3.72	.020	NS	NS	-

[a] Values are means for gilts fed 2.5 times maintenance (2.5 x M, n = 44) and 3.0 times maintenance (3.0 x M, n = 42). At each of the two energy levels, the pigs received 15 graded levels of protein. SEM pooled standard error for the two energy intake levels.

[b] Linear regression ($y = a + bx$) was used to determine effects of protein and energy intake. NS *not significant* ($P > .05$), * $P < .05$, ** $P < .01$, *** $P < .001$. *The regression coefficient (b)* for the effect of protein intake, if $P < .05$, represents the change in amino acid content per g increase in daily protein intake.

[c] Essential amino acids, tryptophan not included.

weight is given. The contents of most amino acids of this deposited protein were similar to those of empty body protein. The concentrations of lysine, histidine and isoleucine however, were slightly higher, and concentrations of glycine and alanine were slightly lower in the deposited protein, compared to the empty body protein.

Effect of Protein and Energy Intake

The amino acid pattern of the organ protein and to a lesser extent carcass protein, was affected by both protein and energy intake. In the carcass protein valine, alanine and glycine (g/16 g N) increased with extra energy intake, histidine increased with increasing protein intake, and alanine and glycine decreased with increasing protein intake. In the organ protein, lysine, leucine, glycine, and serine

Table 3. Amino acid composition of the organ protein of female pigs at 45 kg as affected by protein and energy intake

	Content, g/16 g nitrogen[a]			Effects[b]		
Amino acid	2.5 x M	3.0 x M	SEM	Energy	Protein	Slope (b)
Lysine	7.67	7.31	.061	***	***	.00478
Methionine	1.64	1.77	.010	***	NS	-
Cystine	1.22	1.26	.009	**	NS	-
Threonine	3.88	3.92	.020	NS	NS	-
Histidine	3.50	3.51	.022	NS	**	.00074
Isoleucine	2.98	3.00	.017	NS	**	.00058
Leucine	8.79	8.64	.036	**	***	.00171
Phenylalanine	4.70	4.76	.022	NS	NS	-
Tyrosine	2.80	2.91	.028	*	NS	-
Arginine	5.22	5.27	.057	NS	**	-.00197
Valine	6.01	6.03	.029	NS	***	.00137
EAA[c]	48.43	48.36	.18	NS	***	.00852
Alanine	6.45	6.37	.030	NS	*	.00085
Aspartic acid	8.98	8.90	.039	NS	***	.00159
Glutamic acid	11.09	11.01	.048	NS	*	.00145
Glycine	6.66	6.49	.058	*	NS	-
Serine	4.53	4.46	.021	*	NS	-

[a,b,c] See footnotes Table 2.

were lower at the high energy level, whereas methionine, cystine, and tyrosine were higher. Lysine, histidine, isoleucine, leucine, valine, alanine, aspartic acid and glutamic acid in the organ protein increased with increasing protein intake, whereas arginine decreased. For significant effects of protein intake, the change in amino acid content per g increase in total protein intake is given in Tables 2, 3, and 4. Furthermore the effect of protein intake on lysine and glycine in organ and empty body protein is illustrated in Figure 1.

The effects on the amino acid pattern in the empty body protein (Table 4), being the sum of carcass and organ protein, were to a large extent a reflection of effects in the carcass protein. The effects of protein and energy intake on the amino acid composition of the deposited protein (Table 5) were qualitatively similar to the effects on empty body protein. However, these effects were between 1.5 and 2 times as large as in the empty body protein.

Table 4. Amino acid composition of the empty body protein of female pigs at 45 kg as affected by protein and energy intake

	Content, g/16 g nitrogen[a]			Effects[b]		
Amino acid	2.5 x M	3.0 x M	SEM	Energy	Protein	Slope (b)
Lysine	6.67	6.61	.040	NS	**	.00154
Methionine	2.09	2.13	.017	NS	NS	-
Cystine	.88	.89	.007	NS	NS	-
Threonine	3.60	3.63	.022	NS	NS	-
Histidine	2.82	2.78	.023	NS	**	.00078
Isoleucine	3.43	3.47	.024	NS	NS	-
Leucine	6.47	6.57	.037	NS	NS	-
Phenylalanine	3.45	3.42	.022	NS	NS	-
Tyrosine	2.48	2.46	.024	NS	NS	-
Arginine	6.48	6.52	.033	NS	*	-.00077
Valine	4.32	4.42	.026	**	NS	-
EAA[c]	42.69	42.89	.23	NS	NS	-
Alanine	6.23	6.36	.026	***	**	-.00085
Aspartic acid	7.86	7.97	.041	NS	NS	-
Glutamic acid	12.19	12.32	.061	NS	NS	-
Glycine	8.89	9.07	.065	NS	***	-.00263
Serine	3.85	3.84	.017	NS	NS	-

[a,b,c] See footnotes Table 2.

DISCUSSION

Distribution of Protein and Amino Acids

At the low and high energy level, 14.8 and 15.8% of total body protein respectively, was in the organ fraction. These values are in good agreement with Wünsche et al. (1983) who reported in pigs of 35 kg, 15.7% of body protein was in the organ fraction. The distribution of individual amino acids between carcass and organs in the latter study, was also in good agreement with the results of the present study (Table 1). The big differences in the distribution of individual amino acids was the result of the considerable differences between amino acid patterns of carcass and organ protein, as discussed below.

Amino Acid Composition

The average lysine content (g/16 g N) of empty body protein of 6.64 at 45 kg is in good agreement with recent results of Moughan and Smith (1987) 6.2,

Table 5. Amino acid composition of protein deposited in the empty body of female pigs between 20 and 45 kg as affected by protein and energy intake

	Content, g/16 g nitrogen[a]			Effects[b]		
Amino acid	2.5 x M	3.0 x M	SEM	Energy	Protein	Slope (b)
Lysine	7.09	7.05	.070	NS	**	.00220
Methionine	2.18	2.27	.030	*	NS	-
Cystine	.83	.85	.013	NS	NS	-
Threonine	3.69	3.76	.039	NS	NS	-
Histidine	3.02	2.97	.040	NS	*	.00117
Isoleucine	3.54	3.65	.043	NS	NS	-
Leucine	6.52	6.71	.064	*	NS	-
Phenylalanine	3.47	3.43	.039	NS	NS	-
Tyrosine	2.50	2.46	.045	NS	NS	-
Arginine	6.41	6.46	.060	NS	*	-.00135
Valine	4.34	4.54	.045	**	NS	-
EAA[c]	43.56	44.12	.40	NS	NS	-
Alanine	5.97	6.17	.046	**	**	-.00131
Aspartic acid	8.03	8.28	.071	*	NS	-
Glutamic acid	12.41	12.70	.108	NS	NS	-
Glycine	8.59	8.89	.118	NS	***	-.00465
Serine	3.85	3.83	.030	NS	NS	-

[a,b,c] See footnotes Table 2.

Campbell et al. (1988) 6.4, Batterham et al. (1990) 6.4, Kemm et al. (1990) 6.3, Chung and Baker (1992) 6.2, and Kyriazakis et al. (1993) 7.0. The concentration of other amino acids in the whole body was also in agreement with these authors. However, between the lowest and highest reported values for each amino acid, a relative difference of 5 to 20% was found. Cystine may be underestimated in the present study because the bodies were scalded and scraped before slaughter and hair protein is extremely rich in cystine (Wünsche et al., 1983).

Considerable differences were present in the amino acid composition of protein in the carcass and organs. Schulz and Oslage (1976) and Wünsche et al. (1983) showed that the amino acid patterns of blood protein, muscle protein and protein in the hide, bone and adipose tissue (connective tissues) are distinctly different. Blood protein is relatively rich in lysine, histidine, leucine, phenylalanine, valine, and aspartic acid, and low in methionine, isoleucine, arginine, glycine, and glutamic acid. Muscle protein is relatively rich in lysine, histidine, methionine, leucine, and isoleucine and low in glycine and proline. Protein in the hide, bone and adipose

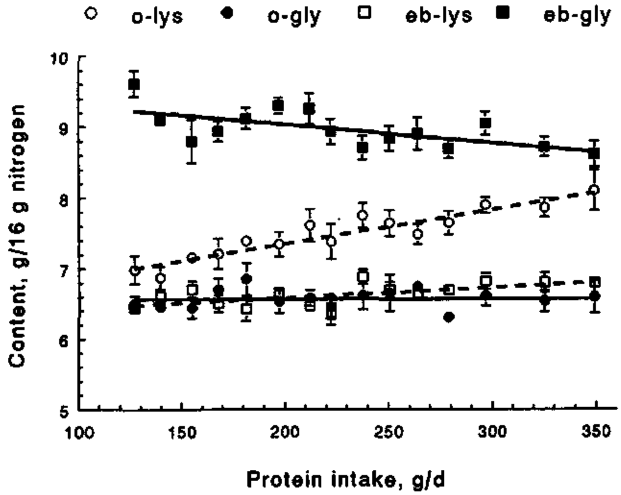

Figure 1. Contents of lysine (o-lys, eb-lys) and glycine (o-gly, eb-gly) in organ and empty body protein respectively, plotted against daily protein intake for gilts fed 15 graded levels of protein at two energy intake levels. Data for the two energy levels were combined, points represent means ± SEM (n = 6).

tissue is relatively rich in alanine, glycine, proline, and hydroxyproline and low in most of the essential amino acids, presumably because of the high proportion of collagen in these tissues (Riis 1983, Williams 1978). These differences in the amino acid pattern of different tissues presumably accounted for the reported differences of the amino acid composition of carcass and organ protein.

Effect of Protein and Energy Intake

Changes in the concentration of a number of amino acids in carcass, organ and empty body protein due to an increase in energy or protein intake, demonstrated that body amino acid composition is dependent on nutrient intake. Changes in amino acids in the empty body with increasing protein intake were also reported by Campbell et al. (1988), Batterham et al. (1990) and Chung and Baker (1992). Generally an increase in some essential amino acids and a decrease in alanine, glycine and proline was found. The present study indicates that these changes were the result of changes in carcass and organ protein (Table 2). The changes in carcass protein presumably reflect an effect of protein intake on lean and adipose tissue content. Bikker et al. (1994a) reported an increase in protein content and a decrease in lipid content with increasing levels of protein intake. Thus at low levels of protein intake, lean tissue (muscle) is reduced relative to other carcass tissues. In addition, Bikker et al. (unpublished data) found a decrease in carcass lean tissue content with an increase in energy intake. Because of the differences in amino acid composition between muscle and non-muscle carcass tissues as reported above, these effects presumably mediated the effect of nutrient intake on carcass amino acid composition. This is supported by results of Krick et al. (1993) with pigs treated with exogenous porcine somatotropin. Carcass protein of hormone treated pigs contained higher levels of most of the essential amino acids and lower levels of glycine and alanine, whereas porcine somatotropin is known to increase carcass muscle percentage.

The changes in concentration of a number of amino acids in the organ fraction, may be the result of the effect of protein and energy intake on the weight of blood and individual organs as reported by Bikker et al. (1994b). The weight of liver and empty intestines, relative to the whole organ fraction, increased with increasing energy intake. The weight of blood, kidneys, pancreas and spleen increased with increasing levels of protein intake. Blood, digestive tract, and liver contain about 5, 4, and 3% of the whole body protein, respectively (Schulz and Oslage 1976). Therefore, these three fractions together contain about 85% of the organ protein. Results of Schulz and Oslage (1976) indicate that the amino acid composition of the liver and the digestive tract is similar to that of muscle tissue. However, the concentration of certain amino acids in blood protein is distinctly different, as reported above. Differences between blood and several organs can to a large extent account for the effect of protein and energy intake on amino acid composition in the organ fraction.

The carcass protein accounts for about 85% of the empty body protein (Table 1). Therefore the changes in empty body amino acid composition with nutrient intake are mainly the result of a change in the proportion of muscle and non-muscle carcass protein as mentioned above. In addition, the composition of body protein can be affected by the increase in the proportion of body protein in the organs with increasing energy intake.

Amino Acid Composition of Deposited Protein

The effects of protein and energy intake on the amino acid pattern of the protein deposited between 20 and 45 kg were larger than the effects on the composition of body protein at 45 kg. This was to be expected because newly deposited protein is directly affected by energy and protein intake, whereas about half of the body protein at 45 kg was already present at the start of the experiment, and therefore not affected by nutrient intake between 20 and 45 kg.

The differences in the amino acid pattern between empty body protein at 45 kg, and the deposited protein between 20 and 45 kg, were the result of slightly higher contents (g/16 g N) of glycine (9.3), and alanine (6.6) and slightly lower values for lysine (6.1), histidine (2.6), isoleucine (3.3), and total essential amino acids (41.5) in the empty body protein of 20 kg pigs at the start of the experiment. A relative low ratio of muscle tissue to connective tissue in the young pig (Riis 1983) could explain these differences. This supposition is supported by Campbell et al. (1988) who reported significantly higher concentrations of glycine, alanine, proline, and hydroxyproline in 8 kg pigs compared to pigs of 20 kg, but not by results of Chung and Baker (1992) for pigs of similar body weights. This indicates that an effect of body weight presumably depends on genotype and feeding strategy. Furthermore the proportion of non-protein nitrogen may also decrease with increasing body weight (Zhang et al., 1986), resulting in lower contents of both essential and non-essential amino acids in the young pig (Moughan and Smith, 1987). Bikker et al. (unpublished data) found a similar distribution of deposited protein in growing (20-45 kg) and finishing (45-85 kg) pigs, fed on the basis of metabolic body weight. These results suggest that the influence of body weight on the amino acid composition of pigs of this improved genotype will be more pronounced in the piglet and the growing pig than in the finishing pig.

Consequences for Protein Requirements

The effect of protein intake on the amino acid composition of the empty body seems to be of little importance for animal husbandry, because in practice animals will usually be fed close to their protein requirements. However, for nutritional research, this effect implies that the marginal efficiency of amino acid utilization, determined under the assumption of a constant concentration of the studied amino acid in body protein (e.g. Heger and Frydrych 1985), can be confounded by an effect of protein intake on amino acid concentration.

Results of Table 5 suggest that for body gain, the requirements of methionine, leucine, isoleucine, and valine relative to lysine, increase slightly with an increase in feeding level. Moreover, Bikker et al. (unpublished data) found that the distribution of deposited protein between organs, lean and non-lean carcass parts may vary considerably with feeding level. The proportion of whole body protein deposition, deposited in the organs, increased from 10 to 16% and in the non-lean carcass parts from 29 to 31 % in growing pigs (20-45 kg), whereas the proportion in the lean tissue decreased from 61 to 53% with an increasing energy level from 2.2 to 3.7 times maintenance. This may exert an effect on the amino acid requirements.

The organs contain about 15% of the whole body protein and therefore have little effect on the amino acid composition of whole body protein. However, owing to the high turnover rate of organ protein, protein synthesis in the organs may account for about 50% of daily protein synthesis (Riis 1983, Simon 1989). The effect of organ protein on amino acid requirements is therefore, presumably, larger than suggested by the proportion of organ protein in the whole body protein. Fuller et al. (1989) found a higher concentration of total essential amino acids in dietary ideal protein for growth than in whole body protein. This may be explained by the high concentration of essential amino acids in the organ protein and the relatively large contribution of organs to the total amino acid requirements, as discussed above. Also taking into account the differences in amino acid composition between actual protein deposition and earlier deposited protein, these findings imply that whole body amino acid composition is not a good measure for the dietary ideal amino acid pattern. This is even more so in situations where the turnover of organ protein makes a relatively large contribution to the total protein synthesis, e.g. in slow growing animals or with diets which increase endogenous losses.

In conclusion, it can be stated that whole body amino acid composition is affected by the level of protein and energy intake. These effects are caused presumably by changes in the proportions of muscle and non-muscle carcass parts, the proportions of blood and viscera in the organ fraction, and the proportions of carcass and organ tissue in the whole body. These changes can affect the amino acid requirements for tissue deposition. A long term aim should be to distinguish between tissue groups with different amino acid compositions, turnover rates and growth rates, in order to determine the whole body amino acid requirements in relation to factors such as body weight, body composition, and feeding level.

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Chapter 4

PROTEIN AND LIPID ACCRETION IN BODY COMPONENTS OF GROWING GILTS (20-45 KG) AS AFFECTED BY ENERGY INTAKE

P. Bikker, V. Karabinas[1], M.W.A. Verstegen, and R. G. Campbell[2]

Department of Animal Nutrition, Wageningen Agricultural University,
Haagsteeg 4, 6708 PM Wageningen, The Netherlands

[1] Present address: Garibaldi 33, 45221 Ioannina, Greece

[2] Bunge Meat Industries, Corowa, Australia

Submitted

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P. Bikker, V. Karabinas, M.W.A. Verstegen, and R. G. Campbell

ABSTRACT

Twenty-eight gilts of a commercial hybrid were used to determine the relationships between energy intake and tissue deposition, and body composition in growing pigs from 20 to 45 kg, with a high genetic capacity for lean gain. The gilts received a single diet at six intake levels (1.7, 2.2, 2.7, 3.2, and 3.7 times maintenance (M); and ad libitum) ranging from 11.3 to 27.2 MJ DE/d. At 45 kg the animals were killed and their bodies dissected into carcass and organ fractions. Carcasses of pigs at 2.2 and 3.7 x M were dissected into lean and other carcass parts. Daily gain (ADG) increased linearly from 371 to 1075 g/d. Gain/feed increased from 500 to 600 g/kg. Deposition rates of protein and lipid increased linearly from 75 to 172 g/d and from 28 to 193 g/d, respectively. The ratio between lipid and protein deposition increased from .3 to 1.1. The relative organ mass and the non-lean carcass parts increased with increasing energy intake, whereas the body lean percentage decreased from 53.9% at 2.2 x M to 47.4% at 3.7 x M. In the carcass and organs, protein content decreased and lipid content increased with increasing energy intake. The proportion of body protein in the lean tissue decreased with increasing energy intake. Protein deposition increased with 5.77 g per MJ increase in DE intake, of which only about 40% was deposited in the lean tissue. Consequently ADG, gain/feed and protein deposition in the pigs are optimized at maximum feed intake, whereas lean percentage, efficiency of lean gain and distribution of body protein are optimal at lower levels of energy intake. An optimal feeding strategy can be designed after definition of the desired product and market circumstances.

Keywords: Pigs, Energy Intake, Protein Accretion, Lipid Accretion, Body Components

INTRODUCTION

Knowledge of the effect of energy intake on performance and body composition of pigs is essential for the development of biologically and economically efficient feeding strategies (Campbell, 1988). According to Whittemore and Fawcett (1976), the distribution of dietary energy between protein and lipid accretion, and consequently performance and carcass quality is determined by the relationship between energy intake and protein deposition. This relationship has been described as linear, curvilinear, and linear-plateau, depending on the maximum capacity for protein deposition (PD_{max}) in relation to the maximum feed intake (Campbell, 1988). For growing female pigs from 20 to 45 kg, Campbell et al. (1983)

determined a linear-plateau relationship with a PD_{max} of 128 g/d. However, in gilts of modern genotype, results of Bikker et al. (1994a) indicated a much higher PD_{max}, of over 160 g/d. Furthermore, the distribution of protein within the body can be affected by feed intake (De Greef and Verstegen, 1993). Therefore the present experiment was designed to determine: 1. the relationship between energy intake and lipid and protein deposition, and 2. the effect of energy intake on body composition and sites of protein deposition, in pigs with a high genetic capacity for lean gain.

This experiment is part of a larger project to study the effects of energy intake, body weight and nutritional history on tissue deposition in improved pigs.

EXPERIMENTAL PROCEDURES

Animals and Design

Twenty-eight 9-10 wks old gilts of a commercial hybrid (VOC Nieuw-Dalland, Venray, The Netherlands) were used in this study. They had an average body weight (BW) of 21.7 ± .3 kg at the start of the experiment. These animals were assigned to four blocks of seven pigs on the basis of BW, and from each block the pigs were randomly allocated to an initial slaughter group and six treatment groups. The four animals of the initial slaughter group were killed at the commencement of the experiment to determine the initial body composition. The six treatment groups represented six levels of feed intake, ranging from 1.7 times the energy for maintenance to ad libitum.

Dietary Treatments

There were six treatment groups, corresponding to six levels of feed intake: 1.7, 2.2, 2.7, 3.2, and 3.7 times energy for maintenance (M) and ad libitum. Digestible energy requirements for maintenance were calculated as .475 MJ DE per kg metabolic body weight ($BW^{.75}$) (ARC, 1981). One experimental diet (Table 1), was used for all treatment groups in order to ensure a constant dietary amino acid profile, to avoid interaction between energy intake and protein quality. This diet was designed to be adequate in protein and amino acids, with an amino acid composition close to that of ideal protein (Wang and Fuller, 1990), to allow determination of the relationship between energy intake and nutrient retention. The ileal digestibility of dietary protein and amino acids was determined at an intake level of 2.5 x M in a trial, involving five entire male pigs, averaging 28.1 ± .6 kg BW and fitted with Post-Valve T-Caecum cannulas (Van Leeuwen et al., 1991). The DE concentration of the diet was measured in a digestibility trial using ten entire male pigs with a BW of 30.7 ± .7 kg. These animals were housed in metabolism cages and received the experimental diet at 2.2 or 3.7 x M. The results of these two trials are included in Table 1.

The diet was analysed for dry matter, nitrogen, ash and amino acids according to procedures described previously (Bikker et al., 1994a).

Table 1. Composition of the experimental diet as fed

Ingredient, g/kg		Nutrient, g/kg[b]	
Barley	218.5	Dry matter	871.2
Wheat	231.6	Crude protein[c]	198.7
Maize	270.6	Ash	43.1
Soybean meal	100.3	Digestible energy, MJ/kg	15.1
Maize gluten meal	12.0	Lysine[c]	11.3
Potato protein	45.0	Methionine + cystine[c]	7.3
Fish meal	40.0	Threonine[c]	8.9
Animal fat	29.5	Tryptophan[c]	2.7
Soybean oil	11.6		
$CaCO_3$	6.8		
Monocalcium phosphate	7.4		
NaCl	2.5		
L-lysine	3.1		
DL-methionine	1.2		
L-threonine	1.9		
L-tryptophan	.5		
Calcium propionate	7.5		
Vitamin mineral premix[a]	10.0		

[a] Contributed the following per kilogram of diet: retinol, 10000 IU; cholecalciferol, 1800 IU; α-tocopherol, 30 mg; menadione dimethyl-pyrimidinol bisulfite, 4 mg; thiamin, 1 mg; riboflavin, 5 mg; niacin, 25 mg; pantothenic acid, 12 mg; pyridoxine, 1 mg; vitamin B_{12}, 40 μg; ascorbic acid, 50 mg; choline, 200 mg; copper, 20 mg; cobalt, .25 mg; iodine, .50 mg; iron, 80 mg; manganese, 30 mg; selenium, .15 mg; zinc, 100 mg. This mixture also supplied 20 ppm salinomicine per kilogram of diet.

[b] Analysed content.

[c] Determined ileal digestibility coefficients: crude protein, .81; lysine, .86; methionine and cystine, .84; threonine, .82; and tryptophan, .82.

Housing and Management

The pigs were housed individually in pens with half slatted floors in an insulated building, at an air temperature between 18 and 22°C. The pigs were offered the experimental diet in two equal portions per day, at 800 and 1600. The diet was pelleted and offered in dry form. The animals had free access to water. The pigs were weighed twice a week on Monday and Thursday, prior to feeding, and the daily feed allowances were adjusted to the expected gain for the following period of three or four days respectively. Feed refusals were collected and weighed twice a week.

Slaughter Procedures and Carcass Analyses

At a BW of 45 kg, the animals were killed by electrical stunning and exsanguination. The blood was collected, the viscera separated and the contents of the stomach and intestines removed. Blood and viscera were weighed, combined (organ fraction) per animal and stored in a plastic bag at -20°C. The cleansed and eviscerated carcass, including head and feet (carcass), was split longitudinally and the two halves were weighed and stored in plastic bags at -20°C.

The right side of the carcasses of the animals from the feeding levels 2.2 and 3.7 x M, was dissected into trimmed major joints (further referred to as lean fraction) and other carcass parts (further referred to as fat fraction) according to the Dutch standard dissection method (Bergström and Kroeske, 1968; Kanis, 1988). The lean fraction comprised four parts, the ham, shoulder, and loin, all without subcutaneous fat, and meat scraps, a group of miscellaneous muscles. The fat fraction consisted of backfat, belly, fat trimmed from ham and shoulder, lard, the first four ribs, head, feet, tail, and backfat scraps (Walstra, 1980). For the animals of the initial slaughtergroup a value of 60.5% lean tissue in the carcass was adopted from De Greef (1992), who used animals with the same genetic background.

The frozen carcass (left plus right halves) and organ fractions were homogenized in a commercial butchers' mincer and sub-sampled for proximate analysis. For pigs from the treatments 2.2 and 3.7 x M, the lean fractions were also homogenized and sub-sampled for proximate analysis. Thereafter, proportional aliquots of the lean and fat fractions and of the left side of the carcass were combined per animal and homogenized to provide a sample of the whole carcass. Composition of the fat fraction was calculated on the basis of the composition of the whole carcass and the lean fraction.

Dry matter, nitrogen, lipid and ash contents in organ, carcass and lean fractions were determined as described previously (Bikker et al, 1994a).

Statistical Analysis

Regression analysis was used to determine linear and quadratic effects of feed intake on performance parameters and body characteristics, using the backward elimination procedure (Draper and Smith, 1981). In addition, a linear-plateau model (Bikker et al., 1994a) was used to derive a possible intrinsically determined maximum rate of protein deposition. Data were analysed by linear (GLM) and derivative-free nonlinear (NLIN, method DUD) regression procedures (SAS, 1989).

RESULTS

Performance

Average DE intake (20 to 45 kg) for the six treatment groups ranged from 11.3 to 27.2 MJ/d for 1.7 x M up to ad libitum (Table 2). The concomitant average daily gain increased linearly ($P < .001$) with increasing feed intake from 371 g/d to 1075 g/d. The relationship between DE intake (DEI, MJ/d) and ADG (g/d) was described as:

$$ADG = -104\ (\pm\ 43) + 43.6\ (\pm\ 2.2) \times DEI \qquad (r^2 = .948,\ RSD = 60.3) \qquad [1]$$

Gain/feed increased linearly ($P < .01$) with increasing feed intake. The quadratic effect just failed to be significant ($P = .06$), but gain/feed was similar for the three highest feeding levels. Backfat thickness increased with the first two increments in feeding level and remained constant, at about 8.3 mm thereafter (Table 2).

Body Composition

Empty body weight as a percentage of live weight, and carcass weight as a percentage of empty body weight decreased ($P < .05$ and $P < .001$), with increasing feeding level. Lean tissue content in the empty and in the carcass also decreased with increasing feed intake ($P < .01$) (Table 3). Rate of carcass gain increased curvilinearly and gain of organs, lean and fat tissue increased linearly with

Table 2. Energy intake and performance of gilts between 20 and 45 kg at six levels of feed intake

	Feeding level, times maintenance energy								Effects[a]	
Parameter	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	L	Q
Feed intake, g/d	750	941	1161	1362	1582	1813	1268	38	-	-
DE intake, MJ/d	11.3	14.1	17.4	20.5	23.8	27.2	19.0	.57	-	-
ADG, g/d	371	488	631	818	959	1075	724	26	***	NS
Gain/feed, g/kg	505	522	547	604	610	600	565	23	**	†
Backfat, mm	6.7	7.3	8.2	8.6	8.2	8.3	7.9	.32	*	*

[a] Linear (L) and quadratic (Q) effects of energy intake. NS not significant, P > .1, † P < .1, * P < .05, ** P < .01, *** P < .001.

[b] Pooled standard error of the six treatment groups.

Table 3. Body composition of gilts at 45 kg, fed at six feeding levels from 20 to 45 kg BW

	Feeding level, times maintenance energy								Effects[b]	
Parameter, %[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[c]	L	Q
Empty body	95.5	97.1	96.5	94.5	94.7	94.9	95.5	.46	NS	*
Carcass	83.5	84.4	83.1	80.8	81.0	80.9	82.3	.57	***	NS
Organs	16.5	15.6	16.9	19.2	19.0	19.1	17.7	.57	***	NS
Lean	-	53.9	-	-	47.4	-	50.6	.66	**	ND
Fat	-	30.5	-	-	33.7	-	32.1	.52	*	ND
Lean in carcass	-	63.8	-	-	58.5	-	61.1	.68	**	ND

[a] Empty body weight (live weight less contents of the digestive tract) as percentage of live weight. Carcass, organs, lean, and fat as percentage of the empty body and lean as percentage of the carcass.

[b] Linear (L) and quadratic (Q) effects of energy intake. NS not significant, P > .1, † P < .1, * P < .05, ** P < .01, *** P < .001, ND not determined.

[c] Pooled standard error of the six and two treatment groups.

increasing feed intake (Table 4).

The chemical body composition (g/kg) of the animals of the initial slaughter group was: water 704 ± 5.3, protein 161 ± 2.0, lipid 96.6 ± 5.8, and ash 28.9 ± .98. These values were used to calculate nutrient retention of the other pigs.

The water, protein, lipid and ash content of the carcass, organs, and empty body of the animals at 45 kg were significantly affected by feed intake (Table 5). Only the ash content of the viscera was not affected (P > .1). These effects were most pronounced for the first two increments in feeding level. For protein and ash

Table 4. Deposition rates of carcass, organs, lean and fat tissue, and efficiency of lean gain in gilts between 20 and 45 kg at six levels of feed intake

Parameter,	Feeding level, times maintenance								Effects[a]	
g/d	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	L	Q
Carcass	299	419	518	612	716	801	561	20.7	***	*
Organs	46.6	55.5	84.3	139	158	180	110	9.6	***	NS
Lean	-	279	-	-	405	-	342	14.1	**	ND
Fat	-	140	-	-	311	-	226	13.5	***	ND
Lean/feed, g/kg	-	298	-	-	258	-	278	13.0	NS	ND

[a,b] See footnotes Tables 2 and 3.

Table 5. Composition of the carcass, organs and empty body of gilts of 45 kg, fed at six feeding levels from 20 to 45 kg

Parameter,	Feeding level, times maintenance								Effects[a]	
g/kg	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	L	Q
CARCASS										
Water	669	656	631	624	629	616	638	7.4	***	NS
Protein	198	191	179	175	177	172	182	2.7	**	*
Lipid	91	114	148	159	152	172	140	8.7	***	NS
Ash	38.6	33.5	33.1	33.8	33.7	33.0	34.3	.98	*	*
ORGANS										
Water	786	781	780	781	782	774	781	4.5	NS	*
Protein	162	159	156	149	154	153	155	1.8	**	NS
Lipid	27.1	36.0	37.7	44.4	39.8	44.7	38.3	4.0	***	NS
Ash	9.8	10.0	9.7	9.7	10.1	10.0	9.9	.16	NS	NS
EMPTY BODY										
Water	689	675	656	654	658	646	663	6.8	***	NS
Protein	192	186	175	170	173	169	177	2.4	**	*
Lipid	81	102	130	137	131	148	121	7.7	***	NS
Ash	33.8	29.8	29.1	29.1	29.2	28.6	30.0	.78	**	*

[a,b] See footnotes Tables 2 and 3.

content of the carcass and empty body, this was reflected by the quadratic effect ($P < .05$) of feed intake. Water and protein content in the carcass, viscera, and empty body, decreased with increasing feeding level whereas lipid content increased in all three fractions. However, the increase in lipid content from 1.7 x M to ad libitum was much greater than the decrease in protein content, about 70 g/kg vs. 20 g/kg.

Deposition Rates

Deposition rates of protein (PD), lipid (LD), and ash in carcass, organs and empty body increased linearly ($P < .001$) with increasing feed intake (Table 6, Figure 1). For water deposition, a quadratic effect ($P < .05$) of feed intake was present. Total daily protein deposition increased from 75 to 172 g. This effect of energy intake was described as:

$$PD = 16.1\ (\pm 7.9) + 5.77\ (\pm .40) \times DEI \qquad (r^2 = .904,\ RSD = 11.1) \qquad [2]$$

The linear increase in lipid deposition in the empty body ranged from 28 to 193 g/d and was described as:

$$LD = -94.0\ (\pm 11.6) + 10.5\ (\pm .59) \times DEI \qquad (r^2 = .936,\ RSD = 16.4) \qquad [3]$$

The ratio between lipid and protein deposition (LD/PD) in the empty body increased linearly from .3 to 1.1 with increasing feed intake. The biggest increase in LD/PD

Table 6. Deposition rates of water, protein, lipid, and ash in the carcass, organs and empty body of gilts between 20 and 45 kg at six levels of feed intake

Parameter, g/d	Feeding level, times maintenance						Mean	SEM[b]	Effects[a]	
	1.7	2.2	2.7	3.2	3.7	ad lib			L	Q
CARCASS										
Water	193	267	304	350	417	445	329	15.0	***	*
Protein	66.7	88.9	98.8	112	135	143	107	4.92	***	†
Lipid	26.6	47.1	92.9	123	134	183	101	11.0	***	NS
Ash	12.8	13.9	16.9	20.6	24.1	26.0	19.1	1.12	***	NS
Lipid/protein	.35	.55	.95	1.09	1.00	1.29	.87	.099	***	NS
ORGANS										
Water	36.1	42.8	65.0	108	123	136	85	8.10	***	NS
Protein	8.5	9.9	14.3	21.0	25.7	28.9	18.1	1.04	***	NS
Lipid	1.5	2.4	4.0	8.0	7.7	10.9	5.8	1.01	NS	***
Ash	.43	.54	.76	1.26	1.56	1.73	1.05	.064	***	NS
Lipid/protein	.12	.25	.29	.39	.30	.37	.29	.053	***	NS
EMPTY BODY										
Water	229	309	369	456	539	580	414	17.3	***	*
Protein	75.3	98.8	113	134	160	172	125	4.95	***	†
Lipid	28.1	49.5	96.9	131	142	193	107	11.9	***	NS
Ash	13.2	14.5	17.6	21.9	25.7	27.8	20.1	1.13	***	NS
Lipid/protein	.32	.52	.87	.98	.89	1.13	.78	.089	***	NS

[a,b] See footnotes Tables 2 and 3.

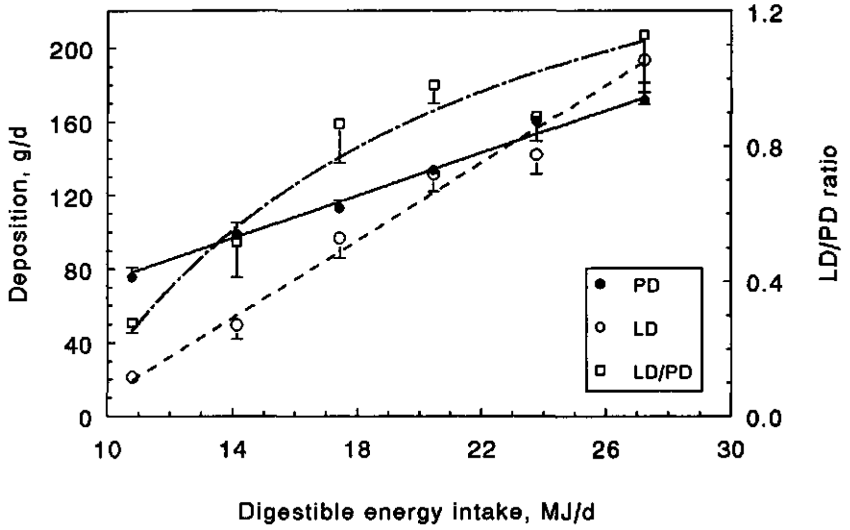

Figure 1. The relationships between daily digestible energy intake (DEI) and rate of protein deposition (PD = 16.1 + 5.77 x DEI), rate of lipid deposition (LD = -94.0 + 10.5 x DEI) and the ratio between lipid and protein deposition (LD/PD). The curvilinear increase in LD/PD was calculated as the ratio between the equations for lipid and protein deposition.

was found with the first two increments in feeding level, but a significant quadratic effect was not found.

Lean and Fat Tissue

Carcasses of animals of two treatment groups, 2.2 and 3.7 x M were dissected. Large differences were present in the composition of the lean and fat fractions (Table 7). Lipid content and LD/PD were three to four times higher in the fat fraction than in the lean fraction, whereas water and protein content were lower in the fat fraction. Results in Table 7 suggest a decrease (not significant) in protein content and an increase (not significant) in lipid content in these two fractions, with increasing feeding level. Protein and lipid deposition and LD/PD increased significantly with increasing feed intake both in the lean and fat fractions. The distribution of body protein was affected by feed intake (Table 8). The proportion of body protein deposited in the organs increased, while the proportion of body protein in the lean tissue decreased with increasing energy intake.

Table 7. Composition of lean and fat tissue at 45 kg and deposition rates of protein and lipid in lean and fat tissue of gilts between 20 and 45 kg at two levels of feed intake

	Lean tissue				Fat tissue			
	Energy level				Energy level			
Parameter	2.2xM	3.7xM	SEM[a]	Effect[b]	2.2xM	3.7xM	SEM[a]	Effect[b]
Content, g/kg								
Water	707	699	3.9	NS	565	532	9.2	†
Protein	199	193	1.3	NS	178	155	8.1	†
Lipid	57.2	68.5	3.7	†	213	269	17.9	†
Ash	33.3	35.4	1.2	NS	33.9	31.2	2.5	NS
Deposition, g/d								
Protein	60.3	85.1	2.2	**	28.6	49.4	3.0	***
Lipid	16.9	34.3	1.3	**	30.2	99.7	8.0	***
Lipid/protein	.29	.40	.029	*	1.11	2.02	.27	*

[a] Pooled standard error of the two treatment groups.

[b] Linear effects of energy intake. NS not significant, $P > .1$, † $P < .1$, * $P < .05$, ** $P < .01$, *** $P < .001$.

Table 8. Distribution of body protein deposited in gilts between 20 and 45 kg, at two levels of feed intake

Fraction, %	2.2xM	3.7xM	SEM[a]	Effect[b]	Slope[c]	Extra PD[d]
Empty body	100	100	-	-	5.77	100
Carcass	89.9	84.0	.51	***	4.42	76.5
Organs	10.1	16.0	.51	***	1.35	23.5
Lean	61.0	53.1	.85	**	2.51	41.2
Fat	28.9	30.8	.96	NS	2.16	35.3
Lean in carcass	67.8	63.3	1.06	*	-	53.8

[a] Pooled standard error of the two treatment groups.

[b] Linear effects of feed intake. NS not significant, $P > .1$, † $P < .1$, * $P < .05$, ** $P < .01$, *** $P < .001$.

[c] Slope, linear increase in protein deposition (g/MJ DE) in the empty body, carcass and organs (based on six treatment groups) and in lean and fat tissue (based on two treatment groups).

[d] Distribution of extra protein, deposited with an increase in feed intake, based on the slopes of the linear regression.

DISCUSSION

Design

In order to determine the effects of dietary protein or energy on protein and lipid accretion, ideally the input of energy and protein should be varied independently, as in Bikker et al (1994a). However, the variation of energy intake over a wide range of intake levels at constant adequate protein intake, would at low energy intake levels lead to diets extremely high in protein. In addition this design would not allow the inclusion of a group of animals receiving feed ad libitum. Therefore in this experiment the effect of energy intake on performance and body composition was determined by feeding graduated levels of one diet with a constant, adequate protein to energy ratio.

Performance and Accretion Rates of Protein and Lipid

The ad libitum feed intake of 27.2 MJ DE/d was similar to that of gilts with the same genetic background in an earlier experiment (Bikker et al., 1994a). With increasing energy intake, ADG increased linearly to 1075 g/d at the ad libitum intake level. This linear increase was in good agreement with findings of many authors, reviewed by the ARC (1981) for pigs in this weight range. The increase in ADG of 44 g/MJ DE was higher than derived by Close et al. (1983), who found 33 g/MJ ME, Campbell et al. (1983), who found 25 g/MJ DE, and others (see review ARC, 1981). Gain/feed was improved with the first three increments in feeding level from 500 to 600 g/kg and remained relatively constant at the higher intake levels. This response was presumably the result of the combined effects of a reduction of the proportion of energy used for maintenance purposes and an increase in the proportion of fat in the body gain (Table 6). These results indicate that the highest performance of these gilts is attained when the animals are given free access to feed.

Protein deposition responded linearly to an increase in daily energy intake from 75 to 172 g/d, with a slope of 5.77 g/MJ DE. A similar response in protein gain to energy intake was reported by Campbell et al. (1988) and Rao and McCracken (1991) for genetically improved boars from 40 to 90 kg. This indicated the high genetic capacity for lean growth of the animals in relation to their feed intake capacity. In contrast, Campbell et al. (1983) reported for unimproved gilts between 20 and 45 kg, a linear increase in protein deposition of 4.19 g/MJ DE until a plateau of 128 g/d was reached, at a daily intake of 29.4 MJ DE. These results indicate that genetic differences between animals can find expression both in the slope, reflecting the distribution of dietary energy at sufficient protein intake, between protein and lipid deposition, and in the maximum capacity (plateau) for protein deposition (PD_{max}). This conclusion is in agreement with Campbell et al. (1988) who compared two lines of boars between 45 and 90 kg BW.

The almost significant ($P = .07$) quadratic component in the relationship between DE intake and protein deposition may indicate that some pigs had reached their PD_{max}. Therefore this relationship was further analysed with a linear-plateau model. Compared to the linear regression, this model showed an improved goodness-of-fit, $R^2 = .937$ ($P < .01$). Model parameters were estimated as: slope, 6.53 ± .41 g/MJ; plateau, 170 ± 6.6 g/d; and point of transition 25.4 ± 1.15 MJ DE/d. However, this plateau was caused by two out of four animals of the ad libitum treatment, which consumed more feed than their counterparts (29.6 vs. 24.8 MJ DE) without showing any further increase in protein deposition. These results may imply that for the pigs used in this study, the energy intake required for PD_{max} was about the maximum daily feed intake.

Lipid deposition increased linearly from 28 to 193 g/d. From the linear increase in protein and lipid deposition, one might conclude that below PD_{max} the ratio LD/PD is constant and independent of energy intake (e.g. Whittemore, 1983). However, LD/PD increased from .3 to 1.1 in the present study. Extrapolation of equations [2] and [3] indicated that at zero lipid deposition, 68 g of protein would be retained. This finding is supported by Close et al. (1983) and Kyriazakis and Emmans (1992a,b), who reported protein deposition rates of 40 to 90 g/d while the lipid deposition was about zero. This preference for protein deposition at low energy intake levels (and consequently different points of intersection of the x-axis for protein and lipid deposition), explains the increase in LD/PD with energy intake, and therefore also in body lipid content, even where protein and lipid deposition increased linearly with increasing DE intake. The LD/PD of .3 at 1.7 x M was in good agreement with Kyriazakis and Emmans (1992a,b), and much lower than .8 to 1.0, often suggested as the minimum LD/PD (e.g. Ellis et al. 1983). Each MJ increase in DE intake resulted in an increase in protein and lipid deposition of 5.77 and 10.5 g/d respectively (Equation [2] and [3]). Thus the LD/PD for extra weight gain, here defined as $\Delta LD/\Delta PD$, was 1.82. With increasing energy intake the LD/PD will approach this value curvilinearly, until the feed intake capacity or PD_{max}

becomes limiting. This is illustrated in Figure 1, which shows the increase in protein and lipid deposition, and in LD/PD, calculated as the quotient of Equation [3] and [2]. These results are in good agreement with Campbell et al. (1983), Rao and McCracken (1991) and Kyriazakis and Emmans (1992a,b). The relationship of LD/PD to energy intake means that a constant LD/PD is not a good criterion to define the genetic capacity of a pig, as suggested by Whittemore (1983) and as also used in several pig growth models. The slope between energy intake and protein deposition, and the ratio ΔLD/ΔPD can be useful alternatives.

Body Composition and Distribution of Protein

The weight of the empty body as a percentage of live weight, decreased slightly with increasing feed intake, owing to an increase in gutfill. Within the empty body, the carcass weight decreased from approximately 84 to 81% with a concomitant increase in weight of the viscera from 16 to 19%. The latter increase was predominantly the result of the response of the food processing organs, including the intestines, liver, and kidneys, to an increased feed intake, and representing increased metabolic activity (Bikker et al., 1994b). The response of metabolically active organs to nutrient intake was also reported by Koong et al. (1983) and Rao and McCracken (1992), but was not found by Gütte et al. (1978). Results of the latter study were obtained by feeding incremental amounts of starch and saccharose in addition to a constant amount of a high protein diet, which was the same for all energy intake levels. These different effects of nutrient intake on organ growth indicate that the dietary composition may be important for the response of organs to an increased feed intake.

The percentage of lean tissue in the empty body decreased from 53.9 to 47.4% with an increase in feeding level from 2.2 to 3.7 x M. This decrease was the result of the above mentioned decrease in carcass weight, and a decrease in the lean percentage within the carcass from 63.8 to 58.5%. The reduction in carcass lean of .55% per MJ increase in DE intake was in agreement with reductions of .3% (Ellis et al., 1983), .4% (Kanis, 1988) and .7% (Gütte et al., 1978) per MJ DE for pigs between 70 and 110 kg. However, Haydon et al. (1989) and Rao and McCracken (1992) found no effect of feed restriction on lean percentage in pigs from 20 to 50 and from 30 to 90 kg respectively. There are two possible explanations for these differences: the genetic capacity of the animals, and the levels of feed intake applied. A restriction in energy intake in animals which have reached PD_{max} will mainly reduce the fat deposition and consequently will increase the lean percentage more than in pigs which have not yet reached PD_{max}. Secondly, in this study an increase in DE intake from 2.2 to 3.2 x M affected protein and lipid content much more than a similar increase from 3.2 x M to ad libitum, due to a curvilinear increase in LD/PD. The choice of energy intake levels therefore influences the effects on LD/PD and body composition which will be found.

In agreement with the decrease in lean percentage, the efficiency of lean gain (lean gain/feed intake) decreased from 298 to 258 g/kg feed, when the feeding level increased from 2.2 to 3.7 x M. Owing to the small number of dissected animals, this effect was not significant (P = .13). Conversely, gain/feed (Table 2) increased from 522 to 610 g/kg with an increase in intake from 2.2 to 3.7 x M. These results indicate that the energy intake level required to optimize efficiency of lean gain was lower than the level required to optimize body gain. This was also found by Kanis (1988) for pigs from 30 to 110 kg.

The effect of feed intake on body tissues suggested an effect of feed intake on the sites of protein deposition. This was confirmed by results in Table 8. Protein deposited in the organs, as a proportion of whole body protein deposition between 20 and 45 kg, increased from 10.1 to 16.0% and the proportion in the lean tissue decreased from 61.0 to 53.1%, when the energy intake was increased from 2.2 to 3.7 x M. Based on the slopes of the linear regression of protein deposition in the empty body, carcass, organs, and lean and fat tissue, it was concluded that of each extra gram of protein deposited only about 40% was deposited as lean tissue. This finding was in agreement with De Greef and Verstegen (1993) for pigs between 25 and 65 kg. Studies in which the source of energy is different and(or) in which protein intake is kept constant may give different results (Susenbeth and Keitel, 1988). Therefore this effect of feed intake on protein distribution needs further evaluation, especially because protein in lean meat is the most valuable for human consumption.

The present study indicates that protein deposition increases linearly with increasing energy intake in growing gilts (20-45 kg) with a high genetic potential for lean gain. However, a decreasing proportion of the protein is deposited as lean tissue. Secondly, the rate of lipid accretion increases more with energy intake than the rate of protein accretion. As a consequence ADG, gain/feed and protein deposition in these pigs are optimized at maximum feed intake. The lean percentage, efficiency of lean tissue deposition, and proportion of body protein deposited as lean tissue, are optimized at lower levels of energy intake. Consequently, an optimal feeding strategy for these pigs can only be designed after appropriate definition of the desired product and market circumstances.

IMPLICATIONS

Daily gain and protein and lipid deposition in growing gilts (20-45 kg) responded linearly to increasing energy intake up to maximum feed intake. The lean tissue percentage, the efficiency of lean tissue gain and the proportion of body protein in the lean tissue, decreased with increasing energy intake. Giving animals free access to feed will therefore optimize daily gain and protein deposition but not body composition. For modelling growth in pigs, extra protein deposition per MJ digestible energy intake or the ratio extra protein/extra lipid deposition with increasing energy intake, can be used as a parameter to define the genetic capacity of the animals.

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Chapter 5

PERFORMANCE AND BODY COMPOSITION OF FATTENING GILTS (45-85 KG) AS AFFECTED BY ENERGY INTAKE AND NUTRITION IN EARLIER LIFE.

1. GROWTH OF THE BODY AND BODY COMPONENTS

P. Bikker, M.W.A. Verstegen, B. Kemp[1], and M.W. Bosch

Department of Animal Nutrition, Wageningen Agricultural University,
Haagsteeg 4, 6708 PM Wageningen, The Netherlands

[1] Department of Animal Husbandry, Wageningen Agricultural University

Submitted

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ABSTRACT

Forty-eight gilts of a commercial hybrid were used to determine the effects of energy intake from 20 to 45 kg, on the relationship between energy intake and weight gain of the body and body components from 45 to 85 kg. Two groups of 24 gilts received a single diet either at 2.2 (low pigs) or 3.7 (high pigs) times maintenance (M) from 20 to 45 kg. From 45 to 85 kg the pigs were fed the same diet at one of six intake levels (1.7, 2.2, 2.7, 3.2 and 3.7 x M and ad libitum). At 85 kg, the animals were dissected into organs, lean and fat tissue. In the low pigs, body and lean tissue gain between 45 and 85 kg increased curvilinearly with increasing energy intake from 432 to 1412 g/d and from 228 to 507 g/d, respectively. In the high pigs, body and lean tissue gain increased from 394 to 1201 g/d and from 238 to 508 g/d, respectively. The percentage lean tissue in the carcass decreased curvilinearly with increasing energy intake from 62.9 to 56.5%, and from 62.5 to 53.9% in the low and high pigs, respectively. Previously restricted pigs gained on average 140 g/d faster ($P < .001$) and their carcass lean tissue content at slaughter was almost 3% higher ($P < .001$). These differences increased with increasing energy level between 45 and 85 kg. The increased gain was largely the result of an increase in organ growth and gut contents, and was only evident up to 65 kg. Accretion rates of lean and fat tissue were not affected by previous nutrition ($P > .1$). Thus the higher lean content at 85 kg in previously restricted pigs was not the result of compensation in lean gain, but was already present at the end of the restriction phase at 45 kg.

Keywords: Pigs, Energy Intake, Body Gain, Body Components, Nutritional History

INTRODUCTION

Compensatory gain in pigs after a period of feed restriction has been studied by many authors during several decades. Nielsen (1964), Owen (1971) and Donker et al. (1986) reported an increase in feed intake and consequently in body gain, in pigs with free access to feed after a period of restriction. Others reported an increase in the efficiency of gain in restrictedly fed animals after a period at a low feeding level (Campbell et al., 1983; Kirchgessner et al., 1984). These studies however, do not allow the determination of the presence and the degree of compensation are affected by the level of feeding in the realimentation period. In addition, little information is available concerning the effect of a previous restriction on the composition of body gain in the realimentation period. This information is even more important since Koong et al. (1983) reported that weights of metabolic organs at slaughter are significantly affected by the feeding strategy. Thus it may be that an increase in organ gain accounted for a large part of the compensatory gain in the reported studies.

Therefore in this study the effects of energy intake from 20 to 45 kg on performance, tissue deposition and composition of gain between 45 and 85 kg have been studied in gilts at six levels of feeding from 45 to 85 kg.

EXPERIMENTAL PROCEDURES

Animals and Design

Forty-eight 9 - 10 wks old gilts of a commercial hybrid (VOC Nieuw-Dalland, Venray, The Netherlands) with an average liveweight of 21.8 ± .2 kg at the start of the experiment, were used in this study. These animals were allocated on the basis of BW among 12 treatment combinations in a 2 x 6 factorial arrangement with four pigs per treatment combination. The respective treatments were level of feeding from 20 to 45 kg, equivalent to 2.2 and 3.7 times energy for maintenance (M), and level of feed intake from 45 to 85 kg, ranging from 1.7 times energy for maintenance to ad libitum. The treatment period from 20 to 45 kg will be further referred to as the nutritional history and the gilts with the low (2.2 x M) and high (3.7 x M) nutritional history will be referred to as low and high pigs respectively. The treatment period from 45 to 85 kg will be further referred to as the fattening period.

Dietary Treatments

The six feeding levels in the fattening period were 1.7, 2.2, 2.7, 3.2, and 3.7 x M, and ad libitum. One experimental diet, adequate in protein and amino acids, was used from 20 to 85 kg for all treatment groups, in order to ensure a constant dietary amino acid profile. This allowed the determination of the relationship between energy intake and tissue deposition. The DE concentration of the diet was measured in a digestibility trial using ten intact male pigs at a BW of 30.7 ± .7 kg and at a BW of 65.7 ± 2.0 kg. These animals were housed in metabolism cages and received the experimental diet at 2.2 or 3.7 times maintenance. Energy digestibility was not affected by the level of feed intake nor by the BW of the animal. The composition of the experimental diet, including the DE concentration and contents of digestible amino acids, has been published previously (Bikker et al., 1994a). The energy content of the experimental diet was 15.1 MJ of DE/kg.

Housing and Management

The pigs were housed individually in pens with half slatted floors in an insulated building, at an air temperature between 18 and 22°C. The pigs were offered the experimental diet in two equal portions per day, at 800 and 1600. The diet was pelleted and offered in dry form. The animals had free access to water. The pigs were weighed twice weekly on Monday and Thursday, prior to feeding, and the daily feed allowances were adjusted to expected gain for the following period of three or four days, respectively. The feed allowances were based on metabolic body weight ($BW^{.75}$), with digestible energy requirements for maintenance calculated as .475 MJ DE per kg $BW^{.75}$ (ARC, 1981). Feed refusals were collected and weighed twice weekly.

Slaughter Procedures and Carcass Analysis

At a liveweight of 85 kg, the animals were killed by electrical stunning and exsanguination. Body components were collected and stored as described by Bikker et al. (1994a). The bodies were dissected into three fractions or tissue groups, referred to as organ, lean and fat fraction. The organ fraction comprised the blood and all organs, including mesenteric fat. The lean fraction comprised the ham, shoulder, and loin, all without subcutaneous fat, and meat scraps. The fat fraction comprised all other carcass parts and consisted mainly of backfat, belly fat, other fat depots, head, feet, and tail (Bikker et al., 1994a).

The body composition of the pigs at 20 and 45 kg was estimated using the data presented in Bikker et al. (1994a). The latter experiment from 20 to 45 kg was conducted in the same period, under similar experimental conditions, and with gilts from the same herd as the present study.

Statistical Analysis

Regression analysis was used to determine linear and quadratic effects of feed intake in the fattening period, on performance, tissue deposition and body composition. The effect of nutritional history on regression parameters was determined using dummy variables and a backward elimination procedure (Draper and Smith, 1981). Data were analysed by linear (GLM) regression procedures (SAS, 1989).

RESULTS

Performance

In the growing period from 20 to 45 kg, daily gain of the high pigs was much higher ($P < .001$) than that of the low pigs, 959 vs. 501 g/d (Table 1). As a result the low pigs were 22 days older at the start of the fattening period. In addition, these pigs had less backfat (Table 1) and a higher ($P < .01$) estimated body lean percentage, 53.9 vs. 47.4% (Bikker et al., 1994a) at 45 kg.

In the fattening period, the average DE intake at the different intake levels, increased from 18.3 to 44.8 MJ/d for the low pigs, and from 18.0 to 41.9 MJ/d for the high pigs (Table 2). The concomitant ADG increased curvilinearly with increasing energy intake to 1412 and 1201 g/d, respectively. Gain/feed also increased curvilinearly with increasing DE intake. The first increments in energy level led to a large increase in feed efficiency, which remained relatively constant at the three highest energy levels. The rate and efficiency of empty body gain also increased curvilinearly. The low pigs showed a better performance in this period than the high pigs, which is reflected by an effect of the nutritional history on the linear component of the relationships for ADG, gain/feed, and rate and efficiency

Table 1. Performance from 20 to 45 kg of gilts at two feeding levels

	Energy level[a]			
Parameter	Low (2.2xM)	High (3.7xM)	SEM[b]	Effect[c]
Days in exp.	47.4	25.8	.86	***
DE intake, MJ/d	14.2	23.6	.15	***
ADG, g/d	501	959	13	***
Gain/feed, g/kg	534	613	9.4	***
Backfat, mm	7.6	8.5	.12	***

[a] Energy level times energy for maintenance (M).
[b] Pooled standard error of the two treatment groups, n = 24.
[c] Effect of energy intake, *** $P < .001$.

of the empty body gain. This implies that the difference between high and low pigs increased with increasing levels of energy intake (DEI), which is illustrated for ADG (g/d) in Figure 1. These relationships were described as:

$$\text{ADG} = -550\ (\pm 167) + [61.4\ (\pm 11.3) - 1.87\ (\pm .37) \times \text{DUM}] \times \text{DEI} - .44\ (\pm .18) \times \text{DEI}^2 \quad (r^2 = .943,\ \text{RSD} = 80.8) \quad [1]$$

in which DUM represents the dummy variable for the nutritional history, with values of -1 and +1 for the low and high pigs respectively. Consequently, the coefficients for the linear component were 63.3 and 59.5 ($P < .001$) for the low and high pigs, respectively. On average, ADG and gain/feed between 45 and 85 kg were 138 g/d and 49 g/kg higher for the low pigs. However, results in Table 3, in which the fattening period was divided in two periods of 20 kg, showed that this improved gain and efficiency were only evident from 45 to 65 kg of BW.

Table 2. Energy intake and performance of gilts between 45 and 85 kg, at six levels of feed intake, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	*ad lib*	Mean	SEM[b]	DE intake	History
DE intake, MJ/d	L	18.3	23.6	29.3	35.5	40.4	44.8	32.0	.52		
	H	18.0	23.9	28.7	34.6	39.2	41.9	31.0			
ADG, g/d	L	432	656	988	1148	1278	1412	986	40	$L^{***}Q^{*}$	ΔL^{***}
	H	394	659	801	907	1127	1201	848			
Gain/feed, g/kg	L	356	419	510	489	478	475	455	19	$L^{***}Q^{***}$	ΔL^{***}
	H	331	416	422	397	434	434	406			
Empty body gain, g/d	L	416	621	916	1073	1195	1298	920	36	$L^{***}Q^{**}$	ΔL^{**}
	H	394	644	783	906	1087	1162	829			
EB gain/feed, g/kg[d]	L	343	397	473	457	447	437	426	17	$L^{***}Q^{***}$	ΔL^{**}
	H	331	407	412	396	418	420	397			
Backfat, mm	L	8.6	9.2	10.3	10.9	12.2	11.5	10.4	.79	L^{***}	ΔL^{***}
	H	8.8	10.3	12.4	13.4	13.0	14.1	12.0			

[a] His., nutritional history, feeding level from 20 to 45 kg, being 2.2 (L) or 3.7 (H) times maintenance.

[b] Pooled standard error of the 12 treatment groups, n=4.

[c] *Linear (L) and quadratic (Q) effects of energy intake between 45 and 85 kg, and effects of the nutritional history on the intercept (ΔI), linear (ΔL) and quadratic (ΔQ) component of the regression equation.* * $P < .05$, ** $P < .01$, *** $P < .001$.

[d] Empty body gain per kg feed intake.

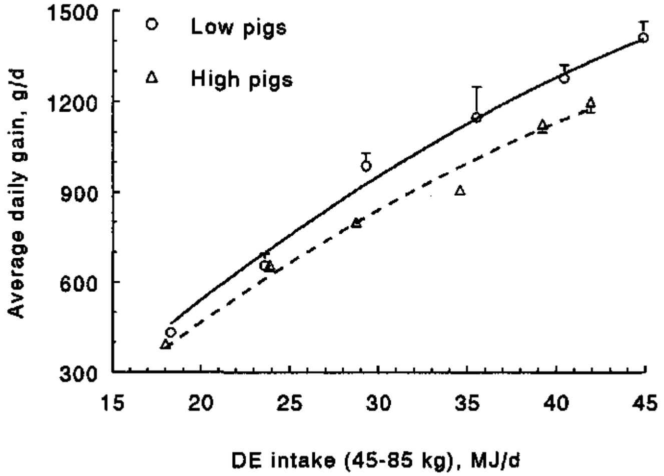

Figure 1. Daily gain from 45 to 85 kg at six levels of energy intake, in gilts which had received either 2.2 (low pigs) or 3.7 (high pigs) times energy for maintenance from 20 to 45 kg

Table 3. Energy intake and performance of gilts from 45 to 65 kg and from 65 to 85 kg, at six levels of feed intake, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
45-65 kg											
DE intake, MJ/d	L	16.3	21.0	26.2	30.6	35.8	42.5	28.7	.64		
	H	16.1	21.4	25.7	30.6	35.4	40.3	28.3			
ADG, g/d	L	400	606	955	1341	1287	1772	1060	58	L^{***}	ΔL^{***}
	H	354	588	729	871	1034	1270	808			
Gain/feed, g/kg	L	370	435	551	662	543	630	532	27	$L^{***}Q^{**}$	ΔL^{***}
	H	332	415	428	430	441	477	421			
65-85 kg											
DE intake, MJ/d	L	20.6	26.5	32.8	38.9	44.8	46.5	35.0	62		
	H	20.6	26.7	32.6	38.7	43.5	43.4	34.2			
ADG, g/d	L	469	716	1024	1007	1271	1158	941	45	$L^{***}Q^{*}$	
	H	454	739	903	949	1234	1152	905			
Gain/feed, g/kg	L	344	408	472	391	428	376	403	20	$L^{***}Q^{***}$	
	H	334	418	419	370	429	402	395			

[a] His., nutritional history, feeding level from 20 to 45 kg, being 2.2 (L) or 3.7 (H) times maintenance.

[b] Pooled standard error of the 12 treatment groups, n=4.

[c] Linear (L) and quadratic (Q) effects of energy intake between 45 and 65 kg and between 65 and 85 kg, and effects of the nutritional history on the intercept (ΔI), linear (ΔL) and quadratic (ΔQ) component of the regression equation. * $P < .05$, ** $P < .01$, *** $P < .001$.

Backfat thickness increased linearly with increasing feeding level (Table 2), and was on average 1.6 mm higher for the high pigs. This difference increased with increasing energy intake (Table 2).

Body Composition

Empty body weight as a percentage of liveweight at slaughter (85 kg), decreased linearly with increasing energy intake (Table 4). Weight of the carcass as a proportion of the empty body decreased linearly and the organ weight increased linearly with increasing feeding level. The lean fraction as a percentage of the empty body and as a percentage of the carcass, decreased curvilinearly with increasing energy intake, whereas the fat fraction increased curvilinearly. The lean tissue as a percentage of both the empty body and the carcass, was on average 2 - 3% higher in the low pigs than in the high pigs. The percentage of fat tissue was 2 - 3% higher in the high pigs.

Table 4. Body composition of gilts at 85 kg, fed at six levels of feed intake between 45 and 85 kg, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[d]	
Parameter	His.[b]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[c]	DE intake	History
Empty body, %	L	97.1	96.8	96.2	96.4	96.4	95.7	96.4	.31	L^{**}	ΔL^{*}
	H	97.2	96.9	96.7	97.2	96.4	96.7	96.8			
Carcass, %	L	86.5	85.6	84.6	83.7	83.5	83.0	84.5	.43	L^{***}	
	H	85.9	86.1	84.6	84.4	83.0	84.2	84.7			
Organs, %	L	13.5	14.4	15.4	16.3	16.5	17.0	15.5	.43	L^{***}	
	H	14.1	13.9	15.4	15.6	17.0	15.8	15.3			
Lean, %	L	54.4	51.9	50.2	49.0	47.1	47.0	49.9	.88	$L^{***}Q^{*}$	ΔL^{***}
	H	53.7	51.6	46.2	45.6	44.4	45.4	47.8			
Fat, %	L	32.1	33.7	34.4	34.6	36.4	36.1	34.5	.89	$L^{**}Q^{*}$	ΔL^{***}
	H	32.2	34.5	38.3	38.7	38.5	38.8	36.9			
Lean in carcass, %	L	62.9	60.6	59.4	58.6	56.4	56.5	59.1	1.02	$L^{**}Q^{*}$	ΔL^{***}
	H	62.5	59.9	54.7	54.1	53.6	53.9	56.4			

[a] Empty body weight (live weight less contents of the digestive tract) as percentage of live weight and weight of carcass, organs, lean and fat tissue as percentage of empty body weight.

[b,c,d] See footnotes Table 2.

Growth of Body Components

The deposition rate of organ tissue increased linearly ($P < .001$) with increasing energy intake, from 46 g/d to 244 g/d for the low pigs, and from 37 to 166 g/d for the high pigs (Table 5). Consequently, there was an increasing difference ($P < .001$) between the low and high pigs. Deposition rates of carcass, and of lean and fat tissue, increased curvilinearly with increasing energy intake in the fattening period. On average, deposition rates of both lean and fat were 15 g/d higher (not significant, $P > .05$) in the low pigs. The efficiency of lean tissue deposition (g/kg) decreased quadratically with increasing energy intake (Table 5). This efficiency was relatively constant at the three highest feeding levels, and was not affected by the nutritional history of the gilts.

The composition of body gain was affected by energy level and nutritional history. In Table 6 the relative contribution of gain of carcass, organs, lean and fat tissue, to the total body gain is given. The results showed an increase in the proportion of organ and fat gain and a large decrease, from about 58% to 40%, in the proportion of lean tissue gain, with increasing energy intake. Furthermore, at each level of energy intake the proportion of organ gain was about 4% higher and lean gain was about 3% lower in the low pigs.

Table 5. Growth rates of body components and efficiency of lean gain in gilts between 45 and 85 kg, fed at six levels of feed intake, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
Carcass, g/d	L	367	538	782	888	993	1064	772	29.7	$L^{***}Q^{**}$	
	H	359	601	699	805	935	1028	738			
Organs, g/d	L	46	81	142	187	211	244	152	11.5	L^{***}	ΔL^{***}
	H	37	53	92	112	166	145	101			
Lean, g/d	L	228	305	426	471	478	507	402	28.6	$L^{**}Q^{*}$	
	H	238	370	355	401	451	508	387			
Fat, g/d	L	139	232	356	417	516	557	369	18.0	$L^{***}Q^{*}$	
	H	121	232	344	404	484	520	351			
Lean/feed, g/kg	L	188	195	220	201	178	171	192	12.9	Q^{**}	
	H	200	234	187	175	174	184	192			

[a,b,c] See footnotes Table 2.

Overall Performance from 20 to 85 kg

In Table 7 are given the overall performance and lean tissue deposition in the growing-fattening period. On average, the low pigs needed 96 d, and the high pigs 79 d, to grow from 20 to 85 kg. As a consequence, the age difference was reduced from 22 d at 45 kg to 17 d at 85 kg due to the compensatory gain in the low pigs. The ADG between 20 and 85 kg increased linearly with increasing DE intake and the linear component was affected by the nutritional history. However, the average daily energy intake was much higher for the high pigs, 27.9 vs. 21.9 MJ. Therefore, the effects of energy intake and nutritional history cannot be derived directly from Table 7. In order to illustrate these effects, the ADG between 20 and 85 kg has been plotted against DE intake, which is shown in Figure 2. At similar daily energy intake, the low pigs gained about 65 g/d faster than the high pigs. Consequently, the gain/feed in the low pigs was also higher. The difference was about 40 g/kg. However, the maximum daily gain in the high pigs was 285 g/d higher than in the low pigs, 1123 vs. 838 g/d, because of the lower energy intake of the low pigs. Further analysis showed that the extra ADG of 65 g/d in the low pigs comprised an increase in organ gain of 21 g/d ($P < .001$), an increase in fat

Table 6. Composition of body gain in gilts between 45 and 85 kg, fed at six levels of feed intake and, with two nutritional histories

		Feeding level, times maintenance								Effects[d]	
Parameter[a]	His.[b]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[c]	DE intake	History
Carcass, %	L	88.8	86.9	84.7	82.8	82.5	81.3	84.5	.93	L^{***}	ΔI^{***}
	H	90.8	91.9	88.4	87.7	85.0	87.6	88.6			
Organs, %	L	11.2	13.1	15.3	17.2	17.5	18.7	15.5	.93	L^{***}	ΔI^{***}
	H	9.2	8.1	11.6	12.3	15.0	12.4	11.4			
Lean, %	L	55.1	49.6	46.0	43.7	39.6	38.6	45.4	1.94	$L^{***}Q^{*}$	ΔI^{*}
	H	60.2	56.5	44.9	43.6	41.0	43.1	48.2			
Fat, %	L	33.7	37.2	38.7	39.1	42.9	42.7	39.1	1.97	$L^{**}Q^{*}$	
	H	30.7	35.4	43.5	44.2	44.0	44.5	40.4			
Lean in carcass, %	L	62.1	57.1	54.4	52.8	48.0	47.4	53.6	2.21	$L^{**}Q^{*}$	
	H	66.3	61.4	50.8	49.7	48.3	49.1	54.3			

[a] Percentage of carcass, organs, lean and fat tissue in the empty body gain and percentage of lean tissue in the carcass gain.

[b,c,d] See footnotes Table 2.

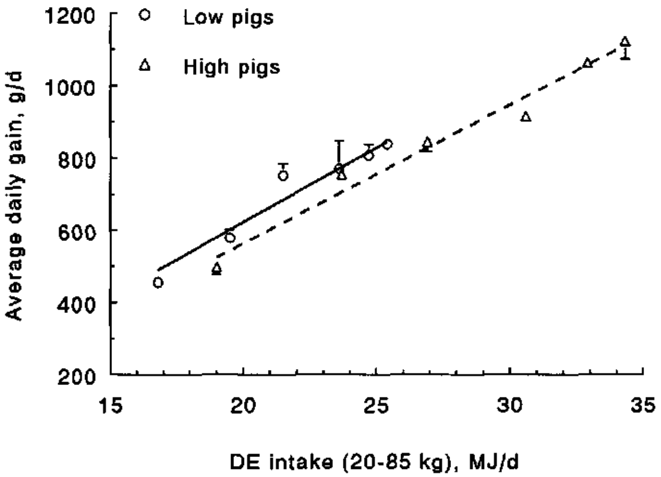

Figure 2. Average daily gain from 20 to 85 kg, in gilts fed at six energy levels between 45 and 85 kg. The low and high pigs received 2.2 and 3.7 times energy for maintenance from 20 to 45 kg, respectively

Table 7. Overall performance of gilts from 20 to 85 kg, fed at two feeding levels between 20 and 45 kg (His.[a]), and at six feeding levels from 45 to 85 kg

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
DE intake, MJ/d	L	16.8	19.5	21.5	23.6	24.7	25.4	21.9	.40		
	H	19.0	23.7	26.9	30.6	32.8	34.3	27.9			
Days in experiment	L	141	111	86	85	80	76	96	3.5		
	H	128	85	74	71	60	58	79			
ADG, g/d	L	446	579	752	771	807	838	699	29.9	L***	ΔL**
	H	499	756	844	916	1063	1123	867			
Gain/feed, g/kg	L	403	448	528	492	494	499	477	17.6	L**Q**	ΔI**
	H	397	482	474	452	489	495	465			
Lean gain, g/d	L	242	293	363	363	360	367	331	19.3	L***	
	H	268	381	367	399	435	476	388			
Lean/feed, g/kg	L	219	226	255	231	220	219	228	11.1	Q**	
	H	213	243	206	197	200	210	212			

[a,b] See footnotes Table 2.

[c] Linear (L) and quadratic (Q) effects of energy intake between 20 and 85 kg, and effects of the nutritional history on the intercept (ΔI), linear (ΔL) and quadratic (ΔQ) component of the regression equation. * $P < .05$, ** $P < .01$, *** $P < .001$.

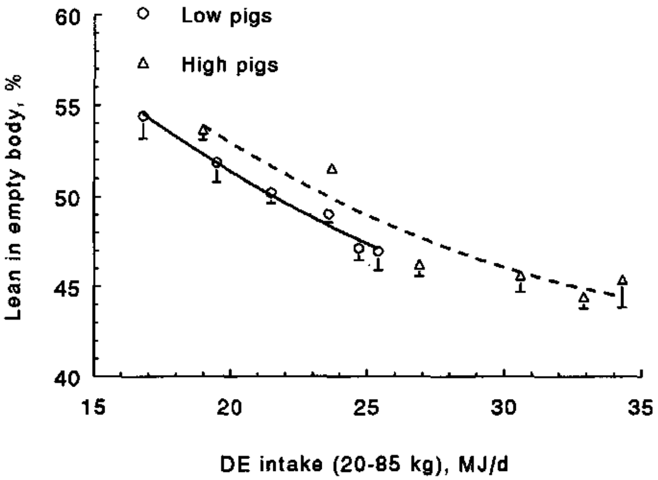

Figure 3. Percentage of lean tissue in the empty body of gilts at 85 kg, fed at six energy levels between 45 and 85 kg. The low and high pigs received 2.2 and 3.7 times energy for maintenance from 20 to 45 kg, respectively

gain of 18 g/d ($P < .01$), and an increase in lean gain of 14 g/d (not significant, $P > .05$). Thus at similar overall daily energy intake, the nutritional history did not affect ($P > .05$) the daily lean tissue deposition nor the efficiency of lean gain (Table 7). Because of the increase in deposition rates of other tissues, the body lean percentage at similar average energy intakes between 20 and 85 kg, was 1.6% lower in the low pigs (Figure 3).

DISCUSSION

In the discussion the effects of energy intake between 45 and 85 kg on body gain, efficiency of gain and body composition is discussed first. Thereafter the effects of the nutritional history on performance and tissue deposition are discussed. Finally, attention is paid to the overall performance between 20 and 85 kg of BW.

Effect of Energy Intake between 45 and 85 kg

Daily gain increased with increasing energy intake. The increase per MJ DE decreased with increasing body weight. On average, ADG increased by 34.2 ± 1.5

g/MJ of DE intake in the present study. For gilts from 20 to 45 kg, Bikker et al. (1994a) reported a linear increase in ADG of 43.6 ± 2.2 g/MJ of DE. The mean slope for lean growth (g/MJ DE), decreased from 12.5 ± 3.1 for 20-45 kg pigs to 9.6 ± 1.0 for 45-85 kg pigs. Consequently, the marginal efficiency of body and lean tissue gain (g/MJ DE) decreased with increasing body weight, presumably because older pigs deposit more lipid and less protein per unit extra energy (Bikker et al., 1994b).

A small quadratic effect was present in the relationship between energy intake and body and lean tissue gain ($P < .05$). Results in Table 3 indicate that this quadratic effect on tissue deposition was only present after 65 kg. The curvilinear effect indicates that either a plateau in lean tissue growth rate was reached, or that the slope for lean tissue growth decreased gradually with increasing energy intake. The results do not clearly show that a plateau in lean tissue gain was reached. Furthermore a gradual decreasing slope can be explained by a decreasing proportion of lean gain in the total body gain (Table 6), and(or) by a change in composition of the lean tissue. Diminishing returns of lean tissue gain with feed intake were also reported by Kanis (1988). The decrease of the lean proportion in the gain (Table 6) showed that at low intake levels, the animals have a preference for muscle gain, whereas the proportion of fat tissue gain increases at higher intake levels. This is in agreement with Davies (1983), who reported that pigs at a high feeding level deposited proportionately more fat and less muscle, relative to animals at a low feeding level. These results strongly challenge the assumption proposed by Whittemore (1986) that the ratio of fat to lean is constant in the nutritionally limited phase of growth.

In addition to the increasing proportion of fat tissue gain, the relative organ gain also increased with increasing feed intake (Table 6). This was mainly the result of growth of the liver, kidneys and digestive tract. An increase in the weights of metabolically active organs, with increasing feed intake, was also reported by Koong et al. (1982 and 1983), Davies (1983), Rao and McCracken (1992) and Bikker et al. (1994a). This effect reflects presumably a functional hypertrophy of the organs in order to process the incremental amounts of feed, and illustrates the adaptive capacity of the animal to the nutritional environment.

As a consequence of the decreasing proportion of lean gain, the lean percentage in the body at 85 kg decreased by .3% per MJ DE intake, with a concomitant increase in backfat (Table 2) and fat tissue content (Table 4). An increase in lean and a decrease in fat percentage with a reduction in energy intake, was also reported by Ellis et al. (1983), Jørgensen et al. (1985), Susenbeth and Keitel (1988), but not by Rao and McCracken (1992). As discussed by Bikker et al. (1994a), the effect of a reduction of energy intake on body composition, depends on the genotype of the pig and the level of energy intake. The latter was confirmed by the presence of a curvilinear effect of DE intake on lean and fat percentage in this study. In agreement with Kanis (1988), and Bikker et al. (1994a), the efficiency of lean tissue gain decreased with increasing energy intake. Because of a curvilinear increase in gain/feed with increasing energy intake, the highest lean efficiency was reached at a lower intake level than the maximum efficiency of body gain. This is also largely in agreement with Ellis et al. (1983), who reported an increase in gain/feed with increasing feed intake, whereas lean efficiency was constant or tended to decrease.

In conclusion, the results of the present study showed an increase in the proportion of organ and fat tissue, and a decrease in the proportion of lean tissue, in the body gain, with increasing energy intake. Consequently the ratio of fat to lean increases substantially with an increase in the level of energy intake, even when the maximum rate of lean deposition has not been reached. As a result, the lean percentage and efficiency of lean gain are optimized at lower feed intake levels than daily gain, gain/feed and lean tissue growth rate.

Effect of the Nutritional History on Performance from 45 to 85 kg

At the end of the restriction period at a BW of 45 kg, the animals on the low feeding level were 22 d older and had leaner bodies than the high pigs. From 45 to 85 kg these low pigs showed a higher daily gain than the high pigs (Table 2). This difference in ADG increased with increasing energy intake. The difference was very small at the two lowest feeding levels, and higher at the other four intake levels. Because of similar intakes of low and high pigs, this compensatory gain was caused by an increased gain/feed (Table 2). For the animals with free access to feed, the increase in DE intake of about 3 MJ/d would have also contributed to the higher gain in these treatment groups. An increased feed intake and daily gain after a period of feed restriction, was also reported by Nielsen (1964), Owen et al. (1971), Donker et al. (1986). This literature does not allow a determination to be made as to whether the compensatory growth was caused by the increased feed intake or by an increased efficiency. However, in the studies of Nielsen (1964), Campbell et al. (1983), and Kirchgessner et al. (1984), previously restricted pigs showed compensatory gain and gain/feed at a similar daily feed intake, as their non-restricted counterparts. These authors reported an increase in daily gain of about 80-100 g/d after a restriction to 55-75% of the control feeding level for several weeks. These references and the present study, show that the rate of gain and feed efficiency are higher after a period of feed restriction. In addition the present study shows that this compensation increases with increasing energy intake in the realimentation phase.

Nutrition and Gain in Body Components

In the present study, the low pigs gained on average, about 140 g/d more between 45 and 85 kg. A large part of this extra gain was caused by increased gut fill (50 g/d, Table 2), and increased organ growth (50 g/d, Table 5). The gain of lean tissue, which is the most important edible product, was only 15 g/d (not significant) higher in the low pigs. The efficiency of lean gain was also not affected by the nutritional history. In most of the above mentioned studies, the deposition of different tissues was not determined. However, Mersmann (1987) and Pond and Mersmann (1990) reported an increased gain of liver, kidneys and the digestive tract in pigs during the rehabilitation period, without significant compensation in body or carcass gain. Furthermore, the data of Drouillard et al. (1991) in energy restricted and refed lambs, suggested a small compensation in non-visceral tissue and a larger compensation in visceral tissue. Carstens et al. (1991) reported compensatory growth in steers which were previously restricted in feed intake. This compensation consisted of gut fill and non-carcass water and protein. Consequently, these results indicate that the compensatory gain after a period of feed restriction is largely caused by a functional increase in organ growth and in the contents of the intestinal tract.

It has been suggested that carcass quality is higher in pigs after a period of restriction and compensation (Robinson, 1964). This was confirmed by this study, because the low pigs had less backfat and fat tissue, and a higher lean percentage, at 85 kg (Table 4). Similar results were reported by Nielsen (1964), Campbell et al. (1983) and Mersmann et al. (1987). However, from the literature it cannot be concluded whether the improved carcass quality is a direct result of the feed restriction in the restriction phase, or an effect of this restriction on the composition of gain during realimentation. This study shows that the higher carcass quality of the low pigs was not caused by an increase in lean gain. Moreover, the proportion of lean gain in the total gain from 45 to 85 kg, was even lower in the low pigs than in the high pigs, because of the increased organ growth (Table 6). The higher percentage of lean tissue in the carcass of the low gilts at 85 kg, was already present at 45 kg, due to the restriction in feed intake from 20 to 45 kg. The lean percentage was still higher at 85 kg, because of the lack of compensation in lean or fat tissue gain. This may have been the reason for the lower fat content in the other studies, since composition of gain was not reported (Nielsen, 1964; Campbell et al., 1983), or no compensation in lean and fat deposition was found (Mersmann, 1987).

Presumably, the above-mentioned compensation took place during the first few days or weeks of the realimentation period, because a compensation in gain was only present between 45 and 65 kg. It seems reasonable to assume that the metabolically active organs adapt to the increased feeding level very soon after the start of the realimentation period. This is in agreement with Owen et al. (1971) who found the highest increase in gain immediately after the end of the restriction period. The energy requirements for this extra gain may be small, because it mainly consisted of water and protein (Bikker et al., 1994b). Presumably the maintenance requirements were somewhat lower during the first days of the realimentation period, because a period of undernutrition can reduce the basal energy expenditure (Ledger and Sayers, 1977; Koong et al., 1983; Ferrell et al., 1985). When feed intake is restored, both the maintenance requirements and the energetic efficiency of gain return rapidly to that of the continuously fed animal (Webster, 1979; Graham, 1975; Schnyder et al., 1982). Furthermore feed and protein intake stimulate growth of certain visceral tissues by suppressing protein degradation (Reeds, 1989), which thereby enables an efficient regrowth of these tissues.

Overall Performance from 20 to 85 kg

The overall performance from 20 to 85 kg shows the combined effects of energy intake on performance between 20 and 45 kg and between 45 and 85 kg. As expected, ADG and gain/feed increased with increasing energy intake. Furthermore, the low pigs were on average 17 d older at 85 kg, which means that only 5 d of the time-lag of 22 d were compensated for by the compensatory gain and feed efficiency. From the results in Table 7, and Figures 2 and 3, it was concluded that at similar average daily energy intake, the distribution of the intake had an effect on rate of gain and body composition. The rate and efficiency of body gain were higher in the pigs with a low intake from 20 to 45 kg and a high intake from 45 to 85 kg, than in pigs with a high intake from 20 to 45 kg and a low intake from 45 to 85 kg. This can be explained by the higher average metabolic body weight, and consequently the higher maintenance requirements of the pigs with the high intake and daily gain below 45 kg (Wenk et al., 1980). At similar average daily energy intake, the mean metabolic body weight between 20 and 85 kg, was 2.2 - 2.6 kg less for the low pigs, which allowed them to use 1 - 1.3 MJ DE/d more for tissue deposition. This largely explains the higher daily gain and gain/feed of these animals. The lean percentage was lower in the low pigs than in the high pigs, at similar energy intake, mainly because of a higher organ mass at 85 kg in low pigs. This indicates that organ mass at slaughter is affected more by the feeding level in the period just before slaughter, than by the feeding level in earlier life, which is in agreement with results of Koong et al. (1982 and 1983) in pigs and Ferrell et al. (1985) in lambs. The overall daily lean gain was not significantly different for low and high pigs (Table 7), indicating that the extra gain in low pigs is of limited benefit for pig production. As a result, at similar average daily intakes, the distribution of the dietary energy between the growing and fattening phase of these gilts, seems of little importance for pig production. However, maximum attainable gain of the body and lean tissue is of course much higher if pigs receive a high feeding level both in the grower and finisher period (Table 7, Figure 2).

In conclusion, this study showed that after a period of feed restriction, compensatory gain and feed efficiency increased with increasing feeding level in the realimentation period. This extra gain was largely accounted for by an increase in the contents of the digestive tract, and by the increased growth of metabolically active organs, which responded to the increase in feed intake. The higher carcass quality at slaughter in restricted and realimented pigs, was caused by the restriction per se and not by an effect of previous restriction on the composition of gain in the realimentation period.

IMPLICATIONS

Lean tissue percentage and efficiency of lean tissue gain decreased with increasing energy intake. Giving animals free access to feed, will therefore optimize body and lean tissue gain but not body composition and efficiency of lean gain. After feed restriction in the growing period, pigs show compensation in the rate and efficiency of body gain, which is mainly caused by an increase in organ growth. The better carcass composition of compensating animals is the result of maintaining the better carcass composition present at the start of the realimentation phase. As a result, compensatory gain after a period of feed restriction is of limited value for the pig industry.

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Chapter 6

PERFORMANCE AND BODY COMPOSITION OF FATTENING GILTS (45-85 KG) AS AFFECTED BY ENERGY INTAKE AND NUTRITION IN EARLIER LIFE.
2. PROTEIN AND LIPID ACCRETION IN BODY COMPONENTS

P. Bikker, M.W.A. Verstegen, and R. G. Campbell[1]

Department of Animal Nutrition, Wageningen Agricultural University,
Haagsteeg 4, 6708 PM Wageningen, The Netherlands

[1] Bunge Meat Industries, Corowa, Australia

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ABSTRACT

Forty-eight gilts of a commercial hybrid were used to investigate the response relationships between energy intake and deposition of protein and lipid in body components of fattening pigs (45-85 kg), as affected by previous nutrition. Two groups of 24 gilts received a single diet either at 2.2 (low pigs) or 3.7 (high pigs) times maintenance (M) from 20 to 45 kg. From 45 to 85 kg, pigs from each of these two groups were fed the same diet at one of six intake levels (1.7, 2.2, 2.7, 3.2 and 3.7 x M, and ad libitum). At 85 kg, the animals were dissected and analysed. Protein content in the whole body decreased curvilinearly from 190 to 166 g/kg ($P < .001$) and lipid content increased from 116 to 210 g/kg ($P < .001$) with increasing energy intake. The mean content of protein was 6 g/kg higher and of lipid 29 g/kg lower (both $P < .001$) in previously restricted pigs. Protein (PD) and lipid deposition (LD) in the whole body, organs, lean and fat tissue increased linearly ($P < .001$) with increasing energy intake. In the whole body PD, increased from 83 to 187 g/d and LD from 46 to 392 g/d. The respective response relationships in g/d were $PD = 21.8 + 3.78 \times DEI$ and $LD = -193 + 13.7 \times DEI$ (DEI is digestible energy intake, MJ/d). The LD/PD ratio increased curvilinearly from .6 to 2.2. Previous nutrition had only small effects on PD and LD. Only PD in the organs was on average 7 g/d higher ($P < .001$) in previously restricted pigs. Thus the higher protein content and the lower lipid content in previously restricted pigs was not the result of compensation, but was already present at the end of the restriction phase at 45 kg.

Keywords: Pigs, Energy Intake, Protein Accretion, Lipid Accretion, Nutritional History

INTRODUCTION

The assignment of dietary energy above maintenance to protein and lipid accretion in growing pigs is largely determined by the relationship between energy intake and protein deposition (Whittemore and Fawcett, 1976). It is not clear how this relationship is affected by body weight (BW) and previous nutrition. Black and Griffiths (1975) reported that in lambs, the slope between protein deposition and energy intake falls with increasing BW, whereas Whittemore (1986) suggested that this slope was largely unaffected by BW in pigs. Furthermore, Campbell (1988) suggested that a plateau in protein deposition could be reached in fattening pigs rather than in growing pigs, but it may be that due to genetic improvements, even older pigs of an improved strain cannot reach a plateau of protein deposition.

Several authors have reported an increased gain after a period of feed restriction (Bikker et al., 1994b). The effect of a previous restriction on subsequent protein and lipid deposition, however, is unclear.

In this study, the relationship between energy intake and deposition and distribution of body protein, has been determined in fattening gilts (45 - 85 kg) in relation to the feeding level from 20 to 45 kg. The results will be compared with those of growing gilts (20 - 45 kg) of the same genotype (Bikker et al., 1994a) to investigate whether the distribution of dietary energy between protein and lipid accretion is affected by the BW of the pigs.

EXPERIMENTAL PROCEDURES

Animals and Feeding

Forty-eight gilts with an average BW of 21.8 ± .2 kg were allocated among 12 treatment combinations in a 2 x 6 factorial arrangement. The respective treatments were the level of feeding from 20 to 45 kg, equivalent to 2.2 and 3.7 times energy for maintenance (M), and the level of feeding from 45 to 85 kg, equivalent to 1.7, 2.2, 2.7, 3.2, and 3.7 x M, and ad libitum. One experimental diet, based on cereals and soybean meal, with an energy content of 15.1 MJ of DE/kg, was used from 20 to 85 kg for all treatment groups. The composition of this diet has been published previously (Bikker et al., 1994a). The treatment period from 20 to 45 kg will be referred to as the nutritional history and the gilts with the low (2.2 x M) and high (3.7 x M) nutritional history will be referred to as low and high pigs, respectively. The treatment period from 45 to 85 kg will be referred to as the fattening period or the realimentation period.

The initial body composition of the pigs at 20 and 45 kg was estimated using the data presented in Bikker et al. (1994a). This experiment from 20 to 45 kg was conducted in the same period, under similar experimental conditions, and with gilts from the same herd as in the present study.

Slaughter Procedures and Carcass Analysis

At a liveweight of 85 kg, the animals were killed by electrical stunning and exsanguination. Body components were collected and stored as described by Bikker et al. (1994a). The bodies were dissected into three fractions or tissue groups, referred to as the organ, lean, and fat fractions. The organ fraction comprised the blood and all organs, including mesenteric fat. The lean fraction comprised the ham, shoulder, and loin, all without subcutaneous fat, and meat scraps. The fat fraction comprised all other carcass parts and consisted mainly of backfat, belly fat, other fat depots, head, feet, and tail (Bikker et al., 1994a,b). The different fractions were homogenized and subsampled for proximate analysis as described by Bikker et al. (1994b). Dry matter, nitrogen, lipid and ash contents in the organ, carcass, lean and fat fractions were determined as described by Bikker et al. (1994a,b).

A more detailed description of the experimental procedures has been given in the first paper of this series (Bikker et al., 1994b).

Statistical Analysis

Regression analysis was used to determine the linear and quadratic effects of feed intake in the fattening period on performance, tissue deposition and body composition of the pigs. The effect of the nutritional history on the regression parameters was determined using dummy variables and a backward elimination procedure. (Draper and Smith, 1981). Data were analysed by linear (GLM) regression procedures (SAS, 1989).

RESULTS

The effects of energy intake and nutritional history on daily gain, feed efficiency, and deposition rates of carcass, organs, lean and fat tissue in these animals have been presented in Bikker et al. (1994b).

Body Composition at 85 kg

At 85 kg, the pigs contained on average 173 g/kg protein and 180 g/kg lipid (Table 1). The composition of all body components was affected by the level of energy intake from 45 to 85 kg. Water and protein content in the empty body, carcass and lean tissue (Tables 1, 2 and 3) decreased linearly or curvilinearly with increasing levels of energy intake. A quadratic effect on lean tissue protein content just failed to be significant (P = .08). The lipid content in all fractions increased curvilinearly with energy intake. Ash content decreased linearly or curvilinearly in all fractions, apart from ash in the lean tissue, which was not affected (P > .1) by energy intake. The curvilinear response relationship indicates that the effects of the energy intake level on the body composition were bigger at low intake levels than at high intake levels.

The composition of all fractions was influenced by the nutritional history. Tissues of the low pigs, contained more water and protein and less lipid at 85 kg BW than tissues of the high pigs. The difference in composition between low and high pigs was small at the lowest intake level, and increased with increasing energy intake. This was indicated by an effect of the nutritional history on the slope rather than on the intercept of the relationships between energy intake from 45 to 85 kg and water, protein and lipid content in the body. On average, the low pigs contained 6 g/kg more protein and 29 g/kg less lipid in their bodies than the high pigs.

Table 1. Chemical composition of the empty body of gilts at 85 kg, fed at six feeding levels between 45 and 85 kg, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
DE intake, MJ/d	L	18.3	23.6	29.3	35.5	40.4	44.8	32.0	.52		
	H	18.0	23.9	28.7	34.6	39.2	41.9	31.0			
Water, g/kg	L	650	626	622	609	587	583	613	10.4	L^{***}	ΔL^{***}
	H	649	618	577	565	581	565	592			
Protein, g/kg	L	192	182	178	172	165	168	176	2.89	$L^{***}Q^{***}$	ΔL^{***}
	H	190	179	163	159	162	164	170			
Lipid, g/kg	L	114	151	154	175	200	193	165	12.3	$L^{***}Q^{*}$	ΔL^{***}
	H	117	163	217	227	214	226	194			
Ash, g/kg	L	34.2	33.8	29.5	29.9	29.9	29.5	31.1	.70	$L^{***}Q^{***}$	ΔL^{*}
	H	34.1	30.7	27.8	29.2	29.0	28.4	29.9			

[a] His., nutritional history, feeding level from 20 to 45 kg, being 2.2 (L) or 3.7 (H) times maintenance.

[b] Pooled standard error of the 12 treatment groups, n=4.

[c] Linear (L) and quadratic (Q) effect of energy intake between 45 and 85 kg, and effect of the nutritional history on the intercept (ΔI), linear (ΔL) and quadratic (ΔQ) component of the regression equation. * P < .05, ** P < .01, *** P < .001.

Table 2. Chemical composition of the carcass of gilts at 85 kg, fed at six feeding levels between 45 and 85 kg, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
Water, g/kg	L	633	605	598	581	556	550	587	11.4	L^{***}	ΔL^{***}
	H	630	598	547	534	547	532	565			
Protein, g/kg	L	197	186	181	176	167	171	180	3.21	$L^{***}Q^{***}$	ΔL^{***}
	H	194	182	166	160	164	166	172			
Lipid, g/kg	L	125	166	172	198	227	219	185	13.4	$L^{***}Q^{**}$	ΔL^{***}
	H	129	179	242	255	243	254	217			
Ash, g/kg	L	38.1	37.9	33.2	33.9	34.0	33.6	35.1	.82	$L^{***}Q^{**}$	ΔL^{*}
	H	38.1	34.1	31.2	32.9	33.0	32.0	33.5			

[a,b,c] See footnotes Table 1.

Retention between 45 and 85 kg

Deposition rates of protein and lipid in the empty body (Table 4, see also Figure 1), carcass, organs, lean and fat tissue (Table 5), increased linearly with increasing energy intake between 45 and 85 kg. Only for protein deposition in the lean tissue was there a tendency (P = .07) towards a quadratic effect. Average protein deposition in the body increased from 83 g/d at the lowest energy level, to 187 g/d for animals with free access to feed. The ratio between lipid and protein

Table 3. Chemical composition of the lean tissue of gilts at 85 kg, fed at six feeding levels between 45 and 85 kg, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
Water, g/kg	L	689	678	680	673	667	666	676	4.78	$L^{**}Q^{*}$	$\Delta I^{*}\Delta L^{*}\Delta Q^{*}$
	H	696	672	662	655	662	658	667			
Protein, g/kg	L	207	202	202	196	191	193	199	2.27	L^{***}	
	H	206	204	192	192	191	194	196			
Lipid, g/kg	L	60.1	79.3	77.3	88.2	98.1	102	84.2	4.70	$L^{***}Q^{**}$	$\Delta I^{*}\Delta L^{*}\Delta Q^{*}$
	H	60.0	82.4	107	108	103	107	94.6			
Ash, g/kg	L	39.1	35.7	36.7	35.5	35.0	38.0	36.6	1.73		
	H	34.9	35.0	33.4	39.1	37.8	32.2	35.4			

[a,b,c] See footnotes Table 1.

deposition (LD/PD), increased curvilinearly from about .6 to 2.2, with the biggest increase at the low feeding levels.

Deposition rates of protein (PD) and lipid (LD) in the empty body were not affected ($P > .05$) by the nutritional history of the pigs (Table 4). The linear relationships with energy intake (DEI, MJ/d), combined for the low and high pigs, were:

$$PD = 21.8\ (\pm\ 11.6) + 3.78\ (\pm .35) \times DEI \qquad (r^2 = .724,\ RSD = 21.1) \qquad [1]$$

$$LD = -193\ (\pm\ 20.3) + 13.7\ (\pm\ .62) \times DEI \qquad (r^2 = .918,\ RSD = 37.1) \qquad [2]$$

Protein deposition in the empty body tended ($P = .08$) to be somewhat higher in the low pigs than in the high pigs. This was mainly due to an increased rate of protein deposition, on average 7.0 g/d, in the organs of the low pigs (Table 5). This difference increased with increasing levels of feed intake. Water and ash deposition in the empty body were higher in the low pigs. The higher water retention of these pigs was also largely accounted for, by an increased water retention in the organs.

Distribution of Deposited Protein and Lipid

The distribution of body protein and lipid, deposited between 45 and 85 kg was

Table 4. Deposition rates of water, protein, lipid, and ash in the empty body of gilts between 45 and 85 kg, at six levels of feed intake, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
Water, g/d	L	256	349	517	576	586	616	483	35.8	$L^{***}Q^{*}$	ΔL^{**}
	H	254	374	385	430	544	544	422			
Protein, g/d	L	83	110	157	172	172	194	148	9.93	L^{***}	
	H	83	123	120	133	165	180	134			
Lipid, g/d	L	53	131	197	273	375	397	238	20.9	L^{***}	
	H	39	131	248	301	338	386	240			
Ash, g/d	L	15.9	23.3	26.4	31.7	35.3	37.4	28.3	1.48	L^{***}	ΔL^{***}
	H	15.4	21.1	20.7	26.8	31.6	32.1	24.6			
Lipid/protein dep., g/g	L	.66	1.18	1.30	1.70	2.23	2.08	1.53	.233	$L^{**}Q^{*}$	
	H	.50	1.08	2.08	2.33	2.05	2.19	1.71			

[a,b,c] See footnotes Table 1.

affected by the level of energy intake (Tables 6 and 7). The proportion of protein and lipid deposited in the carcass and lean tissue, decreased markedly with increasing energy level, whereas the proportion deposited in the organs and in the fat tissue increased with increasing energy intake. Furthermore, the distribution of protein but not of lipid was affected by the nutritional history. In the high pigs, a bigger proportion of the deposited protein was in the carcass and in the lean tissue, whereas a smaller proportion was deposited in the organs.

Retention between 20 and 85 kg

Daily gain (g/d) between 20 and 85 kg BW, increased from 446 to 838 g/d for the low pigs and from 499 to 1123 g/d for the high pigs (Bikker et al., 1994b). In Table 8, the daily retention of water, protein, lipid and ash between 20 and 85 kg is presented. The retention of these nutrients increased linearly with increasing

Table 5. Deposition rates of protein and lipid in different tissues of gilts between 45 and 85 kg, at six levels of feed intake and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
CARCASS											
Protein,	L	75.0	96.7	134	143	140	158	125	8.82	L^{***}	
g/d	H	75.8	113	107	115	140	159	118			
Lipid,	L	49.9	124	186	258	355	374	225	19.6	L^{***}	
g/d	H	37.6	124	233	285	319	365	227			
ORGANS											
Protein,	L	7.9	13.4	22.7	28.5	31.5	36.2	23.4	1.93	L^{***}	ΔL^{***}
g/d	H	6.8	9.5	13.1	17.7	25.0	21.2	15.6			
Lipid,	L	2.7	7.4	11.1	15.0	19.8	23.1	13.2	1.69	L^{***}	
g/d	H	1.7	7.0	14.2	15.8	19.4	21.3	13.2			
LEAN TISSUE											
Protein,	L	49.7	63.0	88.5	92.1	87.0	93.4	78.9	6.78	L^{***}	
g/d	H	51.6	79.2	67.8	77.0	84.5	98.7	76.5			
Lipid,	L	14.3	33.1	44.1	60.4	76.3	89.7	53.0	3.20	L^{***}	
g/d	H	12.3	35.5	54.3	60.8	66.6	76.7	51.0			
FAT TISSUE											
Protein,	L	25.4	33.7	45.7	51.3	53.1	64.3	45.6	3.65	L^{***}	
g/d	H	24.2	34.0	39.4	38.2	55.6	60.1	41.9			
Lipid,	L	35.6	90.6	142	198	279	285	172	18.3	L^{***}	
g/d	H	25.3	88.5	179	224	252	288	176			

[a,b,c] See footnotes Table 1.

Table 6. Distribution of protein deposited between 45 and 85 kg, among different body tissues, as a percentage of whole body protein deposition, in gilts at six feeding levels, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
Carcass, %	L	90.5	87.8	85.6	83.5	81.6	81.2	85.0	.92	L^{***}	ΔL^{***}
	H	91.8	92.3	89.1	86.7	84.9	88.0	88.8			
Organs, %	L	9.5	12.2	14.4	16.5	18.4	18.8	15.0	.92	L^{***}	ΔL^{***}
	H	8.2	7.7	10.9	13.3	15.1	12.0	11.2			
Lean, %	L	59.9	57.3	56.5	53.6	50.7	47.8	54.3	2.00	Q^{***}	ΔI^{*}
	H	62.5	64.8	56.4	57.6	51.2	54.5	57.8			
Fat, %	L	30.6	30.6	29.1	29.9	30.9	33.4	30.7	1.71	Q^{**}	
	H	29.3	27.5	32.8	29.0	33.7	33.5	31.0			

[a,b,c] See footnotes Table 1.

energy intake between 20 and 85 kg. At similar average daily energy intake between 20 and 85 kg, lipid deposition (g/d) was 17.4 g higher ($P < .05$) in the low pigs, which was indicated by an effect of the nutritional history on the intercept of the linear relationship between energy intake and lipid deposition. Most of this extra lipid was deposited in the fat tissue. Daily water and protein deposition in the organs (data not shown) were 15.8 and 3.0 g higher in the low pigs

Table 7. Distribution of lipid deposited between 45 and 85 kg, among different body tissues, as a percentage of whole body lipid deposition, in gilts at six feeding levels, and with two nutritional histories[a]

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
Carcass, %	L	95.7	94.5	94.3	94.5	94.7	94.2	94.6	.62	L^{*}	
	H	96.1	94.7	94.2	94.7	94.2	94.6	94.8			
Organs, %	L	4.3	5.5	5.7	5.5	5.3	5.8	5.4	.62	L^{*}	
	H	3.9	5.3	5.8	5.3	5.8	5.4	5.2			
Lean, %	L	30.7	26.1	22.8	22.3	20.5	22.7	24.2	2.26	$L^{***}Q^{**}$	
	H	33.8	27.3	22.3	20.5	19.7	20.2	24.0			
Fat, %	L	65.0	68.4	71.4	72.2	74.2	71.5	70.5	2.09	$L^{***}Q^{**}$	
	H	62.4	67.4	71.9	74.2	74.5	74.3	70.8			

[a,b,c] See footnotes Table 1.

Table 8. Deposition rates of water, protein, lipid, and ash in the empty body of gilts between 20 and 85 kg, fed at two feeding levels from 20 to 45 kg and at six levels from 45 to 85 kg

		Feeding level, times maintenance								Effects[c]	
Parameter	His.[a]	1.7	2.2	2.7	3.2	3.7	ad lib	Mean	SEM[b]	DE intake	History
DE intake 20-85 kg, MJ/d	L	16.8	19.5	21.5	23.6	24.7	25.4	21.9	.40		
	H	19.0	23.7	26.9	30.6	32.8	34.3	27.9			
Water, g/d	L	272	331	425	424	423	429	384	23.7	L^{***}	
	H	305	428	430	465	544	554	454			
Protein, g/d	L	87	105	131	129	128	135	119	6.5	L^{***}	
	H	97	134	132	142	164	176	141			
Lipid, g/d	L	52	94	122	146	179	179	129	10.0	L^{***}	ΔI^{*}
	H	59	133	209	239	257	285	197			
Ash, g/d	L	15.8	19.6	21.2	21.8	23.2	23.5	20.8	.87	L^{***}	
	H	17.2	22.6	22.1	26.1	29.3	30.0	24.6			
Lipid/protein dep., g/g	L	.61	.90	.95	1.16	1.42	1.33	1.06	.120	$L^{**}Q^{*}$	
	H	.63	1.00	1.58	1.71	1.57	1.65	1.36			

[a,b] See footnotes Table 1.

[c] Linear (L) and quadratic (Q) effect of energy intake between 20 and 85 kg, and effect of the nutritional history on the intercept (ΔI), linear (ΔL) and quadratic (ΔQ) component of the regression equation. * $P < .05$, ** $P < .01$, *** $P < .001$.

($p < .001$). The rates of water and protein deposition (g/d) in the body were 22 and 6.0 g higher in the low pigs, but these differences were not significant ($P > .1$). As a result of these effects body protein content at 85 kg (Table 1) was 4.5 g/kg lower in the low pigs than in the high pigs, when compared at similar average daily energy intake between 20 and 85 kg. Water content was slightly lower and lipid content was somewhat higher in the low pigs, but these differences were not significant.

DISCUSSION

Effect of Energy Intake between 45 and 85 kg

Protein and lipid deposition increased linearly with increasing energy intake, with increments of 3.8 and 13.7 g/MJ of DE, respectively. This indicates that an intrinsically determined maximum in protein deposition (PD_{max}) had not yet been reached. The PD_{max} may be above the range of protein deposition observed here. Therefore, the feed intake probably limited expression of the genetic potential. Similar results were reported for genetically improved entire male pigs by Campbell and Taverner (1988) and Rao and McCracken (1991). Campbell and Taverner (1988), reported a linear increase in protein deposition to 189 g/d at an energy intake of 41 MJ of DE/d. Rao and McCracken (1991) determined a linear increase in protein deposition to 230 g/d, determined by nitrogen balance, at about 38 MJ of DE/d. In the latter two studies, the respective increments in protein deposition were 5.3 and 4.4 g/MJ DE. Therefore it was concluded that in male and female pigs of improved genotype between 45 and 85 kg, the relationship between energy intake and protein deposition is essentially linear up to high levels of feed intake, rather than linear-plateau as reported for unimproved pigs by Campbell et al. (1985) and Dunkin et al. (1986). However, big differences in the slope and the level of the linear relationship, were found between this study, Campbell and Taverner (1988) and Rao and McCracken (1991). These differences were presumably the result of different selection strategies, and of differences between male and female pigs.

The ratio between lipid and protein deposition (LD/PD) increased curvilinearly from about .5 at the lowest intake level to 2.2 at the higher intake levels. This increase in LD/PD with increasing energy intake has been reported earlier for young and older animals (Campbell et al, 1983b; De Greef et al., 1994; Bikker et al., 1994a). Nevertheless, it is often assumed that below PD_{max} the LD/PD ratio is constant and independent of energy intake. This assumption has been used in several pig growth models (Moughan et al., 1987; Pomar et al., 1991; Werkgroep TMV, 1991). Results of our study imply that models based on this assumption will underestimate protein deposition, and overestimate lipid deposition, at low intake levels.

The curvilinear increase in LD/PD ratio with increasing energy intake caused a curvilinear increase in body lipid content and a curvilinear decrease in body protein content with increasing energy intake (Tables 1, 2 and 3). Body composition was relatively constant at the higher feeding levels. These effects of energy intake on body composition were in good agreement with Campbell and Taverner (1988) and Bikker et al. (1994a). In addition, our study showed that these effects of energy intake on body composition were present in all dissected body tissues, carcass, organs, lean and fat tissue.

Very little information is available concerning the effect of energy intake on the distribution of deposited protein within the body, whereas with regard to human consumption protein deposited in the lean tissue is the most valuable. In the present study, a quadratic decrease of 18% in the proportion of body protein deposited in the lean tissue, was found when energy intake increased from the lowest to the highest feeding level (Table 6). An increasing proportion of the deposited protein was found in the organs, and, to a lesser extent, in the fat tissue. Based on linear regression analysis, we found that from each extra gram of deposited protein with increasing energy intake, 25% was deposited in the organs, 39% in the lean tissue and 37% in the fat tissue. The drop in the proportion of protein deposited in the lean tissue with increasing energy intake, agreed with the results of growing female pigs in Bikker et al. (1994a) and with the results of growing and fattening male pigs of similar genotype in De Greef and Verstegen (1993).

In conclusion, protein and lipid deposition increased linearly, and LD/PD and lipid content increased curvilinearly with increasing energy intake. The proportion of body protein deposited in the lean tissue, decreased with increasing energy intake. These results imply that maximization of protein deposition is accompanied by a deterioration in the body composition, even in pigs of improved genotype.

Effect of the Nutritional History

Several authors reported an effect of a previous restriction in feed intake on body gain in the realimentation period, as discussed in Bikker et al. (1994b). However, information of the effect of a feed restriction in the growing period on protein and lipid deposition in pigs in the fattening period was not available. In this study, the previous feed restriction had only a small, insignificant effect on daily rate of whole body protein deposition. This effect was largely caused by a higher rate of protein deposition in organ tissue between 45 and 85 kg in the low pigs than in the high pigs. Water retention, but not lipid retention, in the organs was also higher in the low pigs. These differences between the low and high pigs increased with increasing energy intake, indicating a functional hypertrophy of metabolically active organs, with increasing feed intake. These results are in good agreement with Carstens et al. (1991), who reported compensatory gain in steers after a period of feed restriction. This compensation was largely caused by an increased gut fill and an increase in protein and water retention in non-carcass tissues. Drouillard et al. (1991) found an increase in gain of water, protein and lipid in visceral tissue but not in non-viscera, after a period of energy restriction in lambs. Stamataris et al. (1991) studied the effect of feed restriction between 6 and 12 kg on nutrient retention in pigs with free access to feed from 12 to 24 kg. They reported an increase in feed intake, body gain and deposition of protein, and ash but predominately of lipid, in previously restricted pigs. In agreement with the present study, this extra protein was deposited in the organs. An increase in the rate of lipid deposition due to the previous restriction, was not found in our study. Only the low pigs with free access to feed, which had a higher feed intake than the high pigs, used this extra energy for both protein and lipid deposition. The reason for the difference between our study and Stamataris et al. (1991) is not clear. Due to a big increase in feed intake, the previously restricted pigs in Stamataris et al. (1991) presumably had reached their maximum protein deposition. It can also not be excluded that the lipid reserves of these young pigs at the end of the restriction were so low that repletion of these reserves was more necessary than in the present experiment.

With increasing energy intake, protein deposition in the organs of previously restricted pigs was progressively higher than in pigs previously fed at a high energy level. There was no evidence that protein deposition in the carcass is higher due to a previous feed restriction. As a consequence, the distribution of deposited protein was affected by the nutritional history (Table 6). In previously restricted pigs, more of the total amount of deposited protein was retained in the organs and less in the carcass and lean tissue. The similar LD/PD from 45 to 85 kg for low and high pigs, indicated that the distribution of dietary energy between protein and lipid deposition was not affected by the nutritional history. Consequently, the lower lipid content at 85 kg in previously restricted animals (Table 1), as found in this study and reported earlier (e.g. Campbell et al., 1983a), was not the result of compensation in protein or lipid deposition. It was a direct result of the restriction between 20 and 45 kg, which was still present at 85 kg. Finally these results suggest that if PD_{max} has not been reached, an increase in maximum feed intake in the realimentation phase results in an increase in both protein and lipid deposition.

The effect of the nutritional history on overall deposition between 20 and 85 kg can be derived from Table 8. Average rates of protein and lipid deposition were considerably higher in the high pigs because of their higher feed intake. However, if the pigs were compared at similar daily energy intake, lipid and protein deposition were 17 g/d ($P < .05$) and 6 g/d (not significant) higher in the low pigs. The calculated daily energy retention was about 830 kJ/d higher in the low pigs. Possible reasons for this increased energetic efficiency have been discussed in the first paper of this series (Bikker et al., 1994b). It can be concluded that at similar daily energy intake, the distribution of the total energy allowance between the growing and the fattening period has only a small effect on tissue deposition.

Effect of Body Weight

Black and Griffiths (1975) concluded that in lambs nitrogen, retention increased linearly with increasing energy intake, at a rate that decreased with increasing liveweight. Results of nitrogen balance trials with pigs in four weight ranges (Dunkin and Black, 1985) suggested an effect of BW on the relationship between energy intake and nitrogen retention in pigs also, but the design of that study did not allow firm conclusions to be drawn. To determine the effect of BW on protein and lipid deposition, the results of the present experiment were compared with those obtained with pigs from 20 to 45 kg (Bikker et al., 1994a). These two experiments were conducted simultaneously, with pigs of the same herd, in the same stable, using the same experimental diet. The relationships between energy intake and protein deposition, lipid deposition and LD/PD are presented in Figure 1a, b and c. Since the nutritional history did not affect protein and lipid deposition in the empty body from 45 to 85 kg, results of the high and low pigs in this weight range were combined. The slope for protein deposition decreased markedly with increasing BW from 5.77 ± .40 to 3.78 ± .35 g/MJ DE. Reversely, the older pig retained more lipid with each MJ increase in energy intake. The slope for lipid deposition increased from 10.5 ± .59 to 13.7 ± .62 g/MJ DE. As a result, the ratio LD/PD increased with increasing energy intake, from .3 to 1.1 in the growing pigs and from .5 to 2.2 in the fattening pigs. Thus, at similar rates of protein deposition, the fattening pigs retained twice as much lipid as the growing pigs.

In the pigs used in this study, BW had a considerable effect on the slope of the relationship between energy intake and protein deposition. However, it may be that depending on the selection strategy, and consequently the genotype of the pig, an effect of BW is expressed mainly on the slope, or on the level of the dose-response relationship between energy intake and protein accretion. In addition, the genotype presumably influences the magnitude of the effect of BW. The reported effect of BW on protein deposition has two important implications. At similar rates of protein

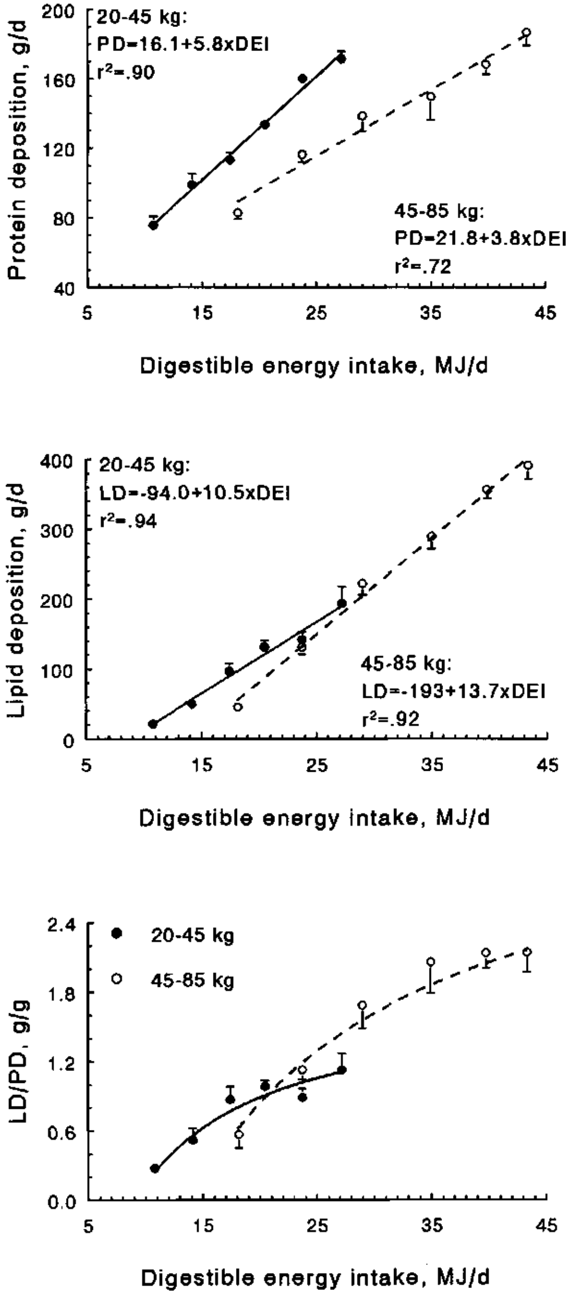

Figure 1. Relationships between energy intake and rate of protein deposition (a), rate of lipid deposition (b) and the ratio between lipid and protein deposition (LD/PD)(c) in gilts from 20 to 45 kg and from 45 to 85 kg of BW

deposition the finisher pigs become fatter than the grower pigs, and because of the higher LD/PD in the finisher pigs, the required protein/energy ratio in the diet decreases with increasing BW.

IMPLICATIONS

In the gilts used in this study, protein and lipid deposition increased linearly and body lipid content increased curvilinearly with increasing energy intake. Therefore, maximization of protein deposition is accompanied by an increase in lipid content of the body. The increment in protein deposition with increasing energy intake, diminished with increasing body weight. Consequently, at similar rates of protein accretion, the lipid deposition increases with increasing body weight. Therefore, finishing pigs become fatter than growing pigs. After a feed restriction in the growing period, compensation in protein retention is likely to occur only in the organs. There was no evidence of a beneficial effect of a previous restriction on carcass protein accretion.

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GENERAL DISCUSSION

GENERAL DISCUSSION

INTRODUCTION

The life of an animal starts at conception with a unicellular stage. From that point the animal grows and develops in order to reach its mature size and shape. For several reasons this growth to maturity is an essential part of the animal's life. It reduces the chance of predation, it enables the animal to participate in the reproduction and to protect its progeny etc. In general terms growth and development to maturity serve the survival of the individual animal and its species. In pig production, however, animals seldomly reach their mature body weight. The pigs are raised in order to be slaughtered between 80 and 120 kg, well below their mature weight of 300 to 400 kg. For biologically and economically efficient meat production, the pigs should attain their slaughter weight with a good growth rate and an efficient conversion of nutrients into body tissues. In addition, the carcasses should contain a high content of lean meat. These three criteria, growth rate, feed conversion and lean meat percentage are highly influenced by the applied feeding strategy, i.e. the feed allowances and the composition of the diet. The general aim of this study was to determine how protein and energy intake separately affect the accretion and distribution of protein and lipid in body components and how they influence the composition of body tissues in pigs with a high genetic capacity for lean gain. Pigs from 20 to 45 kg and from 45 to 85 kg were studied in order to determine the effects of body weight and of a previous feed restriction on these response relationships between nutrient intake and tissue deposition.

Some general aspects of growth and development will be discussed first in order to show the framework within which this study was conducted. Secondly, the effects of protein and energy intake on growth and development of the body and body tissues and on the deposition and distribution of protein and lipid will be discussed. Thereafter the effects on the feed conversion and on the efficiency of dietary energy and protein utilization are addressed. In each of these sections the effects of body weight and previous nutrition will be included. Finally some possible implications of the results of this study for defining efficient feeding strategies, for animal breeding, and for modelling animal growth will be discussed.

GROWTH, GROWTH CURVES AND EFFICIENCY OF BODY GAIN

Growth is usually understood as a largely irreversible increase in size and weight of the body, whereas development refers to changes in the shape, form and functioning of the body as the growth of the animal progresses. Growth and development are based on processes of cell proliferation (hyperplasia), cell differentiation and cell filling and enlargement (hypertrophy). Presumably the first two processes are mainly responsible for the prenatal and early post-natal growth of the animal, whereas post-natal growth is mainly a result of hypertrophy, e.g. of muscle fibres. Brody (1945) distinguished two principal phases in the age curve of growth, the relationship between age and body weight: a self-accelerating phase of growth with an increasing slope and a self-inhibiting phase of growth with a decreasing slope. He described the first segment, which was mainly determined by a growth accelerating force, with an exponential function assuming constant relative growth ($dW/dt = kW_t$, W = weight, t = time, k = constant). To describe the second segment, which is mainly determined by a growth retarding force, he used the Spillman function with a linearly decreasing growth rate with increasing body weight ($dW/dt = k(A-W_t)$, A = mature body weight). This type of curve between age and body weight, somewhat misleadingly referred to as growth curve, has been called the S-shape or sigmoid growth curve. The concept of an increasing and a diminishing slope in the growth curve appeared useful to describe the increase in body weight in many mammalian species (Taylor, 1980). It should be stressed that a large part of the accelerating growth may take part in utero. A number of mathematical models have been used to describe the sigmoid growth curve (Parks, 1982) of which the logistic and the Gompertz function may be the best known. These two models differ in the relative weight of the animal at the point of inflection between the increasing and diminishing phase of growth. In the Gompertz function, the body weight in the inflection point is .37 times the mature weight and in the logistic function .5 times the mature weight. At this inflection point, the growth rate is maximal. Therefore biologists refer to growth near this maximum growth rate as the growth spurt (Parks, 1982), and this is related to the puberty of the animal. On the other hand Whittemore (1993) argued that since postnatal growth is largely determined by cell enlargement and cell filling rather than cell multiplication, it would be more likely to assume a constant absolute growth rate rather than a constant relative growth rate. For pigs this assumption implies that if piglets are given unlimited nutrition and an excellent environment, it may be that the maximum absolute growth rate can be achieved early in life and be relatively constant through most of the growth period.

In many studies the relationship between age and body weight has been determined for animals of different species which had free access to feed. These growth curves and their parameters are of limited value if the animals cannot eat according to their physiological requirements. For many years people have realized that growth is not only determined by age or body weight but also by nutrient intake (e.g. Hammond 1932). Therefore Parks (1982) proposed an equation, based on the Spillman function, to relate the body weight of an animal to its cumulative feed intake. Subsequently, the feed intake was expressed as a function of age in order to determine the age curve of growth. This approach has the advantage of allowing the calculation of feed efficiency. The model of Parks (1982), indicates that this feed efficiency decreases linearly with an increasing degree of maturity. Taylor (1982) combined genetically standardised curves for growth and feed intake and reported a curvilinear decrease in feed efficiency with increasing maturity. However, again these two approaches apply mainly to ad libitum fed animals and are only suitable for animals which are restricted in their feed intake if the level of feed intake does not affect the feed efficiency. Therefore the determination of the potential growth curve does not give insight to the effects of nutrient intake on growth, development and feed efficiency. Nevertheless it is evident from many studies that feed intake can have important effects on body gain, body composition and feed efficiency (ARC, 1981). These effects are likely to be different for pigs of different genetic capacity for body gain.

The general aim of this study was to determine the interrelationships between protein and energy intake, on body and tissue gain and feed efficiency in pigs with a high genetic capacity for lean tissue deposition. The responses to energy intake were determined in two weight ranges (20-45 kg and 45-85 kg) to also study the effect of body weight and previous nutrition on the relationships between energy intake and animal performance. The results will enable us to better define feeding strategies for genetically improved pigs with a high capacity for lean gain, and to validate and improve models to simulate growth in the pig.

GROWTH AND DEVELOPMENT

Body and Tissue Gain

As described above, an animal grows to reach its mature body weight or protein mass. The potential growth curve can be described satisfactorily with a sigmoidal model, e.g. the Gompertz function. The actual relationship between age and body weight, however, is largely determined by the feed intake of the animal. Results in chapter 4 and 5 showed a linear and curvilinear increase in daily gain with energy intake for gilts from 20 to 45 kg and from 45 to 85 kg respectively. Furthermore, the rate of gain was on average 140 g/d higher for pigs which were previously restricted in feed intake. For some of the treatment groups, the relationship between age and body weight has been presented in Figure 1. This figure illustrates the effect of feed intake on the relationship between age and body weight of the pigs.

Body weight gain can be regarded as the increase in mass of different tissues, e.g. organs, lean and fat tissue, and the contents of the digestive tract. The development of different tissues has been studied by several authors (Hammond, 1932; McMeekan, 1940a,b; Davies, 1983; De Greef, 1992), often using allometric

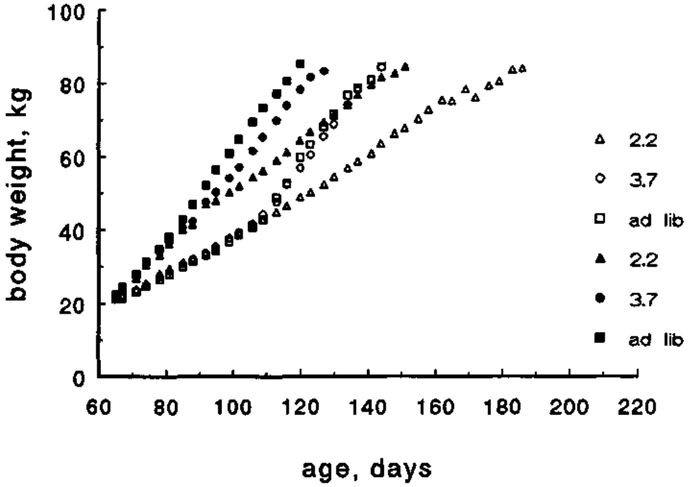

Figure 1. Relationship between age and body weight for pigs at six treatments (Chapter 5). Open and closed symbols represent pigs at 2.2 and 3.7 times energy for maintenance from 20 to 45 kg, respectively. The energy level from 45 to 85 kg is given in the legend.

relationships between a body component and body weight or another component ($W_1 = aW_2^b$; Huxley, 1932). This approach assumes a constant ratio between the relative growth rates of the components to be compared. If, for example, lean tissue mass (W_1) is related to empty body mass (W_2) and $b < 1$, then the relative growth rate of lean tissue is lower than that of the empty body, and consequently the proportion of lean tissue in the body will decrease with increasing body weight. Results of these studies generally indicate that the proportion of lean tissue in the empty body or in the carcass decreases with increasing body weight (Walstra, 1980; Davies, 1983; Whittemore et al., 1988).

In the present study, the lean tissue content in the empty body was about 2% lower at 85 kg than at 45 kg and the lean content in the carcass was 3-4% lower at 85 kg. The fat tissue in the empty body and in the carcass was about 4% higher at 85 kg. These results also indicate a decrease in body and carcass lean percentage with increasing body weight. However, it must be realised that feed intake in most studies increased with increasing body weight, and consequently part of this decreasing lean percentage may be related to an increasing feed intake (see below).

An effect of feed or energy intake on tissue deposition was evident in the present study. The carcass growth rate between 20 and 45 kg and between 45 and 85 kg increased curvilinearly with increasing energy intake. The rate of gain of the lean and fat tissue between 45 and 85 kg also increased curvilinearly with increasing energy intake. The relative increase in growth rate with energy intake was higher for fat tissue than for lean tissue, and consequently the percentage of lean tissue in the body gain decreased with increasing energy intake. This is illustrated in Figure 2. As a result, the lean tissue percentage decreased quite dramatically with increasing energy in both the growing and the fattening pig. The biggest decrease was observed at the lower intake levels (Chapter 4 and 5). These results are in agreement with the view of Hammond (1932) that fat tissue develops later and faster than muscle tissue, and is therefore more influenced by nutrient intake.

Whittemore (1986), however, proposed a constant ratio between fat and lean tissue, independent of the feed intake, for animals in the nutritionally limited phase of growth, i.e. at feeding levels below those required to reach the maximum rate of lean tissue gain. According to this assumption, the animal will not fatten and body composition will be relatively constant over a wide range of body weights

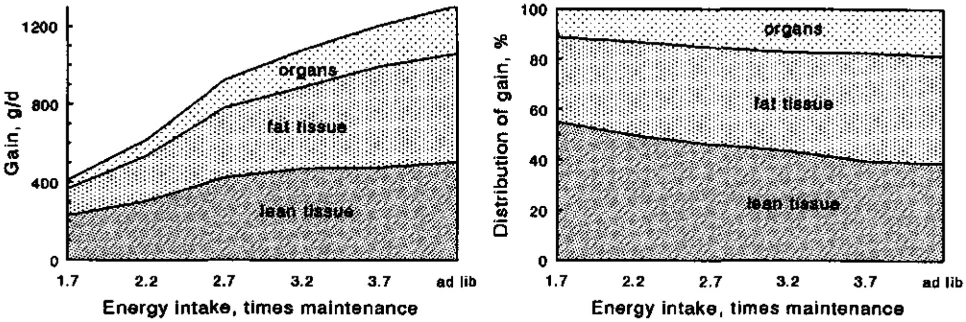

Figure 2. Daily gain of organs, lean and fat tissue from 45 to 85 kg, absolute and as percentage of the empty body gain in pigs previously fed at a low feeding level.

until feed intake is sufficient to maximize lean tissue gain. Theoretically this supposition can be combined with studies which report a decrease in lean tissue percentage with increasing energy intake or body weight (e.g. Davies and Lucas, 1972; Walstra, 1980; Ellis et al., 1983; Whittemore et al., 1988), provided that the pigs in those studies had reached a maximum lean tissue deposition rate. However, the present study showed that the lean percentage decreases gradually with increasing energy intake even when the animals have not reached a maximum in lean tissue gain. The ratio between fat and lean tissue accretion increased from .5 to .8 and from .6 to 1.1 between 20 and 45 kg and between 45 and 85 kg respectively. **In conclusion, lean tissue accretion increased curvilinearly and lean tissue percentage decreased curvilinearly with increasing energy intake. Therefore even in pigs with high genetic capacity for lean gain as used in this study, the maximization of lean gain is accompanied by a decrease in body and carcass lean content.**

In order to distinguish between the effects of body weight and energy intake on body composition and lean tissue deposition, the maintenance energy requirement was determined as the energy intake at zero energy retention. Subsequently, body composition and tissue deposition of the growing (20-45 kg) and fattening (45-85 kg) pigs were compared at similar energy intake above maintenance. The most important results are presented in Table 1.

At similar daily energy intake above maintenance, the daily gain of the total body, the empty body and the organs was higher in pigs between 20 and 45 kg

Table 1. Mean differences in tissue deposition and body composition between growing (20-45 kg) and fattening (45-85 kg) pigs compared at similar daily energy intake above maintenance

Criteria	Difference[a] growing-fattening	Significance[b]
GAIN, g/d		
Live weight	108	***
empty body	66	***
organs	43	***
lean tissue	29	NS
fat tissue	0	NS
protein retention	18.9	***
lipid retention	-25.5	***
BODY COMPOSITION		
Organs in body, %	3.4	***
Lean in body, %	-1.0	NS
Lean in carcass, %	0.9	NS

[a] Difference calculated as amount from 20-45 kg minus amount from 45-85-kg.
[b] NS not significant, $P > .05$, *** $P < .001$.

than between 45 and 85 kg. These differences increased with increasing feed intake. As a result of these effects, the percentage of organ tissue in the body was 3.4% higher in the young pigs. The lean content in the body and in the carcass was only 1% lower and 1% higher, respectively, in the young pigs. A bigger decrease of 2-4% in lean content in the body and in the carcass with increasing body weight was reported above. Consequently, the larger part of this decrease was not the result of an increase in body weight per se but the result of the higher feed intake of the heavier animals. Nevertheless, owing to an increase in the ratio between lipid and protein deposition with body weight (discussed below) body gain per MJ of energy decreased with increasing body weight. These findings are in agreement with results from the relationship between energy intake daily gain of body and tissues. The increase in body gain (slope) with energy intake decreased from 43.6 g/MJ of DE between 20 and 45 kg to 34.2 g/MJ between 45 and 85 kg. The slope for lean tissue gain decreased from 12.5 to 9.6 g/MJ. **Consequently, in the weight range from 20 to 85 kg, body gain per unit of extra energy intake diminishes with increasing body weight. The lean tissue content also decreases with increasing body weight, but this is to a considerable extent the result of the higher feed intake of heavier animals.** This conclusion is supported by the results of Davies (1983) and De Greef et al. (1994). The latter reported only small differences in body composition at different body weights in pigs which received a constant and rather low amount of energy for body gain. Davies (1983) reported a bigger decrease in body muscle content with increasing body weight in pigs at a high feeding level than in pigs at a low feeding level.

Effects of Previous Nutrition

Body gain from 45 to 85 kg was higher in animals which had been restricted in energy intake from 20 to 45 kg at 2.2 times energy for maintenance (low pigs), compared to pigs previously fed 3.7 times maintenance (high pigs). Furthermore, these low pigs had a higher percentage lean tissue, a lower percentage fat tissue, and similar organ weights at 85 kg compared to the high pigs. These differences, however, were already largely present at 45 kg as a result of the feed restriction. For example, the lean content in the carcass was, on average, 5% higher in the low pigs at 45 kg (Chapter 4, Table 3), and 3% higher in low pigs at 85 kg (Chapter 5, Table 4) compared to the high pigs. Significant compensation in accretion rate was only determined for the organ tissue. As discussed in Chapter 5, many authors have reported compensatory gain after a period of feed restriction. Most of these studies, however, do not allow the determination of which tissues are deposited during compensation, when differences in body composition were developed, and whether maximum protein or lean tissue growth rate was reached in the realimentation phase. This information is necessary to gain insight into the mechanisms of compensation. Presumably in many of those studies a large portion of the compensatory gain can be caused by a response in the size and weight of metabolically active organs to nutrient intake. Our experiment did not indicate that the lean to fat tissue ratio in the gain was affected by previous nutrition. After a period of feed restriction, animals presumably follow the normal growth rate and tissue deposition according to their body weight, apart from an increase in organ size. If in the realimentation phase the voluntary feed intake of previously restricted animals is higher than that of previously generously fed animals, the compensating animals may become fatter. This is even more likely when they have reached a maximum protein or lean tissue growth rate. This view is supported by the work of Lister and McCance (1967) who restricted young piglets to keep their body weight constant for one year. In the realimentation period they followed a similar growth curve as the ad libitum fed control animals, but they did not reach the same mature body mass. When animals are restricted at a younger age than in the present study or when they are restricted in protein intake at a high energy intake, there is probably a compensation in lean or fat tissue deposition (Kyriazakis et al., 1991; De Greef et al., 1992).

The organs, especially the metabolically active organs, appear to be quite sensitive to the amount and type of ingested nutrients. In general, the organs can be regarded as early maturing tissue in the sense that the relative organ mass decreases with increasing body weight (this study, Walstra, 1980; Davies, 1983; De Greef, 1992). Nevertheless, in both the growing and the fattening pigs in this study the relative organ mass increased with increasing feed intake. In addition, it seems likely from the rapid increase in daily gain in animals changed from a low to a high feeding level at 45 kg and from the above mentioned increase in organ gain in realimented pigs, that the metabolically active organs respond quite rapidly to an increase in feeding level. This assumption is supported by the results of an energy restriction and subsequent realimentation on weights of specific organs of Pond and Mersmann (1990). Conversely, animals at a high feeding level to 45 kg and a low feeding level thereafter had a high organ mass (19% of body weight) at 45 kg and a low organ growth (9% of total body gain) from 45 to 85 kg.

In addition, results of this study showed that the response to nutrient intake differs between organs and also depends on the type of nutrients. The organs involved in digestion and absorption of nutrients, especially intestines, liver, kidneys and pancreas, showed the biggest increase in weight with increasing energy intake. Furthermore when protein and energy intake were varied independently, the kidneys and pancreas responded mainly to increasing protein intake, whereas the liver and the small intestine were mostly affected by non-protein energy intake (Table 2).

Effects of quantity and type of ingested nutrients on organ mass in pigs have been found by several authors. (Koong et al., 1982, 1983; Pond et al., 1988, Rao and McCracken, 1992) These effects presumably reflect the adaptive capacity of the animal to process the ingested nutrients.

In conclusion metabolically active organs respond rapidly in size and weight to a change in daily nutrient intake. Together with an increase in digestive tract contents, this response can largely account for the increase in body weight gain (compensation) after a period of feed or energy restriction as reported in many studies. An increase in lean or fat tissue gain during rehabilitation was not found. Therefore the lean content which is higher at the end of the restriction phase may still be higher at the end of the realimentation phase. This could explain the higher

lean content as sometimes reported for previously restricted animals and also found in our study.

Table 2. Weight of individual organs at 45 kg as affected by protein, energy and feed intake

	Experiment 1					Experiment 2		
	Weight, g		Effects[b]			Weight, g	Effects[b]	
Organ	2.5xM[a]	3.0xM[a]	Energy	Protein	b1	Mean	Feed	b2
Liver	891	965	***	*	28.1	912	***	28.2
Kidneys	187	190	NS	***	25.1	185	***	4.61
Pancreas	68.8	75.2	NS	***	12.4	91.7	*	1.74
Small intestine	980	1081	***	NS	10.2	1031	***	25.6
Large intestine	670	705	*	*	33.9	759	*	11.0

[a] First and second column: intake levels 2.5 and 3.0 times energy for maintenance respectively.

[b] Linear regression ($y = a + bx$) was used to determine effects of protein and energy intake. NS not significant, $P > .05$, * $P < .05$, ** $P < .01$, *** $P < .001$. The slopes b1 and b2 represent the increase in organ weight per 100 g crude protein intake/d and per MJ of DE intake/d, respectively.

DEPOSITION AND DISTRIBUTION OF BODY PROTEIN AND LIPID

Maximum Protein Deposition

It is well established that protein accretion can be constrained by energy intake, protein intake and the animal's intrinsic capacity for protein deposition (PD_{max}). The PD_{max} is mainly determined by the intrinsic factors age, body weight, sex, and genotype of the animal. Male pigs have a higher capacity for protein deposition than females, whereas females can deposit more protein than castrated male pigs (Campbell et al., 1983b, 1985; Campbell and Taverner, 1988a). Animals intensively selected for body gain or lean tissue deposition have a higher maximum protein retention than pigs of an unimproved genotype (Campbell and Taverner, 1988a). The relationship between body weight and PD_{max} is still a matter of debate. Different theories for this relationship can be distinguished. The first theory is that PD_{max} increases gradually with increasing body weight until a maximum is reached between 60 and 100 kg, and decreases thereafter (Thorbek, 1975). Whittemore (1994) used the derivative of the Gompertz function to describe maximum protein deposition versus liveweight, thus representing a relatively flat-topped response between 20 and 120 kg. It may be, that potential protein deposition increases rapidly in young pigs and remains largely constant from about 20 to 100 kg of body weight (Carr et al., 1977; Moughan et al. 1987). This assumption is in reasonably good agreement with the earlier mentioned theory of Whittemore (1993) that body weight increases linearly with age in a large part of the growth period in nutritionally unlimited pigs.

It must be realised that an increase in protein deposition with increasing body weight in restricted or ad libitum fed pigs does not necessarily imply an increase in PD_{max}. It may also simply reflect the increase in feed intake with increasing body weight. No convincing evidence for one of these concepts has been published. However, the high rates of growth and protein deposition in young pigs as reported by Campbell and Taverner (1988b), Kyriazakis and Emmans (1991), and others suggest that animals following the gradual increase in protein deposition with body weight (Thorbek, 1975) are more restricted by nutritional or environmental conditions than by their intrinsic capacity for protein deposition. This highlights the importance of an adequate nutrition and understanding of the effects of nutrient intake on protein and lipid deposition. These effects will be discussed in the following paragraph.

Protein and Energy Dependent Phases

Protein and lipid deposition are largely determined by both protein and energy intake. It was the aim of this study to determine the separate effects of protein and energy intake in growing (20-45 kg) and fattening (45-85 kg) pigs in order to determine interactions with body weight and previous nutrition. Since protein/energy requirements are higher in young pigs (e.g. Campbell et al, 1988) and supply of dietary protein is therefore more critical in this period, it was decided to determine the effect of protein intake in the grower pig only.

The results discussed in Chapter 1 and 2, supported the concept of protein and energy-dependent phases in protein deposition. At low levels of protein intake, relative to energy intake, protein deposition is limited by protein intake and increases with incremental amounts of dietary protein. Under these conditions an increase in the intake of non-protein energy does not affect protein retention, but will only increase lipid deposition. Likewise, a decrease in protein intake at constant energy intake reduces protein deposition and stimulates lipid accretion. Consequently the ratio between lipid and protein deposition (LD/PD) will increase. At high levels of dietary protein, an increase or decrease in protein intake did not significantly affect protein deposition. An increase in non-protein energy in this energy-dependent phase will increase both protein and lipid deposition. At each level of energy intake, protein deposition reaches a maximum, presumably because the animal's metabolism strives to realize a certain (minimal) ratio between lipid and protein deposition. Consequently it uses part of the dietary energy for lipid retention. This LD/PD ratio in the energy-dependent phase increases with increasing energy intake (Chapter 1), as discussed below. **The concept of protein and energy dependent phases in protein deposition is supported by the results of this study. This concept implies that if the level of feed intake is increased, an increase in protein deposition will reflect the response to dietary protein on a low protein diet and the response to dietary energy on a diet abundant in protein.**

The smoothness of transition between the protein and energy dependent phases remains a point of debate. Even when the relationship follows an abrupt transition in an individual animal, variation between animals as in our study, or variation due to body weight as in Fuller and Garthwaite (1993), is possibly the reason that a curvilinear or gradual transition is observed. The experiment described in the Chapters 1 and 2, and similar experiments reported in the literature therefore, do not elucidate the biological response of protein deposition of the pig to protein intake which lies in the region of the optimum protein/energy ratio. Nevertheless they contribute to the search for a mathematical model for a satisfactory description of the response curve.

Effects of Energy Intake and Body Weight

The relationship between energy intake and protein deposition has been described as linear (Campbell and Taverner, 1988b; Close et al, 1983), curvilinear (Schneider et al, 1982) and linear-plateau (Campbell et al, 1985). Whether a maximum in this response curve can be found, depends on the potential protein deposition of the animal and its feed intake capacity. Results of Campbell and Taverner (1988b), Campbell and Dunkin (1983a), and Campbell et al. (1983, 1985), indicate that a maximum protein accretion can more likely be found in older pigs than in young pigs, and in females and castrates rather than entire male pigs. On the other hand, recent work of Campbell and Taverner (1988a), and Rao and McCracken (1991), suggest that in modern pigs of improved genotype, maximum protein deposition may be beyond the limits of appetite even at body weights up to 90 kg. Before the present study no adequate information was available concerning the effects of body weight and previous nutrition on the relationship between energy intake and protein deposition. Therefore it was decided to determine this relationship in pigs from 20 to 45 kg and from 45 to 85 kg. The latter pigs were fed either a high or a low feeding level from 20 to 45 kg.

Rate of protein deposition increased linearly with increasing energy intake between 20 and 45 kg and between 45 and 85 kg to a rate of 172 and 187 g/d, respectively. Although data of two pigs with free access to feed from 20 to 45 kg suggested some curvilinearity (Chapter 4), no convincing evidence for a plateau in protein deposition was found. These results are in good agreement with those obtained for male pigs by Campbell and Taverner (1988a) and Rao and McCracken (1991). **The data of these three studies (Figure 3) with pigs of high genetic capacity for lean gain indicate that PD_{max} cannot be reached in genetically improved pigs below about 80 to 90 kg.**

Daily lipid accretion also increased linearly with increasing energy intake up to 200 and 400 g/d. This was to be expected since a linear increase in protein deposition implies that from each unit of extra energy, a constant part is used for protein accretion and consequently a constant remaining part can be used for lipid retention. Thus the ratio between extra lipid and extra protein retention (ΔLD/ΔPD) per unit increase in energy intake is constant. This also means a constant ratio

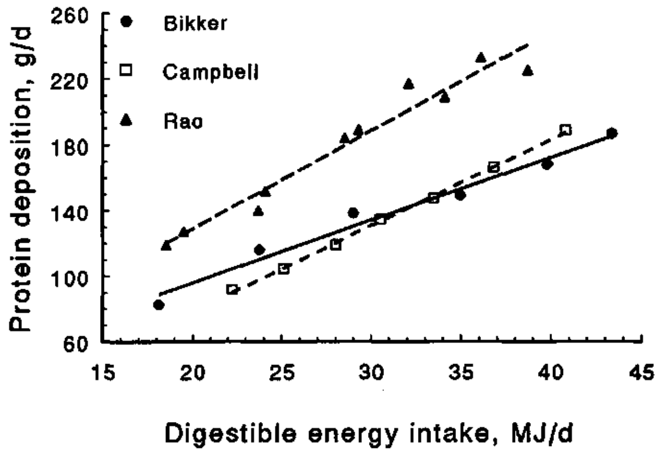

Figure 3. Protein deposition as affected by energy intake in pigs with high capacity for lean gain, from 45 to 85 kg. Data from this study, Campbell and Taverner (1988) and Rao and McCracken (1991).

between total lipid and protein deposition (LD/PD) provided that protein and lipid accretion are zero at maintenance energy intake. However, extrapolation on the basis of the regression equations indicated a positive protein deposition at the expense of lipid breakdown at maintenance energy intake (see also Figure 4). A preference for protein deposition at low intake levels is supported by experimental results of Close et al. (1983) and Kyriazakis and Emmans (1992a,b). These authors reported considerable daily rates of protein deposition (40 to 90 g/d), while lipid deposition was minimal or even negative. In our study LD/PD at the lowest energy intake level was .3 and .5 in the growing and fattening pigs respectively, whereas ΔLD/ΔPD was 1.8 and 3.6, respectively. Consequently LD/PD is low at low intake levels and increases curvilinearly with increasing energy intake (see also Figure 4). This finding is supported by the experimental results of Campbell et al. (1983a), De Greef et al. (1994), and others. **As a result of the increase in LD/PD with increasing energy intake, body lipid content will increase curvilinearly and body protein content will decrease curvilinearly with incremental amounts of dietary energy. These effects of energy intake are also present in pigs of an improved genotype, which cannot reach their maximum protein deposition capacity.**

Body Weight

Whittemore (1986) suggested that the relationship between energy intake and protein deposition is largely constant and independent of the body weight of the pig. This assumption is unlikely to be correct, because body lipid content has been often reported to increase with increasing body weight (e.g. Whittemore et al., 1988). Lipid content can only be higher at higher body weights, without a change in this relationship if the pigs had a feed intake above that required to reach PD_{max}. In the present study, the lipid content in the body ranged from 80 to 150 g/kg at 45 kg and from 115 to 221 g/kg at 85 kg. These results show an increase in lipid content with increasing body weight even in pigs well below their PD_{max}. Since the daily energy allowance was based on the metabolic body weight of the pigs, this increase is again the result of the combined effects of body weight and energy intake. Nevertheless, the regression equations showed a marked decrease in the slope for protein deposition, with increasing body weight from 5.8 to 3.8 g/MJ of DE, and an increase in the slope for lipid retention from 10.5 to 13.7 g/MJ of DE (Figure 1 in Chapter 6). A decline in the slope for protein deposition is in agreement with results reported in lambs by Black and Griffiths (1975). To separate the

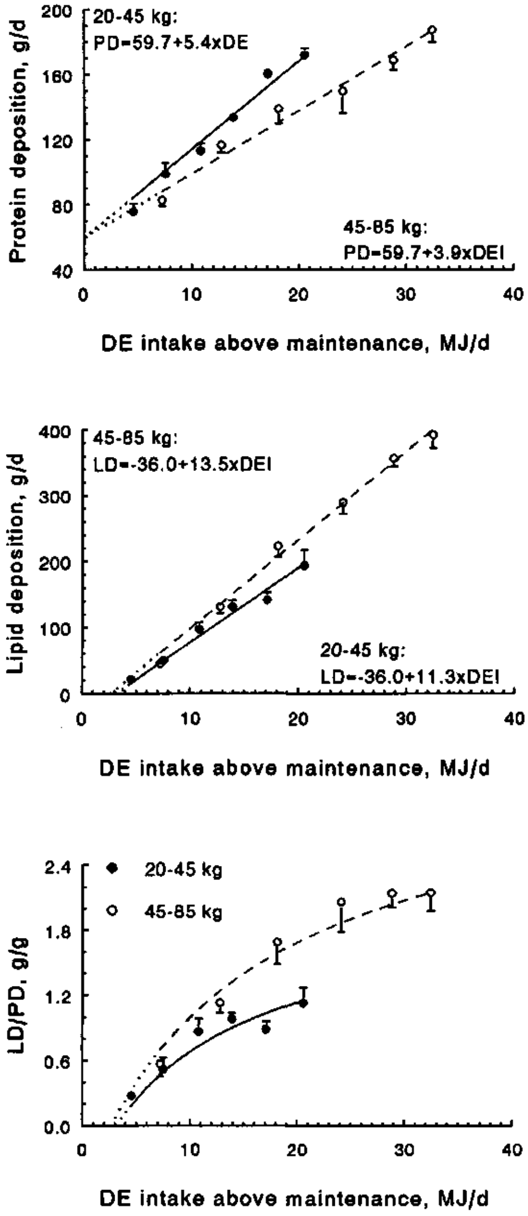

Figure 4. Relationships between energy intake above maintenance and protein deposition (PD), lipid deposition (LD) and LD/PD from 20 to 45 kg and from 45 to 85 kg.

effects of body weight and energy intake, the effects of energy intake above maintenance on the rates of protein and lipid retention were also analysed. The results as plotted in Figure 4, confirmed the decreasing slope for protein deposition and the increasing slope for lipid retention with increasing body weight. In addition, no significant effects of body weight were found for the intercepts, which represent deposition rates at maintenance energy intake. **These results imply that at a constant daily energy intake for production fattening pigs deposit more lipid and less protein than growing pigs. Consequently, lipid content increases with increasing body weight. This effect of body weight is small at very low levels of energy intake and considerable at high energy levels.** On average, the body lipid content was 30 g/kg higher in pigs at 85 kg than in pigs at 45 kg, at similar daily energy intake for production from 20 to 45 kg and from 45 to 85 kg. The young pigs also retained more water in addition to the higher protein deposition, and so gained on average about 100 g/d more than the fattening pigs on a similar amount of production energy (see Table 1). **In practice, the pigs are fed ad libitum or relative to their body weight. Therefore the differences between growing and fattening pigs will be even bigger. At the three highest feeding levels the LD/PD in the fattening pigs was about twice as high as in the growing pigs.**

Distribution of Protein and Lipid

Little attention has been paid in the literature to the distribution of deposited protein and lipid between body components. Nevertheless, only protein in the edible parts of the body, especially the lean meat, is valuable for human consumption. The increase in LD/PD and body lipid content and the decrease in body protein content with increasing energy intake has already been discussed. Most of the protein, on average 55%, was deposited in lean tissue and most of the lipid, on average 70%, was deposited in fat tissue (Chapter 4 and 6). Consequently, the effects of increasing energy intake on protein and lipid content correspond with a decrease in lean tissue percentage. In addition an effect of energy intake on the distribution of protein and lipid within the body was found. At the lowest energy level the distribution of deposited protein was on average: organs 10%, lean tissue 60%, and fat tissue 30% (Chapter 4 and 6). It was calculated with linear regression, that from incremental amounts of protein with increasing energy intake, about 25% was deposited in the organs, 40% in the lean tissue and 35% in the fat tissue. Consequently, the proportion of protein deposited in organs and fat tissue increased, and that in the lean tissue decreased with increasing energy intake. In growing pigs (20-45 kg) the proportion of total daily protein retention which was deposited as lean tissue decreased from 61 to 53%. In fattening pigs this proportion decreased from 61 to 51%. Results of the first experiment (Chapter 1), confirmed the increase in the proportion of organ protein with increasing energy intake. This experiment also showed that the distribution of protein between carcass and organs was not affected by the protein intake of the animals. The proportion of lipid deposited in the lean tissue decreased from 35 to 25% in the young pigs and from 32 to 21% in the older pigs (Chapter 4 and 6). **Consequently, the decrease in lean tissue percentage with increasing energy intake is not only a reflection of an increasing LD/PD but also of a shift in the distribution of nutrients among the different body tissues.** The ratio between lean tissue deposition and protein retention decreased with increasing energy intake from about 2.8 to 2.5 and from 2.9 to 2.7 between 20 and 45 and between 45 and 85 kg respectively. This implies that the decrease in body lean tissue content with increasing energy intake is larger than the decrease in body protein content. This may partially explain why a linear increase in protein deposition and a curvilinear increase in lean tissue accretion with energy intake were found.

Effects of Previous Nutrition

Several authors have suggested that the relationships between energy intake and rates of protein and lipid deposition in pigs are affected by a previous restriction in protein or energy intake (Black et al., 1986; Kyriazakis and Emmans, 1992; De Greef et al., 1992). Indeed there is evidence that after a period of protein restriction at a high energy intake level, animals retain more protein and less lipid (Kyriazakis and Emmans, 1991; De Greef et al., 1992). Kyriazakis and Emmans (1982c) concluded that if the ratio between protein and ash or between protein and lipid in the body was reduced, the animal has an increased preference for protein accretion during rehabilitation.

After a period of feed or energy restriction, body protein content is higher and body lipid content is lower than in generously fed animals (e.g. this study). In addition the restricted animals are older at the same body weight. There is little evidence that these changes related to an energy restriction have a major effect on subsequent protein and lipid deposition. The previously restricted animals (low pigs) in this study, showed similar relationships between energy intake and total protein and lipid accretion from 45 to 85 kg to their generously fed counterparts (high pigs). Only protein deposition in the organs was increased after the previous restriction, which presumably reflected an adaptation in order to enable the animal to process the increased amounts of feed. This assumption is supported by our observation that the increase in organ growth was higher at high feeding levels in the realimentation period.

Protein and lipid deposition in the carcass from 45 to 85 kg, were similar for high and low pigs. Therefore the previously restricted animals were still leaner at 85 kg. Hence the lower fat content at slaughter as sometimes reported in animals restricted in feed intake during a part of the growing phase (e.g. Campbell et al., 1983b), may well be the result of the absence of compensation in the realimentation phase. These results are in good agreement with the theory of compensatory growth presented by Kyriazakis and Emmans (1992) apart from their proposition that restricted animals will replete their body lipid stores. **It would seem likely that the effects of energy intake on protein and lipid deposition in the carcass are not affected by a previous energy restriction. Only protein retention in the organs will be increased as a direct response to an increased nutrient intake. However, if the previously restricted animals eat more, the LD/PD may be increased as discussed earlier in this chapter. If due to an increase in feed consumption the intake required to reach PD_{max} is exceeded, this will cause a rapid increase in LD/PD. In conclusion it seems that protein and lipid retention in the carcass are determined more by body weight and energy intake than by age or previous nutrition.**

EFFICIENCY OF NUTRIENT UTILIZATION

Efficiency of Body Gain and Lean Tissue Accretion

The first experiment in this study (Chapter 1) showed a curvilinear increase in gain/feed with increasing protein intake up to 565 and 604 g/kg at the low and high energy level. This curvilinear response allowed the calculation of an optimum protein/energy ratio in the diet. Below the optimal protein/energy ratio gain/feed deteriorated with decreasing protein levels due to an increase in lipid accretion and a decrease in protein retention. At adequate levels of protein intake, gain/feed increased curvilinearly with increasing energy intake, both in growing and finishing pigs (Chapter 4 and 5). Gain/feed was relatively constant at the three highest energy intake levels, which is in agreement with the curvilinear increase in LD/PD with energy intake. This result agrees well with other studies with improved animals (Campbell and Taverner, 1988a; Rao and McCracken, 1991). In studies with pigs with a low capacity for protein gain (unimproved animals) a decrease in gain/feed at high energy intake levels was found, presumably because the animals had reached their maximum protein deposition capacity and deposited excessive amounts of lipid (e.g. Campbell and Taverner, 1988a).

Gain/feed increased with increasing energy intake from about 500 to 600 g/kg in growing pigs and from 340 to 470 g/kg in fattening pigs (Figure 5a). In order to compare these two groups of pigs, the gain per kg of feed above maintenance was also calculated. The results as plotted in Figure 5b, showed a decrease in gain/production feed with increasing body weight and energy intake. These results are in good agreement with the earlier discussed increase in the ratio LD/PD with increasing body weight and energy intake. At low levels of energy intake and in growing pigs, relatively more of the energy was used for protein deposition. Because of the concomitant water retention, the body gain and gain/feed were higher than in heavier pigs and at high levels of energy intake. Furthermore, the decrease in body gain/production feed with increasing energy intake (Figure 5b) indicates that the increase in body gain/total feed with energy intake (Figure 5a) was caused by a reduction in the proportion of energy used for maintenance.

The lean tissue feed conversion (lean/feed) was also higher in the young pigs than in the fattening pigs, on average 278 vs. 192. Contrary to the gain/feed, the

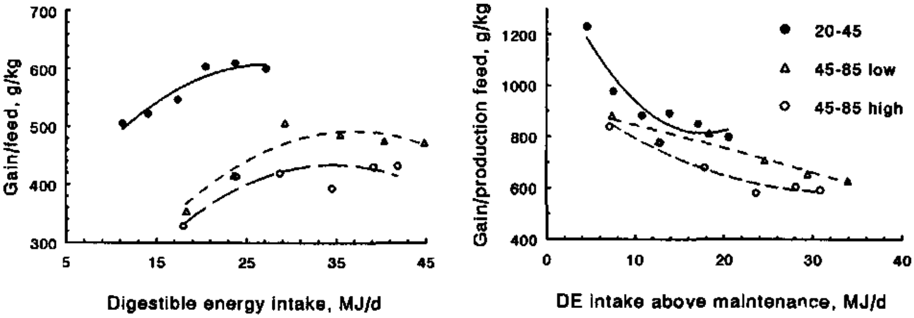

Figure 5. (a) Gain/feed vs. energy intake and (b) gain/production feed vs. energy intake above maintenance in pigs from 20 to 45 kg and in pigs from 45 to 85 kg previously fed either a high or a low energy level.

lean/feed decreased with increasing energy intake (Chapter 4, Table 4 and Chapter 5, Table 5). This decrease was a reflection of the decreasing proportion of lean gain in the total body gain with increasing energy intake. **Consequently the efficiency of nutrient conversion into lean tissue is optimized at a low feeding level and efficiency of nutrient conversion into total body mass is optimized at a high feeding level.**

Animals which had been restricted in feed intake from 20 to 45 kg (low pigs) showed a slightly improved gain/feed from 45 to 85 kg. As discussed earlier, this was mainly the result of an increased organ growth. The lean tissue deposition per kg of feed was not significantly affected by the nutritional history.

Overall, from 20 to 85 kg, the gain/feed was slightly higher in the low pigs than in the high pigs when compared at the same average daily energy intake from 20 to 85 kg (see also Chapter 5, Figure 2). This was presumably the result of the somewhat lower average body weight and maintenance requirements of low pigs compared to high pigs (see Chapter 5 and 6). However, only organ and fat tissue gain and body lipid retention were significantly higher in low pigs at similar average daily intake from 20 to 85 kg (Chapter 5, Table 7 and Chapter 6, Table 8). This increase in fat tissue and lipid gain presumably reflects the increase in LD/PD with increasing body weight. Furthermore, as already discussed, the organs presumably responded to the increasing amounts of feed to be processed between 45 and 85 kg. Lean tissue gain from 20 to 85 kg was similar in low and high pigs when compared at the same average intake level, and consequently the percentage lean tissue in the body at 85 kg was slightly (about 1.6%) lower in the high animals. **It was concluded that at a similar average daily energy intake between 20 and 85 kg, the feeding strategy (a high level from 20 to 45 kg and a low level from 45 to 85 kg, or vice versa) had only small effects on the performance of the pigs. The pigs which received first a low feeding level and thereafter a high feeding level showed a slightly higher gain and gain/feed, a similar rate and efficiency of lean tissue gain and a somewhat reduced body lean content, compared to pigs fed according to the reverse feeding strategy.**

Energetic Efficiency

It is generally accepted that the energetic efficiency for lipid accretion (k_f) is higher than for protein accretion (k_p), but there is a large variation in the estimates from different studies reported in the literature. For k_f, most of the estimates range from .7 to .8, and for k_p from .4 to .7 (ARC, 1981). In the present study, the ratio between lipid and protein accretion (LD/PD) increased with increasing body weight. Therefore an increase in the overall efficiency of energy retention as protein plus lipid (k_{pf}) with increasing body weight was expected. Furthermore, it has been suggested in the literature, that after a period of feed restriction the energetic efficiency of body gain is increased. Therefore the effects of body weight and previous nutrition were determined for the relationship between metabolizable energy intake and energy retention. The results as presented in Figure 6, showed that efficiency of energy utilization (k_{pf}) between 45 and 85 kg was not significantly affected ($P > .1$), by a feed restriction from 20 to 45 kg. Consequently, these results did not confirm the supposition that there would be an increased energetic efficiency during realimentation after a period of feed restriction. If the energy expenditure was reduced during feed restriction, it was presumably rapidly increased after a change in the feeding level.

The k_{pf} between 45 and 85 kg was higher ($P < .001$) than between 20 and 45 kg, 0.64 vs. 0.60. This is in good agreement with the higher ratio between lipid and protein accretion in heavier animals, because lipid is retained more efficiently than protein.

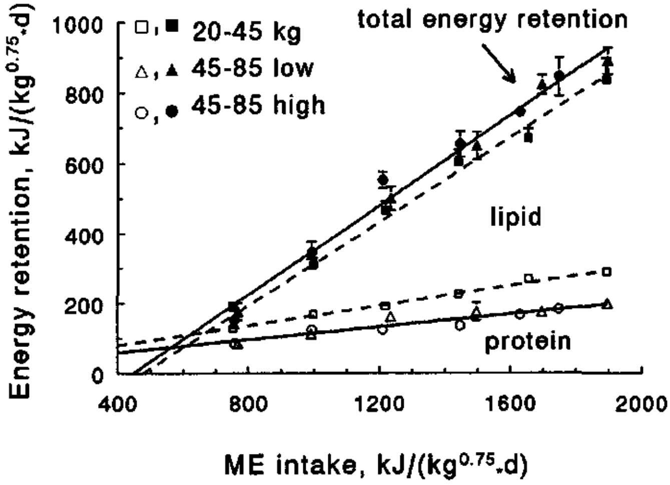

Figure 6. Relationships between metabolizable energy intake and energy retained as protein and lipid in pigs from 20 to 45 kg (dotted line) and in pigs from 45 to 85 kg previously fed either a low or a high energy level.

A linear relationship between energy intake and energy retention as in Figure 6 and thus a constant k_{pf}, has often been reported (Susenbeth and Menke, 1991). It was concluded that this constant k_{pf} combined with a considerable increase in LD/PD (Figure 4) implied that k_p or k_f was not constant (Susenbeth and Menke, 1991; Reeds, 1991). However, it should be stressed that with linear regression, k_{pf} is not based on the total energy retention, but on the marginal increase in energy retention (slope) with increasing energy intake. Due to the linear increase in protein and lipid retention, the ratio between protein and lipid in this extra gain (ΔLD/ΔPD) is constant, as already discussed. Therefore a linear increase in energy retention and a constant k_{pf} is to be expected. This calculated k_{pf} is specific for the extra tissue deposited with an increase in energy intake. If the composition of this extra deposited tissue (ΔLD/ΔPD) is altered, e.g. when relatively more lipid is retained, presumably another k_{pf} will be found. This is supported by the higher k_{pf} determined in the fattening pigs compared to the growing pigs in this study.

Koong et al. (1982, 1983) reported a positive correlation between fasting heat production and weights of organs of the gastro-intestinal tract, liver and kidneys. In the present study an increase in organ weights with increasing energy intake was found. In order to determine a possible relationship between organ mass and energy expenditure, first the metabolizable energy requirements for maintenance were calculated. A value of 456 kJ/(kg$^{.75}$*d) for ME_m was found, using linear regression between metabolizable energy intake and energy retention. Subsequently, energetic efficiencies for energy retention as protein and lipid were determined as $k_p = .43$ and $k_f = .77$ with multiple linear regression. Thereafter, maintenance energy for each individual animal was calculated as ME-intake minus energy used for protein and lipid accretion, using these estimates for k_p and k_f. Consequently, all factors influencing the energy expenditure which were not explained by protein and lipid accretion, were accounted for in the estimate of maintenance. Despite the large variation between animals, a significant increase ($P < .001$) in the estimates of ME_m with increasing energy intake was found, as shown in Figure 7. This increase might be related to the increased organ weights, reflecting an increased metabolic rate at high energy levels. Energy expenditure by the metabolically most active tissues (organs) presumably is higher than energy expenditure related to the carcass (Koong et al., 1982, 1983). Furthermore, an increase in the proportion of total body protein which was deposited in the organs, was found with increasing energy intake. Since turnover of organ protein is much higher than turnover of protein in

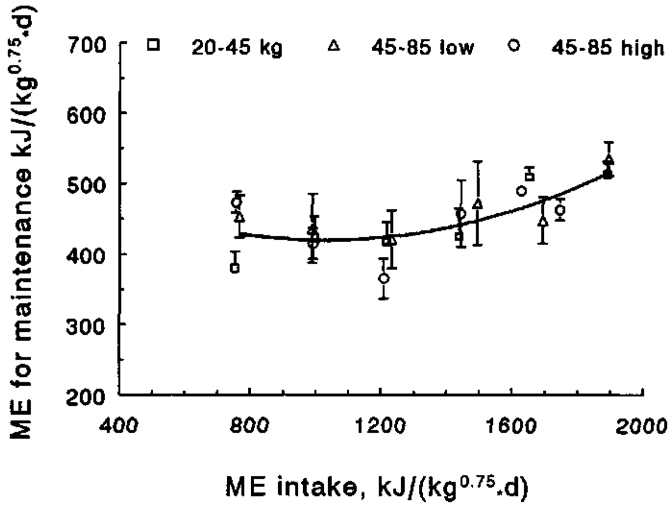

Figure 7. Effect of energy intake on calculated metabolizable energy requirements for maintenance in pigs from 20 to 45 kg and in pigs from 45 to 85 kg previously fed either a low or a high energy level.

other tissues (Simon, 1989), this may have contributed to the increased heat expenditure of the animals at the high intake levels.

In conclusion, there was no evidence in this study of an increased energetic efficiency in pigs which were previously restricted in their feed intake. Furthermore the fattening animals showed a higher efficiency of energy retention (k_{pf}) than the growing pigs, which can be explained by the higher ratio between lipid and protein deposition in the heavier animals. Finally, an increase in feed intake seems to increase the heat expenditure of the pigs, which may be explained by an increase in the weight and activity of metabolically active organs.

Efficiency of Nitrogen Utilization

An efficient retention of dietary nitrogen becomes increasingly important because of an increasing awareness of the negative effects of excreted nitrogen. In the first experiment of this thesis, the efficiency of utilization of ileal digestible protein and lysine, being the first limiting amino acid, was measured as 58 and 74% respectively (Chapter 2). These results, compared with a gross efficiency of total protein utilization of about 30% in practice (Coppoolse et al., 1990), indicate scope for a considerable improvement in nitrogen utilization, especially by better adjusting the amount and pattern of dietary amino acids to the requirements of the animal. Because of the different optimal amino acid patterns for maintenance and production (Fuller et al., 1989), this ideal amino acid pattern is not constant, but depends on the amounts of dietary protein used for maintenance and production. In addition, the present study showed that the whole body amino acid pattern is not constant but is affected by protein and energy intake (Chapter 3). This effect was presumably mediated by the effect of nutrient intake on the growth of different tissues with different amino acid compositions. Consequently it would be expected that factors which influence the growth and turnover of organs and tissues (e.g. nutrient intake, anti-nutritional factors, body weight, and environmental stressors), also have an effect on amino acid requirements and the optimal amino acid pattern. More emphasis needs to be put on the use of different amino acids for accretion of protein in different body components.

The results of experiment 1 (Chapter 1), illustrated the importance of an appropriate definition of the optimal protein/energy ratio. A dietary protein/energy below this optimum will increase the body lipid content, whereas above this optimum the efficiency of nitrogen utilization will diminish rapidly. If an optimum protein or amino acid to energy ratio is to be determined, different methods can give very different results for the same set of data as illustrated in Figure 1 and Table 6 in Chapter 1. In this experiment the linear-plateau model is to be preferred above the quadratic model, mainly because there is no evidence that the increase in lysine/DE from .62 to .82, gave any improvement in performance or protein deposition. Nevertheless these two methods and others, of which some can be rejected on theoretical grounds (Baker, 1986), have been used to determine amino acid requirements. In any case both researchers and nutritionists should be aware of the difficulties and pitfalls of the determination of nutrient requirements. When applying a requirement figure, the method of determination should be taken into account. For optimizing the amino acid utilization, it is preferable to model the relationships between nutrient intake and amino acid flow in the animal by applying experimental results to biological concepts. This allows the inclusion of amino acid flow to different tissues, the sites and reasons of amino acid losses, effects of genetic, nutritional and environmental factors, etc. At this stage, our knowledge in these areas is far from sufficient to realize these aim, but if there is agreement concerning this aim, it will give direction to future research. At this moment it is possible (and it is being done), to include those dose-response relationships between protein and energy intake and protein and lipid deposition which are thought to give the best description of the biological mechanisms, in a mathematical model. Stochasticity can be used to account for variation between animals and the consequences for simulation of one animal or a group of animals. This approach will allow the optimization of energy intake and amino acid/energy ratios, taking into account market conditions and nitrogen excretion.

The efficiency of utilization of faecal digestible protein for protein accretion in the second experiment (Chapter 4 and 6), decreased from .57 between 20 and 45 kg, to .38 between 45 and 85 kg. This decrease in observed nitrogen utilization with increasing body weight has also been reported by other authors (Berschauer et al., 1980; Rao and McCracken, 1991). As discussed above, nitrogen utilization in the energy dependent phase is a reflection of the energy available for protein synthesis and not of the potential protein utilization of the animal. Therefore, the decrease in efficiency with increasing body weight in the present study, was presumably the result of a dietary protein content which was much higher than the requirements of the heavier animals. There is little evidence of a diminishing potential protein utilization with increasing body weight. Results of Rao and McCracken (1990) suggest a similar nitrogen utilization in pigs of 40, 60 and 80 kg of body weight when fed a low protein diet. In addition, a balance study in our laboratories with pigs at 25, 55 and 85 kg did not confirm a decrease in nitrogen utilization with increasing body weight (Bikker, Karabinas, and Van Laar, unpublished data).

This study did not allow a direct evaluation of the effect of feed intake, and thus of the production level, on the utilization of dietary protein. In order to estimate the effect of feed intake on protein utilization, a simple calculation was performed. Maintenance requirements of .268 g nitrogen/($kg^{.75}$*d) (Fuller et al., 1989) and an efficiency of digestible protein utilization of .60 were adopted. Moreover, it was assumed that the dietary protein/energy perfectly matched the requirements at each energy intake level. Subsequently, the maximum nitrogen utilization and the minimum nitrogen excretion were calculated, at each level of energy intake for the pigs between 45 and 85 kg in this study. The results have been plotted in Figure 8.

The gross efficiency of protein utilization (protein gain/protein intake) increased slightly with increasing feed intake due to a dilution of protein requirements for maintenance. On the other hand, with increasing feed intake, a decreasing proportion of the retained protein was deposited in the lean tissue. Therefore protein intake above maintenance is retained with a decreasing efficiency in lean tissue (lean protein gain/[protein intake - maintenance protein]). These two effects compensated each other to some extent and as a result, the gross efficiency of lean protein retention decreased slightly with increasing feed intake. Figure 8 clearly shows that even at a rather high overall protein utilization (50-55%), the efficiency of lean tissue protein gain is unlikely to exceed 30%.

As a next step, the nitrogen excretion per kg of body gain and per kg of lean tissue gain was calculated. Figure 8b shows that for each kg of body and lean tissue gain, about 25 and 55 g nitrogen was excreted in the urine. In addition, nitrogen retained in non-lean body tissues was included in the nitrogen losses because of their low value for human consumption. As a result the nitrogen losses increased to 80 g per kg lean tissue gain. On the basis of the decreasing efficiency of lean protein gain (Figure 8a), one might have expected an increase in nitrogen excretion per kg lean tissue gain with increasing feed intake. This would be the case if the body and lean tissue protein content were constant. However, due to the decrease in protein content, both in the body and in the lean tissue, the calculated nitrogen excretion per kg lean tissue or body gain, decreased with increasing feed intake. This apparent positive effect, however, was counterbalanced by a presumably undesired increase in lipid content of the total body and the lean tissue. Therefore an optimal feeding strategy can only be designed after definition of a set of criteria in a combination considered as optimal.

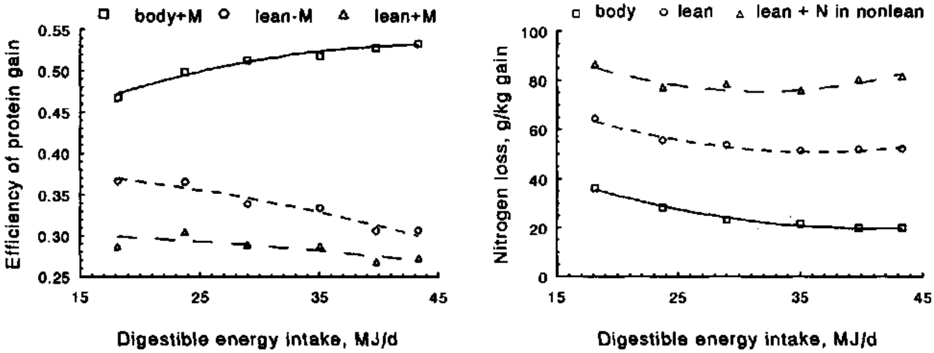

Figure 8. (a) Efficiency of protein utilization for protein gain in the body and the lean tissue. "+M" protein requirements for maintenance taken into account. "-M" efficiency above maintenance. (b) Nitrogen loss in the urine per kg of body and lean tissue gain, and nitrogen retained in non-lean tissues also included in the losses.

In conclusion there is considerable scope for improvement in nitrogen utilization in the pig industry, mainly by better adjustment of the amount and pattern of dietary amino acids to the requirements of the animal. Optimum protein and energy allowances depend among others, on the body weight and genotype of the pig, on the response criteria to be optimized and on the method of determining requirements. This rewards the use of models which simulate the rate and composition of body gain of the pig in response to nutrient intake. These models allow to take animal and environmental factors into account and enable the calculation of optima after definition of the desired or acceptable combinations of response criteria (e.g. daily gain, carcass quality, nitrogen excretion). Obviously the value of these models depends on the adequacy of the description of the animal characteristics. This highlights the importance of research aimed at a better understanding and quantification of the flow of nutrients to different organs and tissues within the body, the metabolic fate of these nutrients, and the (endocrinological) regulation of the nutrient flows.

IMPLICATIONS

In this section, some important consequences of the effects of protein and energy intake, and body weight on protein and lipid retention in body tissues, as found in this study, are discussed.

Protein and Energy Dependent Phases

The observed efficiency of protein utilization in the energy dependent phase of protein deposition, is partially determined by the dietary protein/energy ratio relative to the optimum protein/energy ratio. Consequently, an increase in protein retention and utilization in this phase does not necessarily imply that the potential protein utilization has also been improved. It may simply imply that the control animals received an excess of protein. Several measures like fattening entire male pigs instead of castrates, improvement of the feed conversion of a pig by breeding, and the application of metabolic modifiers have been claimed to improve protein utilization. However, it may be that only the assignment of dietary energy to protein and lipid accretion has been changed. In other words, these measures may have reduced the minimum lipid to protein ratio. Such an effect may be valuable for lean meat production, but without an increase in potential protein utilization, the optimal protein/energy ratio in the diet will be proportionately increased. **Therefore measures and products which claim to improve protein utilization, be it metabolic modifiers, selection for an improved gain or gain/feed or dietary ingredients, should be tested both in the protein and energy dependent phase.**

Modelling Animal Growth

Some aspects of modelling animal growth with regard to optimizing protein allowances and nitrogen utilization have already been discussed. In addition, this study has shown that the relationships between energy intake and protein and lipid deposition, are considerably affected by the body weight of the pig. **An appropriate modelling of the effects of energy intake and body weight on lipid and protein deposition, LD/PD and ΔLD/ΔPD should receive priority in those models which are based on a constant LD/PD ratio.** Different possibilities to realize this have been discussed by De Greef (1992). In essence these methods are not very different. They all imply that the genetic capacity of the animal is not sufficiently defined by its maximum capacity for protein deposition, and a minimal ratio between lipid and protein deposition. An extra parameter is required to define the relationship between energy intake and protein retention below PD_{max}.

Breeding and Selection

During the last few decades the daily gain and gain/feed have been much improved by breeding and selection. The genetic capacity for protein deposition of improved animals approaches or even exceeds 200 g per day (this study, Campbell and Taverner, 1988a; Rao and McCracken, 1991; De Greef et al., 1992). Although improvements in gain are economically important, for sustainable animal husbandry, an efficient conversion of feed ingredients into edible tissues seems even more important. It depends very much on the selection strategy whether an increase in daily gain coincides with an increase in gain/feed or lean gain/feed. Selection for gain where animals are allowed restricted amounts of feed, for example, will result in a greater improvement in feed efficiency and lean tissue percentage than under ad libitum feeding conditions. Furthermore, little attention has been paid to the efficiency of protein utilization. Since pigs generally have been selected on adequate or even high protein diets, it is unlikely that the potential protein utilization has been significantly improved (Kyriazakis et al., 1994). In addition, the biological backgrounds of variation in nutrient utilization, in nutrient flow to different organs, and the mechanisms involved, are not well understood. Therefore in animal breeding programmes, considerable attention should be paid to the determination of biological parameters affecting nutrient utilization and to an improvement in the conversion of nutrients into edible carcass parts, especially lean tissue.

Feeding Improved Genotypes

Protein retention increased linearly with increasing energy intake in the growing and the fattening pigs. This indicates that an intrinsicly determined maximum protein deposition lies beyond the limits of appetite in this type of pig. Therefore the animals can be fed ad libitum without reaching PD_{max}, and thus without depositing excessive amounts of lipid. Nevertheless LD/PD and lipid content increased curvilinearly with increasing energy intake, and the lean tissue percentage in the body and the carcass decreased curvilinearly. These results indicate that even in these pigs with a high genetic capacity for protein deposition, it is not possible to simultaneously maximize both lean tissue gain and lean tissue content. In addition, gain/feed was highest at high feeding levels, whereas lean gain/feed was highest at low feeding levels. However, LD/PD, lipid content, lean tissue percentage and lean gain/feed were relatively constant at the three highest feeding levels. **Therefore a severe restriction in feed intake, below 75% of the ad libitum intake, is required if body composition and lean tissue feed conversion are to be improved. This will have major negative consequences for the daily rate of body, lean tissue and protein gain.**

If lean percentage is to be increased by feed restriction, this can be realized by a severe restriction in either the growing or the fattening phase. Because lean and fat tissue deposition were not increased after a previous feed restriction, the higher lean percentage in restricted pigs at 45 kg was still present at 85 kg. At a constant average daily energy intake between 20 and 85 kg, the distribution of energy between the growing and the fattening phase had only a relatively small effect on body gain and lean percentage. Body gain was slightly lower and lean percentage slightly higher in animals restricted in the fattening phase. The lean tissue growth rate between 20 and 85 kg was not significantly affected. The main reason for this lack of an effect of energy distribution is that the type of relationship between energy intake and LD/PD and body composition was very similar in the two weight ranges in this study. **Therefore in these pigs, the effect of a feed restriction is determined more by the energy levels which are applied, than by the weight range in which the pigs are restricted.** Finally these results indicate that the time delay caused by a feed restriction is not compensated for, by an increased growth in the realimentation phase. **There is little or no evidence in the literature, that a period of growth retardation by feed restriction in pigs is advantageous because of compensation in a later period. In each stage of growth, the animals should be adequately fed without expecting them to later compensate for deficiencies in their nutrition.**

The results of this study have shown a diminishing slope for the relationship between energy intake and protein deposition, and consequently an increasing LD/PD with increasing body weight. At similar daily rates of protein deposition, the fattening pigs retained about twice as much lipid as the growing pigs. Thus the fattening pigs required considerably more energy to deposit one gram of protein and the concomitant amount of lipid. Presumably this will have consequences for the required dietary protein/energy ratio. In Chapter 1 a simple factorial model was proposed to determine the lysine/energy requirements given known protein and lipid accretion rates. This model allows simulation of the effects of, for example, energy intake, body weight, sex, and genotype, if their effects on protein and lipid retention have been determined. This model was used to calculate the ileal digestible lysine/energy requirements for the pigs used in this study in different weight ranges and for pigs of different sex and genotype from Campbell and Taverner (1988a). The results have been presented in Figure 9. The calculated lysine/DE requirements decreased markedly from about .60 between 20 and 45 kg to .40 between 45 and 85 kg. Because of the linear increase in protein deposition with increasing energy intake, the optimal lysine/DE was only slightly affected by the daily energy intake. The latter result was also found for the improved male pigs in Campbell and Taverner (1988a). However, the unimproved pigs reached a plateau in protein deposition at about 33 MJ of DE/d. If the energy intake was increased beyond this 33 MJ, no further increase in protein retention was found. Therefore the absolute daily lysine requirements remained constant above 33 MJ of DE/d. Consequently, if energy intake increased beyond this point, the required lysine/energy decreased. This explains the decrease in lysine/energy for the unimproved male pigs and the castrates in Figure 9. **In conclusion, the lysine or protein to energy requirements for protein gain, are only slightly affected by the**

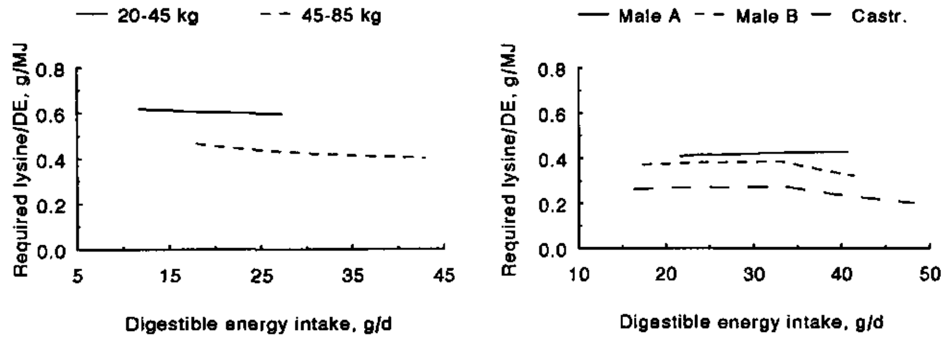

Figure 9. Calculated lysine/DE requirements using Model [4] from Chapter 1 for pigs of different weight from this study and for improved (male A), unimproved (male B) and castrated male pigs from Campbell and Taverner (1988).

level of energy intake in pigs which have not reached their PD_{max}. At energy levels beyond those required to reach PD_{max}, the required protein/energy decreases with increasing energy intake. A higher ratio between lipid and protein deposition due to a higher body weight, or related to sex or genotype, presumably causes a considerable decrease in the required protein/energy ratio. These results emphasize that an adequate knowledge of the pigs' genetic capacity for protein deposition is crucial in order to define an adequate feeding strategy. Future research should aim at a better understanding of the mechanisms involved in the control of the assignment of dietary energy to protein and lipid accretion.

CONCLUSIONS

The following conclusions were drawn on the basis of the results of studies with pigs of high genetic capacity for lean gain, described in this thesis,

Separate protein and energy dependent phases in protein deposition can be distinguished. This concept implies that if the level of feed intake is increased, an associated increase in protein deposition will reflect a response to dietary protein on a low protein diet and a response to dietary energy on a diet abundant in protein.

In genetically improved pigs with a high capacity for lean gain, it is presumed that maximum protein gain (PD_{max}) cannot be reached at body weights below about 80 to 90 kg. The intake capacity probably limits protein accretion and consequently rate of protein (PD) and lipid deposition (LD) respond linearly to energy intake. The ratio LD/PD responds curvilinearly to energy intake.

The proportion of total daily protein deposition which is deposited in the lean tissue decreases with increasing energy intake.

Appropriate modelling of the effects of energy intake and body weight on lipid and protein deposition, LD/PD and ΔLD/ΔPD, should receive priority to models which are based on a constant LD/PD ratio.

Carcass lean content and efficiency of feed conversion into lean tissue, decrease with increasing energy intake. Body and lean tissue gain, gain/feed, and protein deposition, increase with increasing energy intake. Consequently, these different response criteria cannot be optimized simultaneously. Even when PD_{max} has not been reached, maximization of lean gain is accompanied by a decrease in body and carcass lean content and an increase in lipid content.

In pigs of the type as used in this study, the effect of a feed restriction on body composition is determined more by the energy levels which are applied, than by the weight range in which the pigs are restricted. Furthermore a severe restriction in feed intake, below 75% of the ad libitum intake, is required if body composition is to be improved. This will have negative consequences for the daily rate of body, lean tissue and protein gain.

In the weight range from 20 to 85 kg, extra gain of the body and lean tissue per unit of extra energy intake diminishes with increasing body weight. The lean tissue content also decreases with increasing body weight. The latter is mainly due to the higher feed intake of heavier pigs.

With increasing body weight the extra protein gain (slope) with increasing energy intake diminishes and the extra lipid gain with increasing energy intake increases. Consequently, at a constant daily energy intake for production, fattening pigs deposit more lipid and less protein than growing pigs. Therefore, lipid content increases with increasing body weight. When pigs are fed ad libitum or relative to their body weight, the differences between growing and fattening pigs will be even bigger. At the three highest feeding levels in this study the LD/PD in the fattening pigs was about twice as high as in the growing pigs.

Metabolically active organs respond rapidly in size and weight to a change in daily nutrient intake. Together with an increase in gut contents, this response can largely account for the increase in liveweight gain (compensation), after a period of feed or energy restriction as reported in many studies. A significant increase in lean or fat tissue gain during rehabilitation was not found in this study. Therefore the lean content which is higher at the end of the restriction phase may still be higher at the end of the realimentation phase, provided that previously restricted and control animals have a similar feed intake in the realimentation period. This can explain the higher lean content as sometimes reported for previously restricted animals and also found in our study.

There is no evidence that the relationships between energy intake and protein and lipid deposition in the carcass are affected by a previous energy restriction. Protein retention in the organs will be increased during rehabilitation as a direct response to an increased nutrient intake. There was no evidence in this study of an increased energetic efficiency in pigs which were previously restricted in their feed intake.

Fattening animals show a higher efficiency of energy retention (k_{pf}) than the growing pigs which is the result of the increased ratio between lipid and protein deposition in the heavier animals.

There is little or no evidence in the literature that a period of growth retardation by feed restriction in pigs is advantageous because of compensation in a later period. At each stage of growth the animals should be adequately fed. It cannot be expected that the pigs later compensate for deficiencies in their nutrition.

The amounts of lysine or protein relative to energy, required for protein gain, are only slightly affected by the level of energy intake in pigs which have not reached their PD_{max}. A higher ratio between lipid and protein deposition due to a higher body weight, or related to sex or genotype, presumably causes a considerable decrease in the required protein/energy ratio. These results emphasize that an adequate knowledge of the pigs' genetic capacity for protein deposition is crucial in order to define an adequate feeding strategy.

Optimum protein and energy allowances depend on animal factors as well as on the response criteria to be optimized. Animal simulation models will become indispensable to take these factors into account and to calculate optima after definition of the desired or acceptable combinations of response criteria.

Future research should aim at a better understanding and quantification of the flow of nutrients to different organs and tissues within the body, the metabolic fate of these nutrients and the regulation of these nutrient flows.

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SUMMARY

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The primary aim of pig production is to provide food for human consumption. Therefore, in pig husbandry the conversion of animal feeding-stuffs into edible products of high quality should be optimized. Different criteria can be used to determine optimal protein (amino acid) and energy allowances (e.g., maximum lean tissue gain, maximum efficiency of lean gain, and minimum nitrogen excretion), presumably leading to different results. Consequently, optimization requires detailed knowledge of the response relationships between nutrient intake and animal performance, in terms of nutrient retention and body composition. These relationships have been studied in this thesis for pigs of a modern genotype. Special attention has been paid to protein and lipid accretion and to lean tissue gain, as being important criteria affecting the efficiency of production. Knowledge of the response relationships between nutrient intake and tissue deposition, as determined in this study, presumably can best be applied when it is included in simulation models.

Responses to Protein and Energy Intake

Protein and lean tissue gain are largely determined by animal factors like body weight, sex, and genotype, and nutritional factors, especially protein and energy intake. The literature indicates that intrinsic factors define the maximum daily protein deposition capacity of the pig (PD_{max}), whereas nutrient allowances and the feed intake capacity of the pig determine whether this PD_{max} can be reached. The response of protein gain in the animal to incremental amounts of dietary protein at a constant energy intake reflects the digestibility and quality of the dietary protein, the amino acid availability, and the metabolic efficiency of utilization of amino acids for protein gain. At high levels of protein intake, the marginal efficiency (slope) of protein utilization will fall to zero when energy intake becomes limiting. It is a matter of debate what kind of mathematical model can best be used to describe this response relationship. The response of protein accretion to energy intake, at adequate levels of protein intake, reflects the assignment of dietary energy to protein and lipid accretion. This distribution of dietary energy is influenced by the sex and the genotype of the pig. Whether this relationship is affected by previous nutrition (the nutritional history) or by body weight was unclear. Although many studies have reported an increased rate and efficiency of body weight gain after a period of feed restriction, it is often not clear when differences between treatments were developed, nor which tissues gained faster during rehabilitation.

Knowledge of the relationship between energy intake and protein accretion is essential for determination of the effect of an increase in energy intake on rate of gain and body composition. In addition, this relationship determines the possible rate of protein accretion at each level of energy intake, and thus the amino acid requirements at tissue level. Therefore, this relationship has a big influence on the amino acid requirements and the optimal amino acid to energy ratio in the diet. Knowledge of the interrelationships between energy and protein intake on protein deposition is important to determine the efficiency of protein utilization, optimal amino acid/energy ratios, and the effect of the energy intake level on these criteria.

In the first three chapters of this study, protein and energy intake were varied independently in growing pigs (20-45 kg) of a high genetic capacity for lean gain, to determine:

- the optimal ileal digestible lysine/energy allowances for body gain and protein deposition;
- the efficiency of utilization of ileal digestible protein and lysine for protein accretion;
- the interrelationships between energy and protein intake on protein accretion;
- the effects of protein and energy intake on the amino acid composition of the whole body, the carcass and the organs of pigs.

In the investigations described in Chapter 4 to 6, energy intake at adequate levels of protein intake was varied, in growing (20-45 kg) and fattening pigs (45-85 kg), to determine:

- the response relationships between energy intake and protein (PD) and lipid deposition (LD), LD/PD and body tissues;
- the distribution of protein and lipid among different body tissues;
- the effects of body weight on these criteria;
- the effect of a feed restriction from 20 to 45 kg on the responses to energy intake from 45 to 85 kg.

Protein Utilization

In the first experiment protein deposition increased with increasing protein intake to maximum rates of 108 and 128 g/d, at energy intake levels of 2.5 and 3.0 times energy for maintenance (M), respectively. The rates of lysine deposition increased to 8.0 and 9.5 g/d, respectively. The extra protein-free energy allowance of 3.0 MJ of DE/d for pigs fed 3.0 times maintenance, did not affect rates of protein accretion at low levels of protein intake, but improved protein and lysine deposition significantly at high levels of protein intake. These results support the concept of protein and energy dependent phases in protein deposition. The relationships between intake and deposition of protein, and between intake and deposition of lysine were best described by a linear-plateau model. However, no firm conclusion was drawn about the smoothness of transition between the linear and plateau phase. The marginal efficiencies of utilization of ileal digestible protein and lysine (the first limiting amino acid) were estimated as .58 and .74 respectively.

Lysine/energy Requirements

The ileal digestible lysine requirements, determined with a linear-plateau model, were .57 g/MJ of DE for daily gain and gain/feed, and .62 g/MJ of DE for protein deposition. These estimated requirements were similar for the two energy levels. Different methods to determine the amino acid requirements have been discussed. In addition, a simple factorial model to estimate the lysine/energy requirements was proposed in Chapter 1.

Body Amino Acid Pattern

Whole body amino acid contents (g/16 g nitrogen) of the pigs in this study were lysine 6.64, methionine 2.11, threonine 3.62, and total essential amino acids 42.8. The concentrations of essential amino acids were 41.8 and 48.4 g/16 g nitrogen in the carcass and organs, respectively. Concentrations of a number of amino acids, both in carcass, organ and whole body protein, were affected by protein and(or) energy intake. The amino acid pattern of the newly deposited protein was slightly different from that of the empty body protein. The changes in amino acid contents were presumably the result of effects of protein and energy intake on the proportions of muscle and non-muscle carcass tissues, and on relative weights of blood and organs. Possible consequences of these changes for the amino acid requirements were discussed.

Protein and Lipid Accretion in Response to Energy Intake

At adequate levels of protein intake, protein and lipid accretion in the whole body increased linearly with increasing energy intake in the growing (20-45 kg) and fattening (45-85 kg) pigs. In the growing pigs protein and lipid accretion increased from 75 to 172 g/d and from 28 to 193 g/d, respectively, when the energy level increased from 1.7xM to ad libitum. In the fattening pigs protein and lipid deposition increased from 83 to 187 g/d and from 46 to 392 g/d, respectively. These results indicate that in these pigs the feed intake capacity rather than PD_{max} limits protein deposition. The LD/PD ratio increased from .3 to 1.1 and from .5 to 2.2 in the growing and fattening pigs, respectively. Because of the linear increase in rates of protein and lipid accretion, the ratio between extra protein and extra lipid retention ($\Delta LD/\Delta PD$) with each unit of extra energy intake was constant.

Protein distribution was affected by energy intake. The proportion of the daily whole body protein accretion, which was deposited in the lean tissue, decreased from about 61% at the lowest energy level to about 52% at the highest energy level. The proportion of protein deposited in organs and fat tissue increased with increasing energy intake. The higher proportion of protein deposited in the organs and the higher organ weights at high intake levels seem to be associated with higher energy requirements for maintenance.

Body Composition in Response to Energy Intake

Between 45 and 85 kg lean tissue accretion increased curvilinearly with increasing energy intake, from about 230 to 510 g/d. However, the response of organ and fat tissue gain to energy intake was relatively bigger. Both in the growing and fattening pigs the organs responded remarkably to nutrient intake, and the organ percentage increased considerably with increasing energy intake. As a consequence of these effects, the carcass lean content decreased curvilinearly from about 63 to 55% with increasing energy intake. This effect was also found in the growing pigs. Consequently, maximization of lean gain is accompanied by a decrease in the carcass lean content.

Because of the increase in LD/PD with increasing energy intake, body protein content decreased curvilinearly, and body lipid content increased curvilinearly with increasing energy intake. Thus even when PD_{max} is not reached, body lipid content increases with increasing energy intake. However, differences in body lean content and body lipid content were very small at the three highest energy levels.

Therefore, a severe feed restriction, below 75% of ad libitum, is required, if the body composition is to be improved. This will markedly reduce the daily rate of body and lean tissue gain.

Effects of Body Weight

In this experiment the fattening pigs ate more and consequently gained faster than the growing pigs. However, the increase in body and lean tissue gain per unit increase in energy intake decreased with increasing body weight. The respective increases in body and lean tissue gain per unit energy intake were 43.6 and 12.5 g/MJ of DE in the growing pigs, and 34.2 and 9.6 g/MJ of DE in the fattening pigs. When compared at similar average daily energy intake above maintenance, body gain was on average 108 g/d higher in the growing pigs. Lean tissue gain was only 30 g/d (not significant) higher. Carcass lean content was 3-4% lower at 85 kg than at 45 kg. This was largely due to the higher feed intake of the heavier animals. When compared at similar daily energy intake above maintenance, the carcass lean content was only 1% lower at 85 kg than at 45 kg.

The increases in protein and lipid deposition with increasing energy intake (slope of the linear regression) were 5.8 and 10.5, respectively, in the growing pig and 3.8 and 13.7, respectively, in the fattening pig. Consequently, the slope for protein accretion decreased drastically with increasing body weight. At similar energy intake above maintenance, protein accretion was 19 g/d higher and lipid accretion was 26 g/d lower in the growing pigs. Consequently, LD/PD and lipid content increased with increasing body weight. This effect of body weight was higher at high levels of energy intake. At the three highest feeding levels, LD/PD was twice as high between 45 and 85 than between 20 and 45 kg. As a consequence, the efficiency of conversion of nutrients into body or lean tissue decreases with increasing body weight.

The ratio between extra lipid and extra protein retention (ΔLD/ΔPD) increased with increasing body weight, because of a decrease in the slope for protein accretion vs energy intake, and an increase for lipid accretion. The increase in lipid content in the gain in heavier animals caused a higher energetic efficiency (k_{pf}) between 45 and 85 kg, compared to pigs between 20 and 45 kg.

Effects of a Previous Feed Restriction

Animals which had been restricted in feed intake at 2.2xM (low pigs) from 20 to 45 kg, gained on average 140 g/d more from 45 to 85 kg than animals fed at 3.7xM between 20 and 45 kg (high animals). However, a large part of this 140 g compensatory gain was accounted for by an increase in gut-fill, and a response in size and weight of metabolically active organs. Between low and high animals, no significant differences in weight gain of lean and fat tissue from 45 to 85 kg were found. In addition, also in whole body protein and lipid accretion and energy retention no differences were found. Only protein gain in the organs was significantly higher in previously restricted pigs. The differences in weight gain of the body and the organs between low and high pigs, increased with an increasing energy level between 45 and 85 kg. This illustrates the response of metabolically active organs to nutrient intake.

It seems likely that the relationship between energy intake and protein and lipid accretion in the carcass is not affected by a previous energy restriction. Nevertheless, pigs restricted from 20 to 45 kg had a higher lean content and a lower lipid content at 85 kg. However, these differences were already present at 45 kg, due to the energy restriction, and were not the result of differences in tissue deposition between 45 and 85 kg.

Overall, rate and composition of body gain between 20 and 85 kg, compared at a similar average daily energy intake, were only slightly affected by the feeding strategy. Pigs that received a low feeding level up to 45 kg and a high feeding level thereafter, gained slightly faster but had a slightly lower body lean content compared to pigs that first received a high feeding level and thereafter a low feeding level. No differences were found in rate and efficiency of lean tissue gain.

Consequences for Defining a Feeding Strategy for Pigs with High Genetic Capacity for Lean Gain

There is little or no evidence in the literature that a period of growth retardation by a feed restriction in pigs is advantageous because of compensation in a later period. In each stage of growth the animals should be adequately fed without expecting them to later compensate for deficiencies in their nutrition.

The optimal ratio between protein (lysine) and energy for protein gain is only slightly affected by the level of energy intake in pigs which have not reached their PD_{max}. A higher ratio between lipid and protein deposition, due to a higher body weight, or related to sex or genotype, presumably causes a considerable decrease in the required protein/energy ratio. These results emphasize that an adequate knowledge of the pigs' genetic capacity for protein deposition is crucial in order to define an adequate feeding strategy.

The overall effect of a feed restriction in these pigs is more determined by the feeding levels which are applied than by the weight range in which the pigs are restricted. Only a severe restriction will significantly affect the body composition. Such a restriction will have major negative consequences on daily gain and protein deposition.

Optimum protein and energy allowances depend on animal factors, as well as on the response criteria to be optimized. Animal simulation models will become indispensable to take these factors into account, and to calculate optima, after definition of the desired or acceptable combinations of response criteria. An appropriate modelling of the effects of energy intake and body weight on lipid and protein deposition, LD/PD and ΔLD/ΔPD should receive priority in those models which are based on a constant LD/PD ratio.

SAMENVATTING

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Het belangrijkste doel van de vleesvarkenshouderij is de produktie van voedsel voor de mens. In de varkenshouderij dient de omzetting van diervoeders in kwalitatief hoogwaardige vleesprodukten dan ook geoptimaliseerd te worden. Om optimale eiwit- en energiegiften te bepalen kunnen verschillende criteria gebruikt worden, bijvoorbeeld maximale aanzet van vlees, maximale efficiëntie van vleesaanzet of minimale stikstof uitstoot. Deze verschillende criteria leiden zeer waarschijnlijk tot verschillende resultaten. Voor een optimale produktie is een gedegen kennis van de relaties tussen nutriëntenopname (voeding) enerzijds en groei en lichaamssamenstelling van het varken anderzijds dan ook noodzakelijk. In dit proefschrift zijn deze relaties bestudeerd bij varkens met een hoge erfelijke aanleg voor de groei van spierweefsel (vlees). Hierbij is vooral aandacht besteed aan de eiwit- en vetaanzet van de dieren en de groei van spierweefsel, omdat deze in belangrijke mate de efficiëntie van de lichaamsgroei bepalen. Daarnaast is vlees een belangrijke eiwitbron voor menselijke consumptie. De resultaten van dit onderzoek kunnen waarschijnlijk het best toegepast worden door deze te gebruiken voor het testen en verbeteren van computermodellen die de groei van varkens onder invloed van erfelijke aanleg, voeding en milieufactoren (temperatuur, luchtvochtigheid, aantal dieren per hok enz.) voorspellen. Bovendien hopen we dat dit proefschrift de inzichten van de lezer in de verbanden tussen voeding en lichaamsgroei en -samenstelling vergroot.

Effecten van eiwit- en energieopname

Eiwitaanzet en vleesgroei bij varkens worden voornamelijk bepaald door dierfactoren zoals gewicht, sexe en erfelijke aanleg (genotype) en door voedingsfactoren, vooral energie- en eiwitopname. De dierfactoren bepalen de maximaal haalbare dagelijkse eiwitaanzet van het varken terwijl de dagelijkse voergift, de voerkwaliteit en de voeropnamecapaciteit van het dier bepalen of die maximale eiwitaanzet ook daadwerkelijk bereikt wordt. Wanneer een varken bij een vaste energiegift een steeds toenemende hoeveelheid eiwit wordt verstrekt (en dus het eiwitgehalte in het voer toeneemt) zal in eerste instantie de dagelijkse eiwitaanzet toenemen. De toename in eiwitaanzet per eenheid extra opgenomen eiwit hangt af van de verteerbaarheid en de kwaliteit van het voereiwit, de beschikbaarheid van de aminozuren en van de efficiëntie waarmee het dier aminozuren kan benutten voor de aanmaak van lichaamseiwit. Hoe dit verband tussen eiwitopname en eiwitaanzet het best modelmatig beschreven kan worden is niet duidelijk. Wel staat vast dat bij hoge eiwitgehaltes in het voer een extra eiwitgift niet langer resulteert in een toename in de eiwitaanzet van het dier. De eiwitopname is dus in feite te hoog; de energieopname is dan beperkend geworden en het dier heeft eerst meer energie nodig om lichaamseiwit te kunnen maken. Wanneer in die situatie, dus als er voldoende eiwit (aminozuren) in het voer aanwezig is, extra energie (vetten en/of koolhydraten) wordt verstrekt kan het varken deze energie gebruiken om lichaamseiwit aan te zetten. Echter, niet alle extra energie zal gebruikt worden voor eiwitaanzet; een deel van de energie wordt gebruikt voor vetaanzet. De verdeling van energie uit het voer over eiwit- en vetaanzet wordt onder andere bepaald door de sexe en het genotype van het dier. Het was vóór dit onderzoek niet duidelijk of de verdeling van voerenergie over eiwit- en vetaanzet ook wordt bepaald door het gewicht van het dier en de voeding in een voorgaande periode. Het was wel bekend dat als varkens een bepaalde tijd in hun groei beperkt worden, ze daarna soms meer eten en sneller groeien, maar het was niet bekend welke weefsels dan extra groeien en wanneer deze verschillen optreden.

Kennis van de relatie tussen energieopname (bij voldoende voereiwit) en de aanzet van lichaamseiwit is noodzakelijk om te kunnen bepalen wat het effect van een extra voergift op groeisnelheid en lichaamssamenstelling (bijvoorbeeld vleespercentage) zal zijn. Tevens bepaalt deze relatie tussen energieopname en eiwitaanzet hoeveel eiwit bij een bepaalde energiegift maximaal aangezet kan worden en dus hoeveel voereiwit er nodig is. Deze relatie heeft daarom een grote invloed op de eiwitbehoefte (aminozurenbehoefte) van het dier en de optimale verhouding tussen aminozuren en energie in het voer. Kennis van de relaties tussen eiwit- en energieopname enerzijds en eiwitaanzet anderzijds is dus belangrijk om de eiwitbenutting, de optimale eiwit/energie verhouding in het voer en de effecten van energieopname op deze twee parameters te kunnen bepalen.

In het onderzoek beschreven in de eerste drie hoofdstukken van dit proefschrift werden, bij jonge groeiende varkens (20 tot 45 kg), de dagelijks verstrekte hoeveelheden eiwit- en energie in het rantsoen onafhankelijk van elkaar gevarieerd. Het doel hiervan was te bepalen:

- *de optimale verhouding tussen lysine en energie in het voer voor een maximale* groei en eiwitaanzet. Lysine is het aminozuur waaraan in varkensvoeders het snelst een tekort dreigt te ontstaan;
- de benutting van darmverteerbaar eiwit en lysine voor de aanzet van lichaamseiwit;
- de relatie tussen eiwit- en energieopname enerzijds en de aanzet van lichaamseiwit anderzijds;
- de effecten van eiwit- en energieopname op de samenstelling (het aminozurenpatroon) van het lichaamseiwit in het hele dier, het karkas en de organen.

In het onderzoek beschreven in de hoofdstukken 4 tot 6 werd de energieopname bij een constant en voldoende hoog eiwitgehalte in het voer gevarieerd. Dit vond plaats bij zowel jonge (20 tot 45 kg) als oudere (45 tot 85 kg) dieren om te bepalen:

- de relaties tussen energieopname enerzijds en lichaamsgroei, vleesaanzet, vleespercentage, eiwitaanzet, vetaanzet en de verhouding tussen eiwit- en vetaanzet anderzijds;
- de verdeling van eiwit en vet over verschillende lichaamsdelen;
- het effect van het gewicht van het dier op bovengenoemde parameters;
- het effect van een voerbeperking tussen 20 en 45 kg op de relaties tussen energieopname en lichaamsgroei, eiwit-, vet en vleesaanzet tussen 45 en 85 kg.

Eiwitbenutting

In het eerste experiment (hoofdstuk 1 tot 3) werd de varkens een energiegift van 2.5 of 3.0 keer de energie nodig voor onderhoud (energie nodig voor de basale levensprocessen) verstrekt. Bij elk van deze twee energieniveaus varieerde de gemiddelde eiwitgift van 130 tot 350 gram per dag. Bij een toenemende eiwitopname werd een lineaire toename in eiwitaanzet gevonden tot 108 en 128 g/d bij energieniveaus van respectievelijk 2.5 en 3.0 keer onderhoud. De bijbehorende lysineaanzet steeg tot 8.0 en 9.5 g/d. De extra energiegift ter grootte van 3.0 MJ verteerbare energie aan de varkens die 3.0 keer onderhoud gevoerd werden had geen effect op de eiwitaanzet bij dieren die een geringe hoeveelheid voereiwit kregen. Echter, bij dieren met een grote dagelijkse eiwitgift werden de eiwit- en lysine aanzet duidelijk verhoogd door de extra energiegift. Deze resultaten ondersteunen het concept van een eiwit- en een energie-afhankelijke fase in de aanzet van lichaamseiwit. Bij een lage opname van voereiwit wordt de eiwitaanzet beperkt door de eiwitopname en niet door de energieopname. In deze situatie leidt een extra energiegift niet tot een toename in eiwitaanzet, maar een extra eiwitgift wel. Bij een hoge eiwitopname ligt dit omgekeerd en resulteert juist een extra energiegift in een hogere aanzet van lichaamseiwit.

De relaties tussen eiwitopname en eiwitaanzet en tussen lysineopname en lysineaanzet werden het best beschreven met een lineair-plateau model (zie figuur 1, model 1 en 2 in hoofdstuk 2). Het was niet mogelijk op basis van de resultaten eenduidig te bepalen of de lineaire toename geleidelijk dan wel abrupt overgaat in een plateau. Dit wordt deels veroorzaakt door de variatie tussen dieren. Wanneer voor een individueel dier deze overgang abrupt verloopt, kan voor een groep dieren een geleidelijke overgang gevonden worden door de variatie tussen dieren. De hoogte van het plateau in eiwit- of lysineaanzet werd bepaald door de hoeveelheid energie die de dieren ontvingen. De efficiëntie waarmee darmverteerbaar voereiwit en -lysine werden gebruikt voor de aanzet van lichaamseiwit was onafhankelijk van het energieniveau en bedroeg respectievelijk 58% en 74%.

Lysine/energie behoefte

De benodigde verhouding tussen darmverteerbaar lysine en verteerbare energie in het voer voor maximale groei en voerbenutting was .57 g/MJ en voor maximale eiwitaanzet .62 g/MJ voor varkens van 20 tot 45 kg. Deze behoeften waren vergelijkbaar voor de twee energieniveaus. Het voerniveau had dus geen effect op de optimale lysine/energie verhouding. Deze werd bepaald met een lineair-plateau model. Het gebruik van een kwadratisch model leidde tot een veel hogere schatting van de lysine behoefte (figuur 1 en tabel 6 in hoofdstuk 1). Echter, in veevoedingsonderzoek worden beide en andere methoden gebruikt om de behoefte aan bepaalde nutriënten te bepalen, waarbij verschillende methoden tot verschillende behoeftenormen kunnen leiden. Bij de interpretatie van behoeftecijfers dient de methode van bepaling dan ook in de beoordeling betrokken te worden.

Tenslotte is in hoofdstuk 1 een eenvoudig factorieel model afgeleid om de optimale lysine/energie verhouding onder verschillende omstandigheden te kunnen schatten.

Aminozurenpatroon van lichaamseiwit

Het aminozurengehalte van lichaamseiwit van varkens van 45 kg, uitgedrukt in gram per 16 g stikstof (100 g eiwit) was voor lysine 6.64, voor methionine 2.11, voor threonine 3.62 en voor het totaal aan essentiële aminozuren (exclusief tryptofaan) 42.8. Het gehalte aan essentiële aminozuren in het karkas en de organen was respectievelijk 41.8 en 48.4 g/16 g stikstof. Zowel in het karkas, de organen als in het gehele lichaam werd het gehalte van een aantal aminozuren beïnvloed door de eiwit- en of energieopname. Tevens was het aminozurenpatroon van lichaamseiwit aangezet in de proefperiode enigszins verschillend van het al aanwezige lichaamseiwit bij aanvang van de proefperiode (20 kg). Deze veranderingen in aminozurengehalten werden waarschijnlijk veroorzaakt door effecten van energie- en eiwitopname op de verhouding tussen spierweefsel en andere weefsels, met name bindweefsel, en op de relatieve gewichten van bloed en organen. Deze verschillende weefsels en organen vertonen namelijk behoorlijke verschillen in het aminozurenpatroon. Mogelijke consequenties van deze veranderingen in aminozurenpatroon voor de aminozurenbehoefte zijn bediscussieerd in hoofdstuk 3.

Eiwit- en vetaanzet in relatie tot energieopname

In het vervolg van deze studie werd de respons van eiwit- en vetaanzet op energieopname bij een adequate eiwit/energie verhouding bepaald bij groeiende varkens van 20 tot 45 kg en van 45 tot 85 kg. In beide gewichtstrajecten werd een lineaire relatie tussen energieopname enerzijds en eiwit- en vetaanzet anderzijds gevonden. Bij de varkens tussen 20 en 45 kg nam de eiwitaanzet toe van 75 tot 172 g/d en de vetaanzet van 28 tot 193 g/d, bij een toename in energieniveau van 1.7 keer onderhoud tot ad libitum (onbeperkt). Tussen 45 en 85 kg namen de eiwit- en vetaanzet respectievelijk toe van 83 tot 187 g/d en van 46 tot 392 g/d. De verhouding tussen vet- en eiwitaanzet nam toe met een toename in energieopname, respectievelijk van .3 tot 1.1 en van .5 tot 2.2 bij varkens tussen 20 en 45 kg en tussen 45 en 85 kg. De lineaire toename in eiwitaanzet tot aan het hoogste energieniveau (ad libitum) betekent dat de genetisch bepaalde maximale dagelijkse eiwitaanzet niet bereikt werd. Op het hoogste voerniveau werd de eiwitaanzet kennelijk beperkt door de voeropnamecapaciteit van de dieren.

De verdeling van het aangezette eiwit over verschillende lichaamsdelen was niet constant maar werd beïnvloed door de energieopname. Het deel van de dagelijks aangezette hoeveelheid eiwit dat werd aangezet in vlees nam af van circa 61% bij het laagste energieniveau tot circa 52% bij het hoogste energieniveau. Tegelijkertijd nam het aandeel eiwit dat werd aangezet in overige karkasdelen (m.n. huid, spek, kop, buik en poten) en organen toe met een toename van de energieopname. De toename in orgaangrootte en de toename van het aandeel eiwit in de organen bij hoge energieniveaus gaat waarschijnlijk gepaard met een enigszins hogere energiebehoefte voor onderhoud. Dit wordt veroorzaakt door een hogere orgaanactiviteit en de hoge turnover van orgaaneiwit in vergelijking met bijvoorbeeld spiereiwit.

Lichaamssamenstelling in relatie tot energieopname

De vleesaanzet tussen 45 en 85 kg nam kwadratisch toe van circa 230 tot 510 g/d met een toename van de energieopname. De groei van overige karkasdelen en organen steeg echter nog sneller bij een toenemend energieniveau. Vooral de orgaangroei steeg opmerkelijk bij een toenemend voerniveau, zowel tussen 20 en 45 kg als tussen 45 en 85 kg. Als een gevolg van deze effecten daalde het vleespercentage in het karkas van circa 63% bij dieren op de laagste voerniveaus tot 55% bij dieren op de hoogste voerniveaus. Deze daling werd in beide gewichtstrajecten waargenomen. De stijging in vleesaanzet en de daling in vleespercentage bij een toenemend voerniveau betekenen dat wanneer gestreefd wordt naar de hoogste dagelijkse vleesaanzet, dit ten koste gaat van het vleespercentage. Het is dus niet mogelijk bij een bepaalde energieopname de maximale vleesaanzet en een maximaal vleespercentage te realiseren.

Zoals eerder vermeld, nam de verhouding tussen vet- en eiwitaanzet toe bij een stijgend energieniveau. Hierdoor daalde het eiwitgehalte en steeg het vetgehalte in het lichaam, beiden kwadratisch, bij een stijging in de energieopname. Dit betekent dat varkens vetter worden bij een hogere energieopname, zelfs wanneer hun genetisch bepaalde maximale eiwitaanzet niet bereikt wordt. De stijging in vetgehalte en de daling in vlees- en eiwitpercentage waren het grootst bij de drie laagste energieniveaus. De verschillen tussen varkens op de drie hoogste energieniveaus waren klein. Dit betekent dat er een behoorlijke voerbeperking tot een voerniveau beneden 75% van de ad libitum opname nodig is, om het vleespercentage te verhogen en het vetgehalte te verlagen. Zo'n drastische voerbeperking zal echter ook de groei en de vleesaanzet aanzienlijk verlagen.

Effecten van het lichaamsgewicht

De dieren tussen 45 en 85 kg kregen meer voer omdat de voergift werd gebaseerd op het lichaamsgewicht. Deze dieren groeiden dan ook sneller dan de varkens tussen 20 en 45 kg. De stijging in groei en vleesaanzet per eenheid energieopname was echter kleiner bij de zware dieren. Tussen 20 en 45 kg namen de dagelijkse groei en vleesaanzet toe met respectievelijk 43.6 and 12.5 g/MJ verteerbare energie en tussen 45 en 85 kg met respectievelijk 34.2 en 9.6 g/MJ. Wanneer de dieren vergeleken werden bij dezelfde hoeveelheid voer boven onderhoud, dus beschikbaar voor lichaamsgroei, bleken de varkens tussen 20 en 45 kg 108 g/d sneller te groeien. De vleesaanzet van deze varkens was echter slechts 30 g/d hoger (statistisch niet significant). Het vleespercentage in het karkas van de varkens van 85 kg was 3-4% lager dan van de varkens van 45 kg. Dit kon grotendeels verklaard worden door de hogere voeropname van de zwaardere varkens. Bij dezelfde hoeveelheid energie beschikbaar voor lichaamsgroei was het vleespercentage slechts 1% lager bij varkens van 85 kg.

Zoals eerder vermeld stegen de dagelijkse eiwit- en vetaanzet lineair met de stijgende energieopname. Voor de varkens tussen 20 en 45 kg was deze stijging voor respectievelijk eiwit- en vetaanzet 5.8 en 10.5 g/MJ verteerbare energieopname en voor dieren tussen 45 en 85 kg respectievelijk 3.8 en 13.7 g/MJ. Bij een stijgend gewicht van de varkens daalde dus de toename in eiwitaanzet per MJ extra energie. Bij een gelijke hoeveelheid voer voor produktie was de eiwitaanzet 19 g/d hoger en de vetaanzet 26 g/d lager bij de varkens tussen 20 en 45 kg, vergeleken met de varkens tussen 45 en 85 kg. Dit betekent dat bij een constante hoeveelheid produktievoer, de verhouding tussen vet- en eiwitaanzet en het vetgehalte stijgen bij toenemend gewicht van de dieren. Deze stijging is groter bij hoge voerniveaus dan bij lage voerniveaus. Bij de hoogste voerniveaus was de verhouding tussen vet- en eiwitaanzet van 45 tot 85 kg twee keer zo groot als tussen 20 en 45 kg. Door deze effecten daalt de efficiëntie van de omzetting van voer in lichaamsweefsel of in vlees bij een toenemend lichaamsgewicht. Anderzijds stijgt de energetische efficiëntie (k_{pf}) van de aanzet van lichaamsweefsels bij een toenemend gewicht, door de toename in vetaanzet.

Effecten van een voerbeperking in een eerder groeistadium

De varkens waarvan de proefperiode liep van 45 tot 85 kg, waren van 20 tot 45 kg gevoerd op een laag voerniveau (2.2 keer onderhoud) of een hoog voerniveau

(3.7 keer onderhoud). Op 45 kg werden de varkens van deze twee groepen verdeeld over zes verschillende energieniveaus. De dieren die tot 45 kg het lage energieniveau kregen groeiden daarna, van 45 tot 85 kg gemiddeld 140 g/d sneller dan de varkens die tot 45 kg een hoog energieniveau kregen. Een groot deel van deze extra (compensatoire) groei werd echter veroorzaakt door een toename in gewicht en grootte van de organen en in inhoud van het maagdarmkanaal. Er werd geen significant hogere vleesaanzet gevonden bij dieren die tot 45 kg op het lage voerniveau gehouden werden. Ook in de totale dagelijkse eiwit- en vetaanzet tussen 45 en 85 kg werden geen aantoonbare verschillen gevonden tussen dieren van de twee energieniveaus tot 45 kg. Slechts de dagelijkse eiwitaanzet in de organen was duidelijk hoger bij de varkens die tot 45 kg het lage voerniveau kregen. De verschillen in lichaamsgroei, orgaangroei en eiwitaanzet in de organen tussen 45 en 85 kg, ten gevolge van het voerniveau tot 45 kg, werden groter bij een toenemend voerniveau tussen 45 en 85 kg. Dit weerspiegelt de toename in metabolische activiteit van de organen bij dieren die tot 45 kg een laag voerniveau kregen en vanaf 45 kg een hoog voerniveau.

Er waren geen aanwijzingen dat de eiwit- en vetaanzet in het karkas tussen 45 en 85 kg beïnvloed werden door het voerniveau tot 45 kg. Toch was op 85 kg het vleespercentage hoger en het vetgehalte lager bij de dieren die tot 45 kg het lage voerniveau kregen, in vergelijking tot de dieren van het hoge voerniveau. Deze verschillen waren echter al aanwezig op 45 kg ten gevolge van de voerbeperking tussen 20 en 45 kg en waren niet het gevolg van een compensatoire aanzet tussen 45 en 85 kg.

Tenslotte werd bekeken of bij een gelijke gemiddelde energieopname tussen 20 en 85 kg, het uitmaakte of dieren eerst (van 20 tot 45 kg) een hoog en daarna (van 45 tot 85 kg) een laag voerniveau kregen, dan wel eerst een laag en daarna een hoog voerniveau. De verschillen tussen deze twee voerstrategieën bleken gering. De varkens die eerst een laag voerniveau en daarna een hoog voerniveau kregen groeiden gemiddeld van 20 tot 85 kg iets sneller maar hadden op 85 kg een iets lager vleespercentage dan dieren die eerst een hoog en daarna een laag voerniveau kregen. Er waren geen aantoonbare verschillen tussen deze dieren in snelheid en efficiëntie van de vleesaanzet.

Consequenties voor het definiëren van een voerstrategie voor varkens met een hoge genetische aanleg voor vleesaanzet

Er is weinig of geen bewijs, noch in deze studie, noch in de literatuur, dat een voerbeperking gedurende een deel van het groeitraject gunstig is vanwege compensatoire groei in een latere periode. In iedere fase van het groeitraject dienen varkens een adequate voeding te ontvangen. Er mag niet vanuit gegaan worden dat de dieren later wel compenseren voor eerdere deficiënties in hun voeding.

De optimale verhouding tussen eiwit (of lysine) en energie in het voer wordt slechts in geringe mate beïnvloed door het voerniveau bij varkens die hun genetisch bepaalde maximale dagelijkse eiwitaanzet nog niet bereikt hebben. Een hogere verhouding tussen vet- en eiwitaanzet, bij een toenemend lichaamsgewicht of als gevolg van verschillen door sexe of genetische aanleg, leidt zeer waarschijnlijk tot een aanzienlijke daling in de optimale eiwit/energie verhouding in het voer. Een gedegen kennis van de genetische capaciteit voor eiwitaanzet van een varken is derhalve onmisbaar om een adequate voerstrategie te kunnen definiëren.

Bij varkens zoals gebruikt in deze studie wordt het effect van een voerbeperking op de gemiddelde groei in het hele gewichtstraject en op de lichaamssamenstelling bij slachten meer bepaald door de gehanteerde voerniveaus dan door de periode waarin de dieren beperkt worden. Slechts een sterke voerbeperking zal een duidelijk verbetering van de lichaamssamenstelling (meer vlees, minder vet) tot gevolg hebben. Zo'n beperking leidt dan tevens tot een flinke afname in groei en eiwitaanzet.

Zowel dierfactoren als de keuze van criteria die geoptimaliseerd moeten worden (bijv. groeisnelheid, voederconversie of vleespercentage), bepalen de optimale eiwit- en energiegift. Computermodellen die de groei van varkens onder verschillende omstandigheden simuleren zullen onmisbaar worden om deze verschillende aspecten in rekening te brengen. Met behulp van zo'n model kunnen optimale voerstrategieën berekend worden, nadat gewenste of acceptabele combinaties van doelvariabelen zijn gedefinieerd. Uiteraard dient de respons van een dier op de opname van nutriënten op een goede manier in een model weergegeven te worden. Een correcte weergave van de effecten van energieopname en lichaamsgewicht op vet- en eiwitaanzet verdient prioriteit bij die simulatiemodellen die er ten onrechte vanuit gaan dat de verhouding tussen vet- en eiwitaanzet niet beïnvloed wordt door de energieopname.

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CURRICULUM VITAE

Paulus Bikker werd op 13 augustus 1965 te Lexmond geboren. In 1983 behaalde hij het Gymnasium-ß diploma aan het Dr. F.H. de Bruijne Lyceum te Utrecht. In datzelfde jaar begon hij met de studie Zoötechniek aan de toenmalige Landbouwhogeschool te Wageningen. Deze studie werd van december 1988 tot september 1989 onderbroken ten behoeve van het lidmaatschap van de Universiteitsraad van de Landbouwuniversiteit, namens de Christen Studenten Fractie. In november 1989 werd de studie aan de Landbouwuniversiteit afgesloten met als afstudeervakken Veevoeding, uitgevoerd aan de University of Leeds (UK), Gezondheids- en Ziekteleer en Agrarische Bedrijfseconomie. Aansluitend werd hij aangesteld als Assistent in Opleiding (AIO) bij de vakgroep Veevoeding van de LUW, waar het onderzoek beschreven in dit proefschrift werd verricht. Daarnaast was hij van augustus 1993 tot januari 1994 in deeltijd werkzaam als beleidsmedewerker van het Wageningen Institute of Animal Sciences (WIAS).