ENERGY METABOLISM IN THE WEANLING PIG: EFFECTS OF ENERGY CONCENTRATION AND INTAKE ON GROWTH, BODY COMPOSITION AND NUTRIENT ACCRETION IN THE EMPTY BODY

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by

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ABSTRACT

Dietary energy is the largest single cost in pork production. Accurate and current understanding of energy metabolism is crucial to production efficiency. The overall objective of this thesis was to evaluate the effects of dietary energy concentration and energy intake on growth, nutrient deposition rates and energy utilization in weaned pigs. In experiment 1, the optimum total lysine:DE ratio for weaned pigs was estimated at 4.27 and 4.46 g/Mcal for pigs growing from 7.5 to 12.8 kg and 7.5 to 22.5 kg BW, respectively. Experiment 2 determined if a more predictable growth, nutrient deposition and energy utilization in the weaned pig is achieved with NE or with DE. ADG either remained similar or was depressed with increased NE compared to the control ($P < 0.05$). Empty body protein content and deposition (PD) declined relative to the control ($P < 0.05$) and lipid content and deposition (LD) tended to increase ($P < 0.10$). Body composition and nutrient deposition rates were more correlated with determined NE concentration and intake compared with DE. The results of Experiment 3 indicated that amino acid intake impaired the growth of pigs when an energy intake restriction greater than 30% occurred. Experiment 4 investigated the interaction of dietary NE concentration and feeding levels (FL) on body weight gain, tissue (protein, lipid, ash, water) accretion rates and ratios. Growth performance was not affected by NE ($P > 0.05$) but increased with feeding level ($P < 0.001$). Energy intake increased with NE and FL ($P < 0.001$), but the efficiency of energy utilization for growth declined ($P < 0.05$). Empty body protein content declined ($P < 0.05$) while lipid content increased with NE (interaction, $P < 0.05$). Empty body PD was not affected by NE ($P > 0.05$) but both LD and

LD:PD ratio increased (interaction, $P < 0.001$). These data suggest that when amino acid:energy ratio is optimal, increasing dietary energy concentration increased energy intake but does not improve PD and overall body weight gain of weaned pigs. However, body lipid content and LD were increased. Finally, NE offers an advantage over the DE in predicting the body composition and nutrient deposition rates rather than in overall BW gain.

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"In everyone's life, at some time, our inner fire goes out. It is then burst into flame by an encounter with another human being. We should all be thankful for those people who rekindle the inner spirit." --Albert Schweitzer

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DEDICATION

"Weeping may endure for a night, but joy comes in the morning."

This thesis is dedicated to the memories of my sisters, Oluwakemi and Olukoredele, and brother, Oluwaseyi. Many years have passed memories are fresh. I remember your pain, tears and strength. I have learned that pain always come with the strength to bear. I can gracefully say 'I lift up my eyes to the Lord the maker of the universe who has been my own refuge, strength and help in times of pain and trouble.

Ps:121:1; 46:1.

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LIST OF ABBREVIATIONS

AA	Amino acid
ADF	Acid detergent fiber
ADFI	Average daily feed intake
ADG	Average daily gain
AIA	Acid insoluble ash
ATP	Adenosine triphosphate
BW	Body weight
ConP	Constant amino acid intake in proportion to energy
CCK	Cholecystokinin
CF	Crude fiber
CP	Crude protein
d	Day
dl	Deciliter
DCP	Digestible crude protein
DCF	Digestible crude fiber
DE	Digestible energy
DEE	Digestible ether extract
DEc	Coefficient of gross energy digestibility
DE*i*	Digestible energy intake
DE*i*g	Digestible energy intake used for growth
DE*i*m	Digestible energy intake used for maintenance
DM	Dry matter
DNFE	Digestible nitrogen free extract
DRES	Digestible residuals
EBW	Empty body weight
EE	Ether extract
ERL	Energy retained as lipid
ERP	Energy retained as protein
FFSB	Extruded Fullfat soybeans

LIST OF ABBREVIATIONS CONT'D

FHP	Fasting heat production
g	Gram
GE	Gross energy
GIT	Gastrointestinal tract
HDE	High digestible energy
HiFat HiNE	High fat high net energy diet
IGF-I	Insulin-like growth factor-I
RedP	Increased amino acid intake in proportion to energy
ISG	Initial slaughter group
k	Efficiency
kg	Kilogram
k_g	Efficiency for growth
kl	Efficiency for lipid gain
kp	Efficiency for protein gain
LD	Lipid deposition rate
LDE	Low digestible energy
LoCP HiNE	Low crude protein high net energy diet
ME	Metabolizable energy
MedCP MedNE	Medium crude protein medium net energy diet
MedFat MedNE	Medium fat medium net energy diet
ME*i*	Metabolizable energy intake
MEm	Maintenance energy
Mcal	Megacalorie
mg	Milligram
NDF	Neutral detergent fiber
NE	Net energy
NE*i*	Net energy intake
NE*i*g	Net energy intake used for growth
NE*i*m	Net energy intake used for maintenance

LIST OF ABBREVIATIONS CONT'D

ng	Nanogram
PD	Protein deposition rate
PDmax	Genetic potential for protein accretion
PUN	Plasma urea nitrogen
RE	Retained energy
SG	Sugar
ST	Starch
TI	Trypsin inhibitor
wk	Week

1. GENERAL INTRODUCTION

The primary goal of diet formulation is to accurately match energy supply to pigs' energy requirement for maintenance and productive functions. Energy supply below or above pigs' requirement may have an adverse impact on performance, quality of product, the environment, and overall profitability (Chiba, 2000). Without doubt, the efficiency, profitability and sustainability of the pork industry depend on accurate, comprehensive and current knowledge of the influence of dietary energy concentration and intake on growth and whole body nutrient accretion.

The importance of energy in diet formulation cannot be overemphasized. Apart from being the primary driver of growth, energy is an important part of feed evaluation systems, focusing primarily on the quantity of energy that can be derived from ingested nutrients. Energy is the largest single-cost factor in commercial pork production (SCA, 1987; de Lange and Birkett, 2004). Energy and amino acids combined represents more than 80% of feed cost (de Lange et al., 2001a).

In spite of the high cost of dietary energy in production, our understanding of amino acid metabolism, as well as the essential role of minerals and vitamins far exceeds that of energy. An accurate understanding of energy metabolism is essential to take advantage of the rapidly advancing knowledge in amino acid metabolism.

Most research in recent years in terms of energy intake in relation to growth and nutrient deposition has been devoted to the growing-finishing pig (30 to 120 kg). The linear relationship between energy intake and protein deposition rates in modern genotypes of growing pigs suggests that energy intake is greater than the amount needed for maintenance but less than the amount required to achieve the maximum capacity for protein deposition (Campbell and Taverner, 1988; de Greef, 1992; Bikker et al., 1995). Therefore, it is generally accepted that energy intake to maximize lean growth or protein deposition is beyond the capacity of young pigs. In other words, they are unable to eat enough energy to achieve their genetic potential.

At present, there is a very poor understanding of the relationship between dietary energy concentration and intake on the rate of gain, composition of gain and profitability, and the possible effect of energy systems on predictable performance in the weaned pig. In the current understanding, it is generally accepted that the young pig (5 to 25 kg live weight) has limited physical gut capacity for nutrient intake (Campbell, 1987; Whittemore, 1993). Such limitation is suggested to prevent the young pig from achieving its genetic capacity for growth, and especially protein deposition. Van Lunen and Cole (1998) suggested that increasing dietary energy concentration compensate in part for the limitation of gut capacity in young pigs, resulting in increased growth and nitrogen deposition rate. However, the available literature on the effect of dietary energy concentration on growth in weaned pigs (e.g. Tokach et al., 1995; Smith et al., 1999a; Levesque, 2002) fail to support a direct relationship between dietary energy concentration and growth rate. The reasons for this lack of response are not clear.

In terms of energy systems, there is widespread belief that the net energy (NE) by taking into account the metabolic utilization of energy is the closest estimate of the 'true' energy value of feed (Galloway and Ewan, 1989; Noblet et al., 1994; Noblet and van Milgen, 2004) and provides for a predictable animal performance. However, there is lack of empirical data to support this. Consequently, our understanding of energy metabolism in the weaned pig is at best incomplete.

Therefore, it was hypothesized that increasing dietary energy concentration will increase growth performance, tissue gain, and nutrient deposition rates in weaned pigs. Also, for an accurate understanding of energy metabolism in the weaned pig, dietary energy concentration and daily energy intake are two separate topics that need to be studied. It was also hypothesized that diets formulated using net NE improves predictability of animal performance as compared to the use of digestible energy (DE).

In order to study the effect of energy intake on growth, it is essential that other nutrients, especially amino acids are non-limiting. The advances in swine genetics and management practices in the last decade would suggest a greater amino acid/energy requirement for optimal performance in weaned pigs than existing recommendations in the NRC (1998). Also, several inconsistencies exist in literature on the subject. Therefore, it was hypothesized that existing lysine/digestible energy ratios for weaned pigs are inaccurate and limit the expression growth potential.

To study these hypotheses, four experiments were conducted with the overall objective of providing a detailed and accurate understanding of the effect of dietary

energy concentration and intake on growth, nutrient deposition rates and energy utilization in weaned pigs. Specific objectives were:

1. to determine the optimum lysine/digestible energy ratio for the weaned pig,
2. to determine if a more predictable growth, nutrient deposition and energy utilization in the weaned pig is achieved with NE or with DE and thus develop a better understanding of the relative merits of DE vs. NE in diet formulations,
3. to define the interaction between daily energy intake and dietary net energy concentration on body weight gain and on tissue (protein, lipid, ash, water) accretion rates and ratios, and plasma insulin-like growth factor-I concentrations,
4. to evaluate the accuracy of existing factorial estimates of the efficiency of energy utilization for protein and lipid deposition and to determine whether actual (measured) DE intake or estimated NE intake (CVB-based) is more effective in predicting animal growth performance.

The literature review presented in Chapter 2 covers relevant aspects of energy metabolism and energy systems. The experiments are presented in the following chapters: The study in Chapter 3 evaluated the optimum lysine/digestible energy ratios for weaned pigs. In Chapter 4, the study determined if a more predictable growth, nutrient accretion and energy utilization in the weaned pig is achieved with NE or DE. It was aimed at developing a better understanding of the relative merits of DE vs. NE in diet formulations.

The study presented in Chapter 5 evaluated the response of weaned pigs to decreasing daily energy intake, with amino acid intake either declining at a constant

proportion with energy or declining at a reduced rate. This experiment was conducted as a precursor to the following energy study in the thesis (Chapter 6), to help determine how it should be designed. In Chapter 6, the interactive effects of changing NE concentration and daily energy intake on growth, body composition, nutrient accretion rates, energy utilization and plasma insulin-like growth factor-I concentrations are reported. In Chapter 7, the results of the four experiments described in this thesis are discussed, and general conclusions from these studies are presented in Chapter 8. A complete listing of cited literature is provided in Chapter 9.

2. LITERATURE REVIEW

2.1 Introduction

> Energy may be converted from one form to another but is neither created nor destroyed. The disorder or randomness of the universe is continuously increasing, because during energy transformations some energy is degraded to a more random form, heat. First and second law of thermodynamics (Brafield and Llewellyn, 1982).

The first and second laws of thermodynamics hold that all forms of energy are quantitatively convertible to heat (Baldwin and Bywater, 1984) and hence all measurements of energy transactions are made and expressed in terms of heat energy or calories (Armsby, 1917). Animal nutrition is focused on two forms of energy - chemical and heat.

Although it is glibly said that animals consume energy for maintenance and productive functions, animals consume feed ingredients and not energy per se. The energy contained in the feed ingredient as chemical energy is released by partial or complete oxidation following digestive and aborptive mechanisms in the gastrointestinal tract (GIT; Pond et al., 1995). The maximum quantity that any molecule can furnish from its oxidation in the body for the vital activity of maintenance and production is measured by its heat of combustion (Armsby and Fries, 1915).

The oxidation of fats, carbohydrates and protein yield a continuous and controlled supply of energy to the pig. Carbohydrates, protein and fats have an average caloric value of 4.1, 5.7 and 9.4 kcal/g, respectively (Brafield and Llewellyn, 1982; Pond et al., 1995).

The energy generated during the oxidation processes is transformed to heat when utilized to support vital life processes, stored during growth in chemical form, transferred to another animal in chemical form during pregnancy and lactation, or transferred to surroundings during work (Armsby, 1917).

Often a particular feed ingredient may contain an excess of one or more nutrients and be deficient in others. In addition, due to physiological factors in the GIT and digestible and metabolic inefficiencies, no single feed ingredient is used to supply the animal's requirement for nutrients. Therefore, there has been a concerted effort to quantitatively describe the energy value of the vast array of feed ingredients available for selection in practical swine diets. These values are often listed in Tables of feedstuffs (e.g. ARC, 1981; CVB, 1998; NRC, 1998; INRA, 2002) and represent the starting point for feed compounding or least-cost formulation programs.

2.2 Energy: Basic Definition

In the physical sciences, energy is defined as the capacity to perform work, and work in turn as the action of a force moving a mass through a distance. In the biological sciences, it is conceptually easier to view energy in heating units or calories. A calorie is the amount of energy required to raise the temperature of 1 g of pure water from 14 to 15°C at a pressure of 1 atmosphere (Pond et al., 1995).

In general, energy is an abstraction that can only be measured in its transformation from one form to another (Kleiber, 1975). For example, mechanical energy such as kinetic energy of motion can be converted to heat energy, while potential energy can be converted to kinetic energy as the object falls. Chemical energy in plants can be converted to heat energy and chemical energy in animal products.

2.3 Energy Metabolism

Metabolism is the inclusive term for the chemical reactions by which the cells of an organism transform energy, maintain their identity, and reproduce. Metabolism consists of two distinct phases: catabolism and anabolism. In catabolism, molecular substances are degraded to yield products accompanied with the release of energy used up in other biochemical reactions or dissipated as heat. Although both catabolism and anabolism occur simultaneously, when catabolism exceeds anabolism, such as during periods of starvation or disease, weight loss occurs. A state of dynamic equilibrium is reached when the two metabolic processes are balanced. Growth or weight gain occurs when anabolism exceeds catabolism. In this context, Blaxter and Boyne (1978) stated that the loss of body weight in a fasting animal represents a loss of energy equivalent to fasting heat production from the body, while a gain in body weight represents energy retention.

Energy metabolism includes all the transactions that are involved in energy production, protein and fat deposition (Halas, 2004). The fundamental "currency" of energy in tissue is adenosine triphosphate (ATP; Brafield and Llewellyn, 1982; Burrin, 2001; van Milgen and Noblet, 2003) that is supplied in bio-oxidative pathways, for instance, glycolysis and β-oxidation of fatty acids (Crozier et al., 2002).

2.3.1 Regulation of Energy Metabolism

The energy requirement for protein synthesis is essentially a requirement for ATP. The formation of one peptide bond in a protein molecule requires five moles of ATP, including four moles for the bond formation and one mole for transportation across the cell membrane (Van Es, 1980a). Body protein is in a dynamic state (Simon, 1989) and homeostasis is achieved through continual breakdown and re-synthesis referred to as protein turn-over (Knap, 2000). Protein synthesis is regulated by plasma amino acid concentration and insulin activation of the ribosomal protein S6 kinase and messenger ribonucleic acid (mRNA) in translation initiation (Kimball and Jefferson, 2002; Kimball, 2002). Protein degradation depends on catabolic hormones, especially glucocorticoids level (Shah et al., 2000) which in turn vary with plasma glucose concentration (Baldwin and Sainz, 1995).

Body fat content originates from the combined pool of exogenous fat and de novo fatty acid synthesis (Enser, 1991). Exogenous fat is mainly from dietary fat, but also include modified fatty acids and fatty acids synthesized by microbes in the GIT. De novo fatty acids are synthesized from carbohydrates, volatile fatty acid and deaminated amino acids (Halas, 2004). Lipid metabolism is modulated largely by

growth hormone (GH) and insulin-like growth factor-I (Davidson, 1987; Louveau and Gondret, 2004) and depends largely on plasma concentration of glucose, acetate, fatty acids and body fat content (Baldwin and Sainz, 1995).

Exogenous GH consistently decreases lipid deposition in pigs independent of gender, genotype and age (Louveau and Bonneau, 2001). This is primarily due to a decrease in lipogenesis rather than to an increase in lipolysis, and involves a reduction in the adipocyte sensitivity to insulin (Louveau and Gondret, 2004). In addition, the activity and mRNA levels of the enzyme - fatty acid synthase are reduced in GH-treated pigs (Magri et al., 1990; Harris et al., 1993).

The net production of ATP during cellular oxidation depends on the substrate (Burrin, 2001). During fasting, energy from body reserves is mobilized to generate ATP, whereas normally fed growing animals seldom mobilized body reserves (except glycogen) for ATP generating purposes (van Milgen and Noblet, 2003). Blaxter (1989) estimated that a greater number of moles (112-146) of ATP is generated from the oxidation of a mole of long-chain fatty acid compared to 36 moles of ATP generated from a mole of glucose and between 6-42 moles of ATP from a mole of amino acid.

2.4 Function of Energy

In order for the young pig to thrive and grow, it needs a supply of dietary energy. Dietary energy is used for maintenance and productive functions. Maintenance includes basal functions and involuntary activities, such as, muscle tone, feed digestion, blood circulation, tissues replacement (Wenk et al., 2000; Vestergen,

2001), cellular ion transportation for maintaining membrane potential and acid-base homeostasis (Baldwin and Bywater, 1984; Milligan and Summers, 1986). In addition, energy is required for homeothermal functions i.e. the maintenance of body temperature irrespective of the environment in which the pig is placed (Cole, 1995). For example, animals kept below their optimum temperature have about 4% greater energy requirement for maintenance for each 1°C below the lower critical temperature (Close, 1996). Another part of maintenance is the degradation of complex chemical substances into simpler substances that can be eliminated as waste products from the body through the kidneys, digestive tract, lungs and skin.

According to Verstegen (2001) in situations where thermoregulation, detoxification, immune, fever and stress responses are absent (i.e. optimal conditions), energy available for maintenance is distributed into four equal proportions for physical activity, cellular ion (Na^+, K^+) transport activity, protein turnover and other maintenance activity (e.g. waste elimination).

2.4.1 Energy for Maintenance

Maintenance was defined by the ARC (1981) as "the requirement of nutrients for the continuity of vital processes within the body so that the net gain or loss of nutrients by the animal as a whole is zero." In reality, this definition may be suitable only for mature, non-pregnant, non-lactating animals. Growing pigs fed to maintain constant weight deposited protein at the expense of body fat (Black, 1974; Campbell, 1988; Wiesemuller et al., 1988; Kolstad and Vangen, 1996). Thus, growing pigs will

not be in constant energy balance considering the higher heat of combustion of fat that is lost in exchange for protein gain.

Although maintenance energy may be difficult to define or measure unambiguously (van Milgen et al., 2000), it has been widely adopted by animal nutritionists in an attempt to separate the energy cost of maintenance versus that of production and to facilitate the additivity of the two processes (van Milgen and Noblet, 2003).

Maintenance energy (ME_m) is known to vary with pig genotype, body weight (BW) and environmental conditions (van Milgen et al., 1998; Noblet et al., 1999; Kolstad et al., 2002; Le Bellego et al., 2002). The influence of health-status on ME_m is not well documented. However, Williams et al. (1997) estimated similar ME_m in weaned pigs between 6 to 27 kg BW with low and high level of chronic immune system activation. The ME_m is usually expressed as a non-linear function of BW:

$$ME_m = aBW^b \quad (2.1)$$

where a is the intercept and b is the BW exponent, commonly expressed at $BW^{0.75}$.

The 0.75 scaling exponent originated from Kleiber's work (Kleiber, 1932) and was supported by Brody's famous mouse-to-elephant curve (Brody, 1945; Kleiber, 1975). In a recent analysis of the allometry of mammalian basal metabolic rate, White and Seymour (2003) found no support for a quarter-power (b = 3/4) scaling exponent, but instead, for a two-third (b = 2/3) power. Other allometric relationships have been reported specifically for pigs (e.g. 0.62, Schiemann et al., 1989; 0.60, Noblet et al., 1991; 0.647, Hoffman et al., 1992).

Noblet et al. (1999) suggested that when expressed at $BW^{0.75}$, ME_m is underestimated for the growing pig. Consequently, the estimated energy efficiency of protein and lipid deposition would be affected. Since heat production is strongly related to protein rather than lipid metabolism, Tess et al. (1984) suggested that ME_m is better expressed as a function of body protein weight. Schinckel and de Lange (1996) noted that ME_m is better expressed in relation to the distribution of the major tissue groups (viscera, muscle and fat) in the pig's body, since the contribution of these tissue groups to the various processes determines maintenance energy requirement.

Irrespective of the differing opinions on the mode of expressing ME_m, there is a general consensus that ME_m takes preeminence in the energy budget and only when it has been met is energy available for tissue deposition. According to Close (1996), ME_m may represent up to 40 and 10% of the animal's energy and amino acid intake, respectively.

Rijnen (2003) outlined three major approaches used in estimating ME_m: estimates from regressing retained energy (RE) on metabolizable energy intake (ME*i*), multiple regression of ME*i* on energy retained as protein and lipid, and measurement of heat production following a period of fasting.

For example, Close et al. (1983) estimated ME_m from the regression of RE on ME*i* according to the following equation:

$$ME_i = a + (1/k_g)RE \qquad (2.2)$$

where a is the intercept, k_g is the efficiency of energy utilization and ME_m is calculated from the intercept divided by the efficiency.

Campbell and Dunkin (1983a) using a similar approach estimated digestible energy for maintenance (DE_m) from the regression of RE on digestible energy intake (DE*i*):

$$DEi = a + (1/k_g)RE \qquad (2.3)$$

In such estimates, the ME_m or DE_m is by definition the ME*i* or DE*i* at which RE is zero. The ARC (1981) disputed the adequacy of calculating k and ME_m from this regression analysis since a constant k does not reflect the composition of RE or the efficiencies with which the protein and lipid component of RE are deposited. It is now generally accepted that ME*i* is used for protein deposition with a lesser efficiency than lipid deposition (van Milgen and Noblet, 2003). In addition, according to Emmans (1999), when energy intake is just sufficient to achieve a zero RE in growing animals, protein deposition (PD) is positive and lipid deposition (LD) is negative. Thus, the calculated ME_m does not necessarily reflect the ME*i* at which energy retained as protein and lipid are both zero.

2.4.2 Energy for Growth

"If one can imagine the pig giving priority to the various functions for which it needs nutrients, the first would be simply to stay alive, that is to maintain itself." In these words, Close (1996) underscores the importance or the priority that the pig places on maintenance. It is only after such functions pertinent to maintenance have been fulfilled that the pig can build body tissues (lean and fatty tissues) and grow.

In normal growth, the first imperative of the pig is for lean tissue deposition. Although both lean tissue (ham, shoulder, loin, all without subcutaneous fat; Walstra, 1980) and LD increase at a similar rate until the maximum genetic potential for lean growth is reached (Van Lunen and Cole, 2001).

The classical concept of tissue growth in response to feed (energy) intake presented by Close (1996) and Van Lunen and Cole (2001) suppose that lean tissue and growth rate respond in a linear manner with energy intake up to a point at which PD is at a maximum (Figure 2.1). This represents the genetic capacity of the pig for lean tissue growth. Additional energy supplied beyond this point will produce a large increase in LD with little, if any, increase in lean. Lipid deposition, on the other hand, increases at a greater rate above the 'capacity point' than below it due to the greater proportion of the energy needed to fuel protein metabolism below the 'capacity point' (Close, 1996).

Patience et al. (2002), using selected lines of pigs between 25 to 120 kg BW and given various levels of energy intake up to ad libitum, found a quadratic increase in PD of gilts, whereas PD was linearly increased in barrows. Taking into consideration the linear increase in LD in both genders, this would imply that gilts but not barrows might have reached the intrinsic capacity point for lean gain.

A recent study by King et al. (2004) with crossbred pigs (Large White × Landrace) between 80 to 120 kg BW given various levels of energy intake found a linear increase in PD and LD up to ad libitum intake in both gilts and barrows indicating that the intrinsic limit to PD was not attained in this genotype.

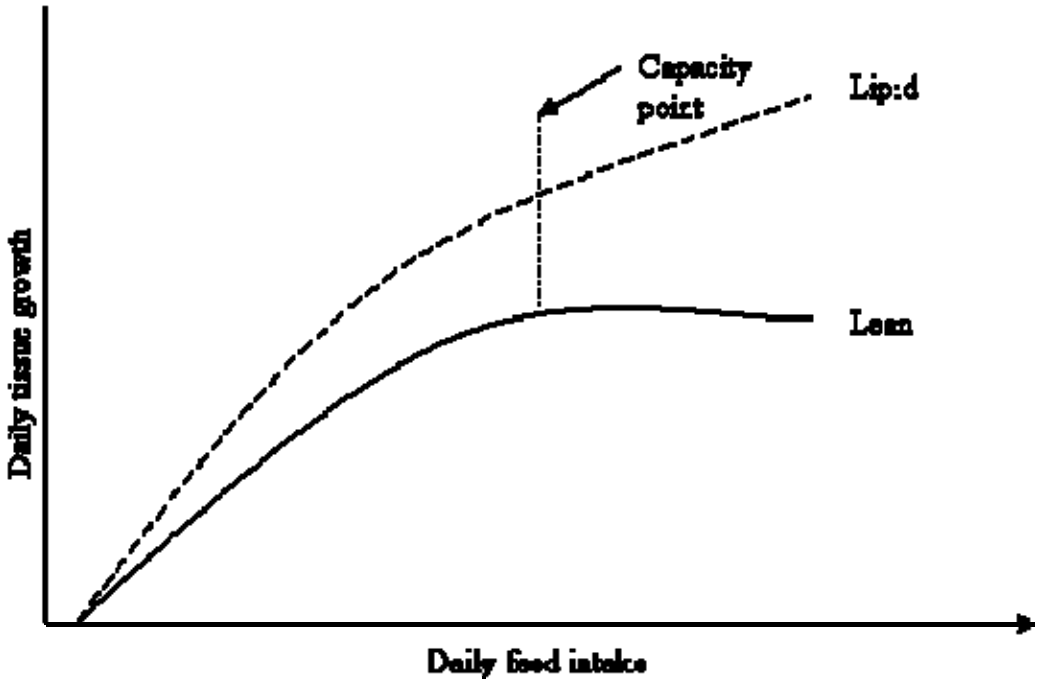

Figure 2.1. The influence of daily feed intake on tissue growth. Adapted from Close (1996).

2.5 Partitioning of Energy

Energy consumed by growing pigs is partitioned to maintenance and to growth according to the scheme in Figure 2.2 with ME*i* plotted against RE. It is generally assumed that greater priority is given to maintenance than to growth. Energy supplied above that needed for maintenance is partitioned into protein and lipid synthesis (Kolstad et al., 2002).

As discussed in section 2.4.1, because it is difficult to justify that energy supplied above maintenance is used for LD and PD with similar efficiency, Kielanowski (1976) utilized a multiple linear regression technique to estimate the ME_m, and the marginal efficiency of using ME*i* over maintenance for daily energy retention as protein (ERP) and lipid (ERL). With this approach, ME*i* is taken as the sum of ME_m and the energy required for PD and LD:

$$ME\mathit{i} = ME_m + (1/kp)ERP + (1/kl)ERL \qquad (2.4)$$

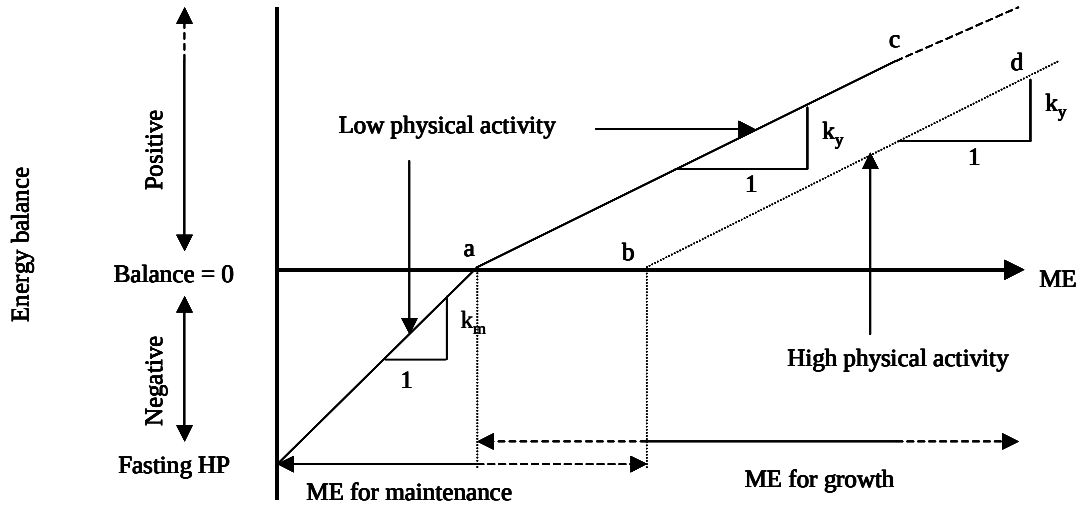

Figure 2.2. Energy retention in relation to the intake of metabolizable energy. a = ME for maintenance at low physical activity; b = ME for maintenance at high physical activity; c = ME for growth at low physical activity; d = ME for growth at high physical activity. Adapted from Wenk et al. (2000).

ME*i* is the dependent variable and ERP and ERL are the independent variables and a theoretical ME_m when no gain or loss of both protein and lipid occurred is estimated from the intercept. The reciprocals of the coefficients of ERP and ERL estimate the marginal efficiency of using ME*i* over maintenance for daily energy retention as protein and lipid (kp and kl, respectively).

This approach is based on the a priori assumption that ME_m is an allometric function. Although it is a refinement of using a common efficiency for the body total retained energy (k_g) in equations 2.2 and 2.3, its main flaw is that the effects of diet on the energetic efficiency of postabsorptive nutrient metabolism are not considered (de Lange and Birkett, 2004). Nonetheless, the partitioning of energy into maintenance, LD and PD has been evaluated in several studies using this approach.

In a study with growing pigs of between 45 to 100 kg BW and different genetic makeup, Quiniou et al. (1996a) estimated kp and kl as 0.49 and 0.81, respectively. van Milgen and Noblet (1999) estimated kp and kl as 0.51 and 0.92, respectively, with growing pigs between 15 to 100 kg BW and diverse genetic makeup. As well, Noblet et al. (1999) estimated kp and kl at 0.64 and 0.83, respectively, with growing pigs of the same BW range. Nieto et al. (2002) estimated kp and kl at 0.30 and 0.81, respectively, with the Iberian pig. Williams et al. (1997) estimated kp and kl at 0.49 and 0.70, respectively, with crossbred weaned pigs (Yorkshire × Landrace dam and Hampshire × Duroc sire) between 6 and 27 kg BW. Earlier, Close et al. (1983) using Large White pigs estimated kp and kl at 0.57 and 0.82, respectively.

The ARC (1981) recommended kp and kl of 0.56 and 0.74, respectively, while the NRC (1998) suggested a kp and kl of 0.53 and 0.76, respectively. The large variation in the literature value for kp and kl (0.303 to 0.644 and 0.74 to 0.916, respectively) and thus the energetic cost of protein and lipid synthesis (Table 2.1) underscore the inherent problem in adequately defining the partitioning of ME*i*.

Table 2.1. Estimated energetic efficiency and the energy cost of protein and lipid deposition

	kp	kl	Energy cost of protein synthesis, kcal/g	Energy cost of lipid synthesis
Close et al., 1983	0.57	0.82	9.93	11.54
ARC, 1981	0.56	0.74	10.11	12.78
Quiniou et al., 1996a	0.49	0.81	11.55	11.68
Williams et al., 1997	0.49	0.70	11.55	13.51
NRC, 1998	0.53	0.76	10.60	12.50
van Milgen and Noblet, 1999	0.51	0.92	11.08	10.33
Noblet et al., 1999	0.64	0.83	8.79	11.38
Nieto et al., 2002	0.30	0.81	18.68	11.65
Mean	0.51	0.80	11.54	11.92

Close et al. (1983) and Nieto et al. (2002) suggested that when dietary protein supply is close to requirement, a higher kp and kl would be expected. This is possibly due to the energy cost of urea synthesis and elimination in pigs fed diets with high crude protein content. Apart from the effects of dietary crude protein and other dietary factors, Birkett and de Lange (2001) indicated that experimental methodology and statistical issues are part of the large variation in reported kp and kl. van Milgen and Noblet (1999) utilized a non-linear multivariate analytical procedure in which the influence of the correlation between LD and PD on parameter estimates is minimized.

Wenk et al. (1998) explained two major limitations to estimating kp, kl and ME_m in growing animals. First, the variation of ME*i* is often not large enough, and consequently the variation in RE within the experiment is inadequate for an accurate estimate of kp, kl and ME_m. Second, ME_m is independent of ME*i* for growth; for instance, PD is only a small fraction of total protein turnover, and ERP and ERL are subjected to physiological limitation that is not easily altered.

Kolstad et al. (2002) indicated that energy is primarily partitioned to lean tissue until the maximum potential for lean growth is reached, and afterward, energy will be deposited primarily as fatty tissue in pigs with ad libitum access to feed containing sufficient protein. The proportion of energy that is devoted to carcass lean and fatty tissue deposition varies with body weight and genotype (de Greef et al., 1994; Kolstad et al. 2002).

Kolstad et al. (2002), who utilized three genetic groups (Landrace, Duroc and Landrace × selected line, LLP) and free access to feed in growing pigs between 25 to 105 kg BW, noted that a higher proportion of energy consumed above maintenance was used for lean growth at lower BW (25 to 50 > 50 to 85 > 85 to 105 kg) while a higher proportion was partitioned into fatty tissue at heavier BW. Differences in genetic groups revealed that Landrace partitioned more energy into lean than Duroc and an LLP strain. van Milgen and Noblet (1999) found that ‘lean boars’ (i.e. synthetic line and Piétrain) maintained a constant partitioning of energy to PD and LD with increasing BW within the 20 to 100 kg BW range, while the proportion of energy partitioned to PD declined linearly with increasing BW in Large White pigs (boars, castrates and gilts).

Thus, the increase in body fatness is mainly due to an increase in the amount of energy available as PD rate declines and is influenced by genetic potential for carcass lean and fatty tissue growth. Since ME is utilized with a greater efficiency for LD than for PD (ARC, 1981), an increase in the proportion of energy that is partitioned to LD will produce a better overall energy efficiency.

2.6 Impact of Energy Intake on Protein Gain

A major constraint to PD in the pig is energy intake (Dunshea et al., 1998). According to Möhn and de Lange (1998), in a stress-free environment and when pigs are given adequate supply and intake of essential nutrients, PD is determined by either energy intake or the genetically determined upper limit to body PD (PDmax).

The relationship between PD and energy intake has been described with a linear-plateau model by several authors (e.g. Campbell et al., 1983; de Greef, 1992; Kyriazakis and Emmans, 1992a; Bikker, 1994; Quiniou et al., 1999). It has formed the basis of several growth models (e.g. Moughan and Smith, 1984; Moughan et al., 1987; Pomar et al., 1991). The model assumes that PD is limited either by the genetic potential for growth (PDmax; plateau) or when energy intake is restricted (linear; Figure 2.3) (van Milgen and Noblet, 1999; King et al., 2004). The linear-plateau relationships was reported for growing pigs between 48 to 90 kg BW (Campbell et al., 1985b), barrows and pigs with poorer genotypes (Campbell and Taverner, 1988) and is more typical of younger pigs with a high potential for PD relative to appetite (Close et al., 1979; Campbell and Dunkin, 1983b).

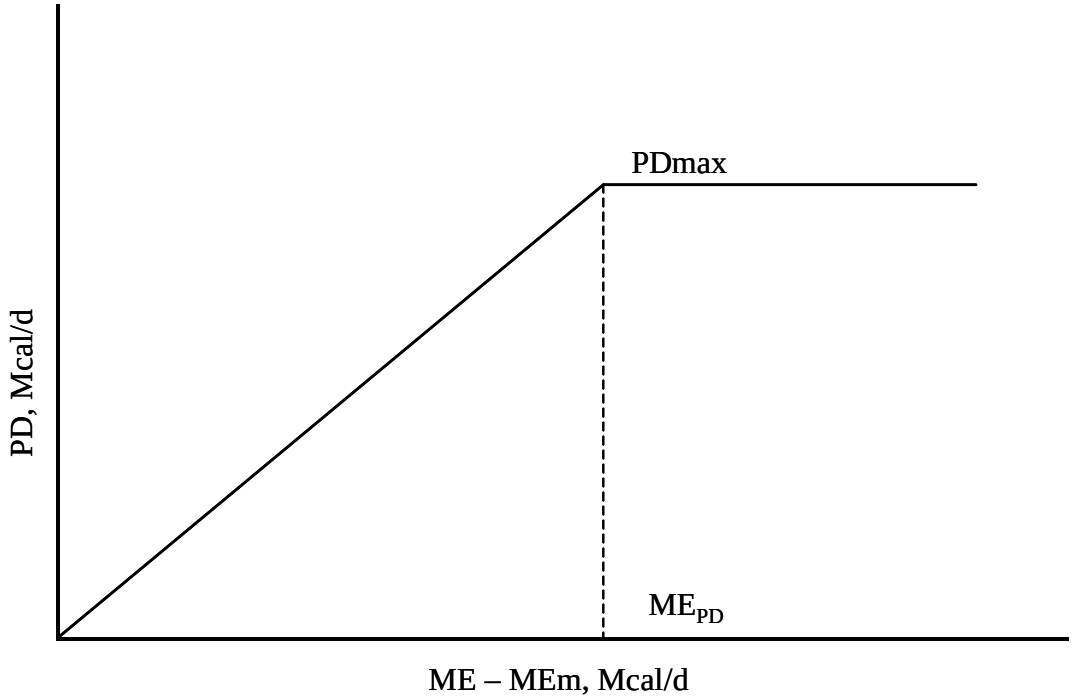

Figure 2.3. The relationship between protein deposition rate (PD) and Metabolizable intake above maintenance (ME – MEm) assuming that either energy intake (ascending line) or genetic potential (plateau) limits PD. The ME_{PD} is the ME intake above maintenance at which the genetic potential starts to limit PD, while PDmax is the corresponding level of PD. Adapted from van Milgen and Noblet (1999).

However, in other studies with pigs of high genetic capacity for lean growth, the pig's upper limit to PD cannot be reached below 80-90 kg BW (Campbell and Taverner, 1988; Rao and McCracken, 1992; Bikker, 1994; Dunshea et al., 1998). King et al. (2004) reported a linear relationship between DE intake and PD in crossbred (Large White × Landrace) boars and gilts between 80 to 120 kg BW. This response is consistent with a linear relationship between PD and energy intake and suggests strongly that there is no intrinsic limit to PD up to 120 kg BW in this genotype. In general, this would suggest that intensive genetic selection of pigs has raised the genetic capacity for PD to heavier body weights and beyond upper limit of appetite (King et al., 2004).

In instances where energy intake is limiting PD, it is assumed that productive energy is partitioned between protein and lipid deposition according to some factor depending on the genotype and gender of the pig (de Greef and Verstegen, 1995). A minimum ratio between protein and lipid deposition rates is assumed (Whittemore and Fawcett, 1976; Moughan et al., 1987). Whittemore (1983, 1986) suggested that the partitioning of energy above maintenance between PD and LD is constant and independent of BW and energy intake level in situations when the expression of lean tissue growth or PD potential is limited by energy intake. On the contrary, recent studies (e.g. Quiniou et al., 1995; Bikker et al., 1996; Coudenys, 1998) indicated that whole body lipid content and consequently lipid:protein ratio increased with BW and/or energy intake.

The slope of the linear relationship between PD and energy intake quantifies the additional amount of protein deposited from each additional unit increase in energy intake, and represents the marginal partitioning of energy intake between PD and LD (Schinckel and de Lange, 1996; Weis et al., 2004). It is a reflection of the pigs' need to deposit a certain amount of essential body lipid even when energy intake limits PD (Schinckel and de Lange, 1996; Möhn and de Lange, 1998).

Möhn and de Lange (1998) summarized the slope of PD per Mcal ME intake reported in various studies. The slopes vary widely across different populations of pigs and ranges from 11.7 to 48.1 g/Mcal.

Weis et al. (2004) in a N-balance study found a linear increase in whole body PD with increasing DE intake and a greater slope (32.9 vs. 21.3 g/Mcal DE) for pigs at 22 than 84 kg BW. According to the authors, this would suggest a greater need to

deposit more lipid per unit of PD as BW increases. Similarly, in a serial slaughter over three 25-kg BW ranges (40 to 65, 65 to 90 and 90 to 115) PD increased linearly, suggesting that energy intake determines PD across BW ranges (Weis et al., 2004).

Bikker et al. (1995), in a comparative slaughter study, found a linear increase in PD with increased DE intake with a slope of 24.1 g/Mcal DE in growing pigs between 20 to 45 kg BW. Also, Quiniou et al. (1996a), in a comparative slaughter study with different genotypes of pigs between 45 to 100 kg BW, detected differences in the slopes of PD per ME intake at 18.4, 19.7 and 25.5 g/Mcal ME for castrated Large White, castrated Large White × Piétrain crossbred and Piétrain boars, respectively.

de Greef et al. (1994) tested the general assumption that there is no effect of energy intake and body weight on lipid:protein ratio in pigs below their maximal PD rate in a serial slaughter study. Pigs were fed either at low or high DE intake (3.01 and 3.89 Mcal/d, respectively) and slaughtered at 25, 45, 65, 85 or 105 kg BW. The lipid:protein ratio increased from 0.74 at 25 kg BW to 0.99 at 105 kg BW in pigs fed at low energy intake, while it increased from 0.82 to 1.32 in those fed at high energy intake. This demonstrates that lipid:protein ratio is influenced by both BW and energy intake. The latter is supported by a linear increase in lipid:protein ratio with increased DE intake reported by Weis et al. (2004).

2.7 Impact of Energy Intake on Lipid Gain

In situations where protein intake (or quality) and pigs' PD capacity are limiting PD, all production energy not utilized for PD is devolved to lipid deposition (de Greef and Verstegen, 1995; Möhn and de Lange, 1998). Considering that energy is retained in growing pigs as lean or adipose tissue, due to the large water content in lean tissue (~80% compared with 15% in adipose tissue), a smaller quantity of energy is required per gram of gain of lean tissue than adipose tissue (1.12 vs. 7.83 kcal; Burrin, 2001).

Body lipid content and deposition rates increase with BW (Campbell, 1987, Bikker, 1994) and energy intake (de Greef and Verstegen, 1993; Close, 1996; Weis et al., 2004). Bikker (1994) found a 4% greater lipid content in the carcass and the empty body of pigs at 85 compared to 45 kg BW. A part of the increase in body lipid content with BW may be related to an increasing energy intake with BW (Bikker, 1994; Weis et al., 2004).

In contrast to the influence of energy intake on PD, the increase in LD with energy intake is generally not affected by genotype or gender (Quiniou et al., 1999). The slope of LD averaged 60.7 g/Mcal DE in pigs over the 45 to 100 kg BW range (Quiniou et al., 1995). On the other hand, Bikker (1994) reported that the slope would increase with increased BW. The slope in pigs between 20 to 45 kg BW was 43.9 g/Mcal DE compared with 57.3 g/Mcal DE in those between 45 to 85 kg BW.

2.8 Energy Systems in Swine Feed Formulation

In view of the great economic importance of energy in animal production (SCA, 1987; Chiba, 2000; de Lange and Birkett, 2004), concerted efforts have been made to develop methods and systems adapted to evaluating the energy content of feed, metabolic utilization of energy and the animal's underlying biological requirements for energy. The primary focus of energy based feed evaluation systems is the quantity of energy that can be derived from ingested nutrients to support the animal's maintenance and productive functions.

All energy systems follow the general scheme of energy utilization in pigs (Figure 2.4). Most of the practical energy systems are marginal systems (Verstegen, 2001), that is, the energy value is based on the ability to deposit a certain unit amount of energy in the body per unit amount of extra feed.

From a practical perspective, energy systems are used in animal nutrition for three basic reasons: 1) allow energy values to be ascribed to a feed ingredient or blend of feed ingredients which can be used to estimate the amount of a given diet needed to meet a particular animal performance (Emmans, 1999) 2) to define the quantity that is required for maintenance, productive functions, diet formulation and to develop feeding programs and 3) to place a relative value on one ingredient vs. another. Ultimately, the quality of such a system is its ability to predict the performance of animals (Noblet, 2000).

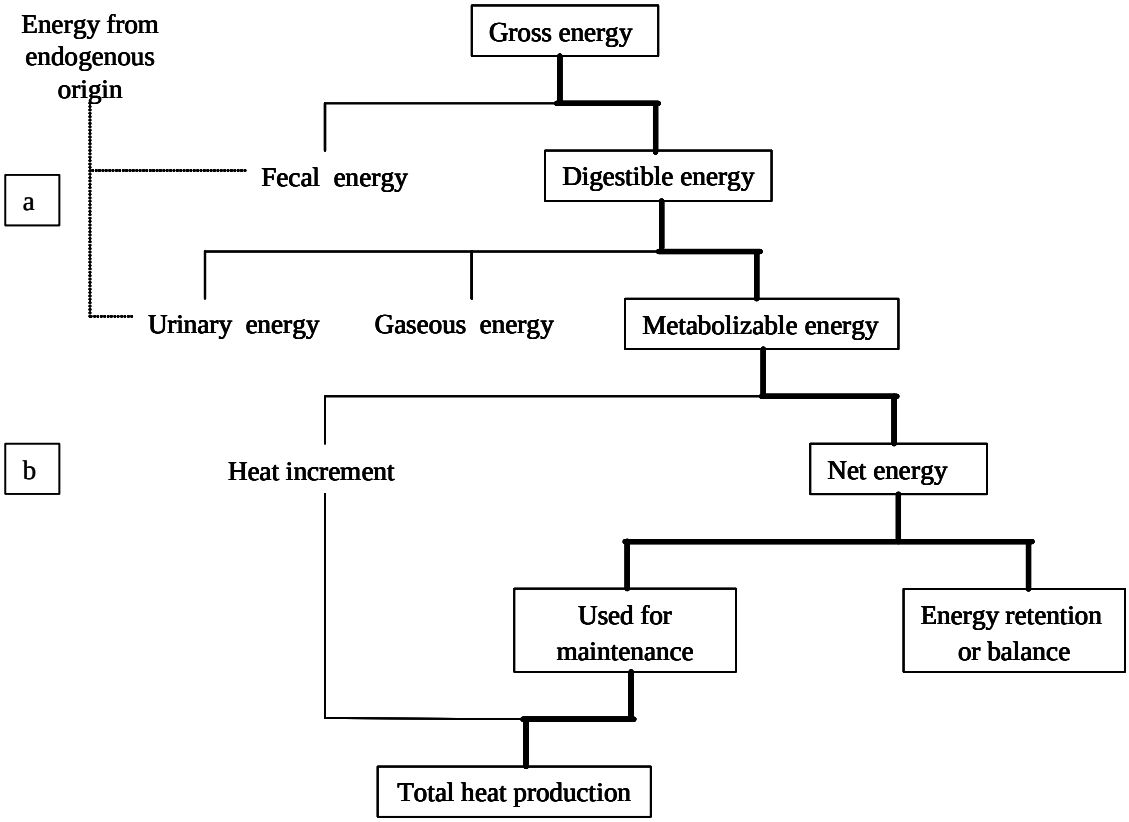

Figure 2.4. Classical description of energy utilization. a) Energy from endogenous sources contribute to faecal energy, Metabolizable energy = digestible energy minus urinary energy (with a portion from endogenous source) and gaseous energy; b) Total heat production = Heat increment plus maintenance energy. Adapted from Wenk et al. (2000).

Van Es (1980b) outlined the desirable properties of a practical energy system: 1) should be precise and generally applicable, 2) should include unconventional rations and high production levels, and 3) should be simple to use. Additionally, Cole (1995) stated that such a system should be versatile enough to accurately describe and rank the wide array of feed ingredients available for pig feed, while at the same time it satisfactorily describes the requirement of the pigs to which it is fed.

2.8.1 Gross Energy

The gross energy (GE) content of feed provides no information on the amount of that energy that is accessible to the pig via the digestive procedure or lost during metabolism. It is rarely used in feed formulation but is used for computational purposes.

GE is the total potential energy content of an organic material when it is completely oxidized. It is usually determined in an adiabatic bomb calorimeter. Alternatively, since the energy supplied by a given feed is from carbohydrates, fat and protein, when the respective content in a feed ingredient is known, the GE concentration can be estimated. One mol of glucose (180 g) yields 674 kcal/mol, with monosaccharides yielding 3.75 kcal/g and polysaccharides (such as starch) yielding 4.16 kcal/g (Wenk et al., 2000). Similarly, the GE content of protein and fat depends on the amino and fatty acid composition, respectively, with an average of 5.64 kcal/g for protein (Wenk et al., 2000). According to Livesey (1984), the GE of free fatty acids (kcal/mol) can be calculated as:

$$GE = 156n - 40d - 101 \quad (2.5)$$

where n is the number of carbon atoms/fatty acid, and d is the number of double bonds.

The GE value of fat can then be calculated from the GE value of 3 moles of free fatty acids, the GE value of glycerol (397 and 22 kcal/mol, respectively) under elimination of 3 moles of water (Wenk et al., 2000). The widely accepted and commonly used GE value of fat is 9.51 kcal/g (Brouwer, 1965).

The NRC (1998) estimated the GE content in feed ingredients using the caloric values of 3.7, 4.2, 5.6, and 9.4 kcal/g for sugar, starch, protein and fat, respectively. If no bomb calorimeter is available but the nutrient composition of feed ingredients and/or diets is known, the GE content can be predicted using existing prediction equations (e.g. Schiemann, 1988; Ewan; 1989; Noblet and Perez, 1993).

2.8.2 Digestible Energy

As a relatively simple modification of the GE, the DE is a measure of the amount of energy that does not disappear during the feed's passage along the digestive tract. It is often referred to as apparent digestible energy since it is not a true measure of the energy values of the nutrients absorbed from the digestive tract. A part of the energy in faeces has been contributed by endogenous sources (e.g. digestive secretions and intestinal cell debris; Figure 2.4) (Just, 1982). In addition, a small amount of gases are produced from hindgut fermentation. DE is determined from the amount of GE consumed and the GE of faecal matter produced. Alternatively, DE can be measured by mixing non-absorbable indicators (e.g. acid insoluble ash or chromic

oxide) into the diet. The digestibility of energy (DEc) expresses the ratio between DE and GE_{feed}:

$$DEc = \frac{GE_{feed} - GE_{faeces}}{GE_{feed}} \quad (2.6)$$

In pigs, up to 25% of ingested energy is found in faecal matter (Boisen and Verstegen, 2000); however, the DEc is known to vary between 70 and 90% for pig diets, with a wider variation, 0 to 100% for raw materials (Noblet and Henry, 1993). The observed variations are due to differences in faecal digestibility of the nutrient's organic matter. Because of the effect of pig's age on its ability to digest fiber, DE values obtained from older pigs will overestimate DE values for younger ones (e.g. nursery pigs) especially in feeds with high fiber content (Shi and Noblet, 1993).

2.8.2.1 Digestible Energy Values for Different Physiological Stages

A comparison of measured versus formulated DE concentrations of compound diets for weaned pigs revealed that measured DE values are mostly lower than formulated values (Figure 2.5). This variation between formulated and determined DE values of compound diets is an issue of considerable importance. As discussed by Levesque (2002), the digestibility coefficients of cereal grains are based on data generated with grower pigs, and may overestimate the DEc for weaned pigs. Specifically, Rijnen et al. (2004) pointed out that DEc values in research with growing pigs would be greater and hence DE concentration for pigs between 10 to 25 kg BW would be overestimated especially for fibrous ingredients and cereal grains with high inclusion levels.

At present, little information about comparative digestibility among the three physiological stages (i.e. weaned pigs, growing pigs and sows) is available.

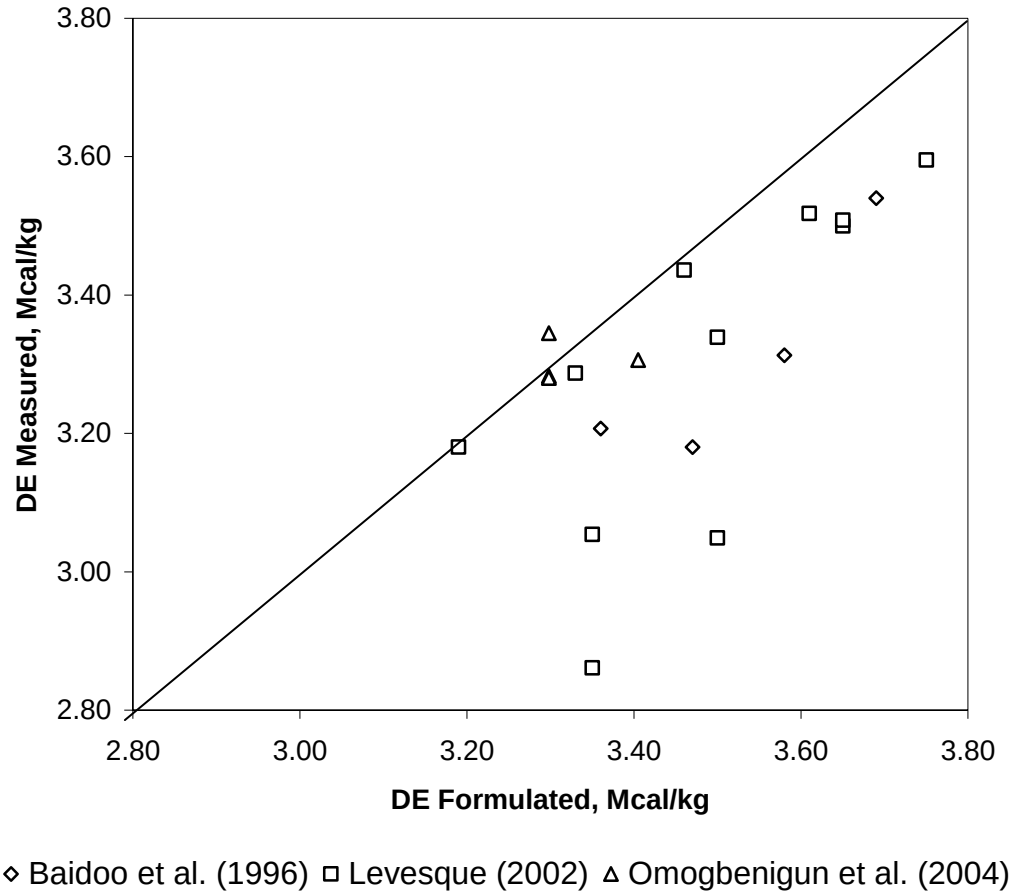

Figure 2.5. Formulated versus measured DE concentration of diets fed to weaned pigs.

Le Goff and Noblet (2001), using the same diets fed to growing pigs and adult sows, compared the apparent energy digestibility. Apparent digestibility was greater in adult sows compared with growing pigs and consequently, a 4% greater DE concentration was determined. Thus, it would be appropriate to ascribe separate values to feed ingredients for these two physiological stages.

2.8.3 Metabolizable Energy

Armsby (1917) defined metabolizable energy as "the gross energy in the feed minus the gross energy of the excreta" and as "energy capable of transformation in the body." Metabolizable energy is estimated as the DE minus urinary energy and gaseous energy (GE_{gas}; mostly CH_4). It is the energy available to the pig for maintenance, cold thermogenesis (when necessary) and for productive purposes.

In pigs and other non-ruminants, the GE_{gas} is usually ignored because it constitutes only a small fraction of DE, between 0.1 and 3% (Verstegen, 1971; Wenk et al., 2000). Therefore, the estimated ME concentration are usually between 0.5 to 3% higher than the real value depending on the amount of plant cell wall content and the age of the animal (Van Es and Boekholt, 1987).

The ME:DE ratio varies with increasing dietary protein content (Noblet et al., 1993). This was explained by Morgan et al. (1975) as due to an increase in the catabolic processes in the animal, and hence, a greater excretion of urinary nitrogen in protein-rich diets. The amount of energy in the urine is dependent on the quality of the protein and the level included in the diet relative to requirement (NRC, 1998). Since the DE does not allow correction for urinary nitrogen loss, the energy value of

protein-rich ingredients compared with cereals is inflated with the DE vs. ME (Morgan et al., 1975).

2.8.3.1 Nitrogen Corrected Metabolizable Energy

Because dietary nitrogen retention can influence the energy lost in urine, a correction to ME values for pigs (Morgan et al., 1975) and poultry (Hill and Anderson, 1958) to either zero or 30% dietary nitrogen retention was suggested. These corrections are an attempt to eliminate the effect of variations in nitrogen retention on the ME:DE ratio. Corrected ME is based on the theory that the ME of a protein source is greater if incorporated into body protein rather than used for fat synthesis or oxidative metabolism (Farrell, 1979).

In view of the fact that most ME determinations are conducted in growing pigs with a positive nitrogen retention, such correction to zero nitrogen retention (Morgan et al., 1975; Wu and Ewan, 1979) is of no justifiable value (NRC, 1998). The correction implies that the protein retained by the animal is not ascribed its full energy value.

2.8.3.2 Disputable Superiority of Metabolizable over Digestible Energy

The ME is presumed to offer an improvement over the DE in feed evaluation and diet formulation because it adjusts for urinary energy that is attributed to protein deamination and excretion. This may be subjected to dispute. First, most of the available ME values for ingredients and diets are estimated as a fixed ratio of 0.96 of

the DE values (ARC, 1981; Whittemore, 1993; Cole, 1995). However, Whittemore (1997) indicated that ME varies from 0.90 of DE for diets with low quality protein to 0.98 of DE in diets with high quality protein fed below requirement. Second, the variation in the ME:DE ratio is in effect not only due to the ingredient, but depends on the animal's ability to utilize the dietary protein for PD as well (Whittemore, 1993). Consequently, dietary protein will be undervalued in fast-growing animals (Baldwin and Bywater, 1984). Third, since the ranking and relative difference between ingredients are the same in the ME as with the DE system (Table 2.2), there is little, if any, benefit of using the ME system over DE.

Table 2.2. Relative digestible, metabolizable and net energy values of selected feed ingredients[a]

Ingredient	DE	Rank by DE	ME	Rank by ME	NE	Rank by NE
Animal fat	261	1	267	1	314	1
Vegetable oil	261	1	267	1	314	1
Fish meal	126	3	118	3	100	6
Soybean meal 48	115	4	108	5	85	8
Corn	111	5	112	4	117	3
Wheat	109	6	108	5	108	4
Pea	109	6	106	7	102	5
Barley	100	8	100	8	100	6
Rapeseed meal	91	9	85	9	66	10
Sugar beet pulp	85	10	83	10	65	12
Meat and bone meal	85	10	77	12	65	12
Corn gluten feed	84	12	82	11	72	9
Wheat bran	73	13	71	13	66	10
Sunflower meal	70	14	66	14	48	14
Soybean hulls	66	15	63	15	44	15

Data from Sauvant et al. (2004). Barley was arbitrarily set at 100. Adapted from Rijnen et al. (2004).

2.8.4 Net Energy

Net energy (NE) is defined as ME minus heat increment (NRC, 1998). The heat increment is the heat produced from metabolic utilization of ME and the energy cost of ingestion, digestion and physical activity (Rijnen et al., 2004). A number of the available NE equations (systems) are listed in Table 2.3.

Essentially, DE or ME represent potential energy, whereas the NE represents utilizable energy. It is not surprising that, at least in theory, the NE system is considered as a superior energy system given the following limitations of the DE and ME systems as outlined by de Lange and Birkett (2004): 1) no consideration is given to the effects of diet on the utilization of DE and ME for various body functions, 2) not all animal effects on diet DE and ME are considered, 3) although ME_m is known to vary with both diet composition and animal state, it is treated as a residual value, 4) large observed variability in the marginal utilization of ME intake for body LD and PD, 5) relatively poor prediction of the efficiency of feed utilization and other animal performance.

Moreover, as suggested previously, one of the attributes of an energy system is its ability to rank ingredients. The hierarchy between feed ingredients is influenced by energy systems (Noblet et al., 1994; Noblet, 2000; Rijnen et al., 2004). This is illustrated in Table 2.2. DE overestimates the energy value of protein and fibrous ingredients while fat and starch sources are underestimated (Noblet et al., 1994; Le Bellego et al., 2001).

Table 2.3. Equations for prediction of the NE concentration of diets for growing pigs from chemical characteristics, and or digestible nutrients, or ME concentration

	Equation	Source
1	NE = 2.56 × DCP + 8.53 × DEE + 2.96 × DCF + 2.96 × DNFE	Schiemann et al., 1972
2	NE = -525 + (0.81 × ME)	Just et al., 1983
3	NE = 0.703 × DE + 1.58 × EE + 0.47 × ST - 0.97 × CP - 0.98 × CF	Noblet et al., 1994
4	NE = 0.700 × DE + 1.61 × EE + 0.48 × ST - 0.91 × CP - 0.87 × ADF	Noblet et al., 1994
5	NE = 2790 + 4.12 × EE + 0.81 × ST - 6.65 × Ash - 4.72 × ADF	Noblet et al., 1994
6	NE = 2875 + 4.38 × EE + 0.67 × ST - 5.50 × Ash - 2.01 × (NDF - ADF) - 4.02 × ADF	Noblet et al., 1994
7	NE = 2.73 × DCP + 8.37 × DEE + 3.44 × ST + 0 × DADF + 2.93 × DRES	Noblet et al., 1994
8	NE = 2.58 × DCP + 8.63 × DEE + 3.23 × ST + 3.04 × SG + 2.27 × DRES	CVB, 1994
9	NE = 2.58 × DCP + 8.63 × DEE + 3.23 × ilealST + 2.92 × ilealSG + 2.27 × DRES	CVB, 2003

NE is in Mcal/kg DM except #1, 8 and 9 in Mcal/kg product; CP, crude protein; EE, ether extract; CF, crude fiber, ST, starch; SG, sugar; DCP, digestible CP; DNFE, digestible nitrogen free extract; DEE, digestible ether extract; DADF, digestible acid detergent fiber; ilealST, ileal digestible starch; ilealSG, ileal digestible sugar; DRES, digestible residuals = digestible organic matter – (DCP + DEE + ST + DADF) all in g/kg DM.

For instance, Noblet et al. (1993) reported a similar DE value for wheat and soybean meal (3.86 and 3.91 Mcal/kg DM, respectively). However, soybean meal contained 34% less NE compared with wheat (1.92 vs. 2.90 Mcal/kg DM). Similarly, the NE value of canola meal was only 53% of its DE value (1.64 and 3.11 Mcal/kg DM for NE and DE, respectively) compared with 75% obtained with wheat (2.90 and 3.86 Mcal/kg DM for NE and DE, respectively) (Noblet et al., 1993). On the other hand, although wheat and tapioca contained a fairly comparable DE concentration (3.86 and 3.79, respectively) the NE value of tapioca was 6% higher than that of wheat (3.09 and 2.90 Mcal/kg DM, for tapioca and wheat, respectively). These clearly indicate that the DE underestimates the energy value of starch ingredients and overestimates that of protein ingredients.

Also, as shown in Figure 2.6, the relatively lower NE:ME ratio of high protein ingredients compared to cereal grains indicates that the NE system ascribes a lower value to protein supplements than cereals as a result of the metabolic inefficiency of their utilization. This underscores the importance of the energy system on the economic evaluation of feed ingredients.

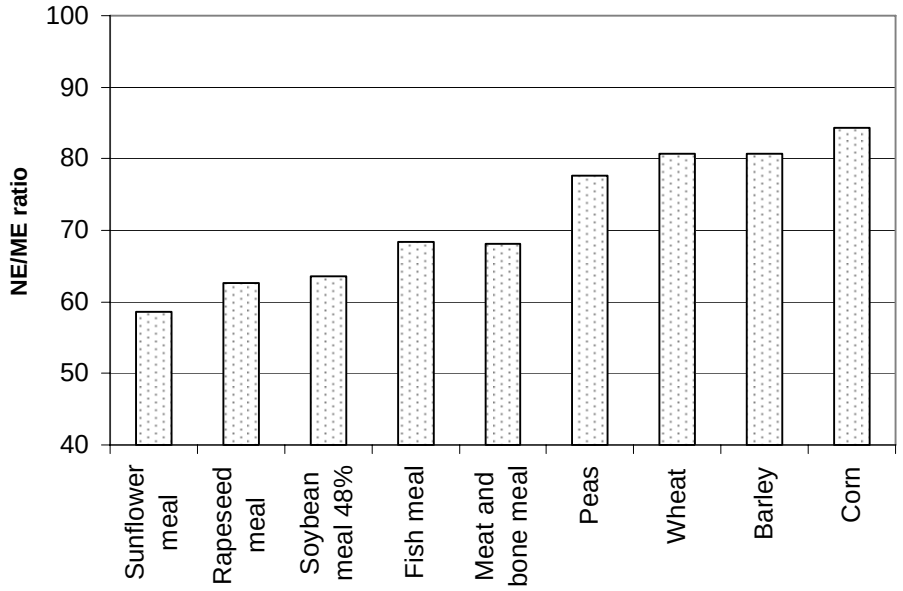

Figure 2.6. The NE:ME ratio of selected feed ingredients. Data from Sauvant et al. (2004).

The NE system has been widely adopted in Europe, especially in the development of feeding programs for growing pigs (Buttin, 1998). The shift from the classical DE or ME to the NE is based on the philosophy that more accuracy in describing the feed's production value for the animals is essential (Chiba, 2000). From a practical standpoint, the application of NE in diet formulation in terms of energy values ascribed to feed ingredients and the potential of using synthetic amino acids in diets when required is recently summed up by Hedges (2003):

Net energy formulations place a higher value on synthetic amino acids than when formulating on a metabolized energy basis. Soybean meal is not a good energy source and the ME system gives bean meal an inflated energy value. Net energy gives a more realistic evaluation of the utilizable energy of corn and soybean meal. Reducing bean meal and using synthetic amino acids with a higher level of corn provides the pig with more utilizable energy than most people realize.

2.8.4.1 Underlying Assumptions of the Net Energy System

Rijnen (2003) summarized the main assumptions of the NE systems: 1) ME_m is assumed to be constant, and NE is the extra RE with an extra unit of a feed ingredient or diet fed above maintenance, 2) additional energy from a certain nutrient is used with a constant efficiency established for that nutrient. In other words, a linear increase in RE with an increase in the intake of a certain digestible component (e.g. protein, lipids, sugar, starch or dietary fiber), 3) for dietary NE estimation, the ratio between ERP and ERL is constant or ERP has to be constant, 4) similar faecal digestibility between physiological stages (piglets, growing-finishing pigs and sows).

Apart from these assumptions, because standardized conditions are imposed in determining NE values of feed ingredients and diets (Boisen and Verstegen, 1998), it follows that a particular NE value is applicable to the particular condition and or pig body weight from which it was determined. Very clearly, it becomes apparent that these assumptions and experimental approaches may limit the full benefit or potential of the NE systems. Moreover, the digestive utilization of nutrients is clearly affected by physiological state. de Lange and Birkett (2004) claimed that some of these limitations could be overcome by using empirical NE systems in which the NE concentration of feed or feed ingredient is predicted from digestible nutrients.

2.8.4.2 Comparison of the French and Dutch Net Energy Systems

Existing NE systems combine the utilization of ME for maintenance and growth by assuming similar efficiencies for maintenance and energy retention. Based on this set of assumptions and experimental conditions, the estimated NE value of feed ingredients may differ (Noblet and van Milgen, 2004). Nonetheless, there is a good correlation in the estimated NE values and ranking of major ingredients between the French and the Dutch NE system (de Lange and Birkett, 2004; Table 2.4). Noblet and van Milgen (2004) who compared other NE systems to the French system indicated that NE Schiemann, NE Just, and NE Dutch are approximately 94, 83, and 96, of the NE French, respectively, for several diets. The lower NE Just/NE French ratio was attributed to the failure of NE Just to compensate for a high dietary fat and starch content and the overestimation of diets with a high crude protein and fiber content. In other words, the inherent flaws apparent in the ME system is not diminished with NE Just.

2.8.4.3 Issues to Consider in Adopting a Net Energy System

From a practical point of view, four major issues face the use of NE in diet formulation. First, there is a lack of empirical results to support the theoretical benefit of diets formulated with NE. Second, there is a wide disparity in available literature and tables of nutritive values for the NE content of feed ingredients (e.g. in NRC, 1998 vs. CVB, 1998 or INRA, 2002). Third, the estimated NE will depend on the type of production, that is, the utilization of energy by the pig for tissue deposition (e.g. fat vs. lean tissues as affected by genotype and stage of growth), the particular

Table 2.4. Estimated net energy concentration (Mcal/kg) of selected feed ingredients according to Noblet et al. (1994) and CVB (2003)[a]

Ingredient	NE French	Relative[b]	NE Dutch	Relative[b]
Vegetable oil	7.90	336	8.15	371
Animal fat	7.39	314	7.62	347
Corn	2.71	115	2.57	117
Wheat	2.44	104	2.30	105
Whey	2.38	101	2.37	108
Barley	2.35	100	2.20	100
Peas	2.31	98	2.24	102
Soybean meal (47.5%)	2.06	87	1.96	89
Soybean meal (45.7%)	1.98	84	1.95	89
Wheat shorts	1.87	80	1.76	80
Rapeseed meal	1.52	65	1.48	67

[a]Adapted from de Lange and Birkett (2004).
[b]Energy concentration relative to barley.

biochemical pathways for nutrient utilization and the heat generated from the reactions (Black, 2000). Thus, it appears that the NE value of feed ingredients and/or diets will vary depending on the way it is used by pigs (Whittemore, 1993). Thus, a single value ascribed to a feed ingredient for all types of production is really spurious. Fourth, if the NE content of ingredients and diets are to be predicted from available equations, the accuracy and suitability of equations for all pigs (e.g. weaned vs. growing) is doubtful.

For instance, the NE French in particular is developed with measurements in growing pigs between 45 to 120 kg BW. NE was calculated as fasting heat production (FHP) plus RE. However, because RE increases with fat deposition, which is considerably higher in the growing pig relative to the weaned pig, the ability of such equations to accurately predict the NE content of diets for weaned pigs is highly uncertain.

In addition, available NE equation may be inaccurate to predict the NE content of feed ingredients with chemical composition very distinct from standard diets (e.g. as used for oils, soy protein and other feed ingredients in NRC, 1998). This may explain the large disparities in some of the NE values reported in NRC (1998) compared with CVB (1998).

The NE Dutch is based on apparent faecal digestibility of nutrients that are present in feed ingredients or diets (Rijnen et al., 2004). The other values used to predict NE content are the fixed partial efficiency of digestible nutrients (Table 2.5). These values originated from the heat production measurements of a wider range of nutrients than those found in practical swine diets (Schiemann et al., 1972; Nehring and Haenlein, 1973; Hoffmann et al., 1993). As stated in section 2.8.2.1, not only is energy digestibility affected by physiological stages, as well, the apparent digestibility of nutrients are influenced by physiological stages (de Lange and Birkett, 2004). This is demonstrated by up to a 17% increase in digestibility of crude fat and fiber in sows compared to growing pigs (Table 2.6). Therefore, even if the absolute partial efficiency for digestible nutrients are different among physiological stages, NE estimated from digestible nutrients would at least allow for different absolute NE values ascribed to feed ingredients and diets for different physiological stages.

Table 2.5. Enthalphy, net energy, heat increment and partial efficiency values used in the Dutch feed evaluation system for pigs[a]

Digestible Nutrient	Enthalpy kcal/kg	NE value kcal/kg	HI kcal/kg[b]	Partial efficiency %
Crude protein	5.64	2.58	3.06	46
Crude fat	9.46	8.63	0.83	91
Starch[c]	4.21	3.27	0.94	78
Sugars[d]	3.79	2.96	0.83	78
Dietary fiber	4.21	2.29	1.92	54

[a]CVB, 2003. Adapted from Rijnen et al. (2004).
[b]Heat increment.
[c]Enzymatically analyzed starch.
[d]Mono and disaccharides expressed in glucose units.

Table 2.6. Apparent faecal digestibility coefficient of energy and nutrients as affected by physiological stages[a]

	Physiological stage		
	Growing pigs	Adult sows	Change, %[b]
Energy	82.1	85.2	3.8
Organic matter	84.8	87.6	3.3
Crude protein	80.3	84.9	5.7
Crude fat	31.6	37.1	17.4
Crude fiber[c]	50.9	59.5	16.9

[a]Adapted from de Lange and Birkett (2004). Original data derived from Le Goff and Noblet (2001) are means of 77 diets.
[b]Percent increase in apparent digestibility coefficient in adult sows relative to growing pigs.
[c]Determined as organic matter minus the sum of crude protein, crude fat, starch and sugars; where apparent faecal digestibility of starch and sugars are assumed to be 100% at both physiological stages.

Recently, CVB (2003) established an equation that included ileal digestible starch and sugars, which is well adaptable not only to conventional ingredients, but as well to those with extreme nutrient composition (de Lange and Birkett, 2004). Such an equation is also able to take advantage of feed processing and/or exogenous enzyme supplementation both of which are known to influence digestibility and hence the NE content of ingredients and diets.

It would appear that the full benefit of the NE system above other systems would require complete characterization of the effects of processing, enzyme supplementation and any interactive effects of ingredient in compounded diets on nutrient digestibility. In addition, due to the effect of body weight on nutrient digestibility and whole body nutrient deposition rates, a separate NE value ascribed to feed ingredients and diets for different physiological stages would be necessary. Therefore, prediction equations (NE system) and estimated NE values would be applicable only to the particular physiological stage for which it was developed.

2.8.5 Effective Energy

Emmans (1994) proposed the effective energy system, which is suggested to have practical application across various animal species. For monogastrics, it operates based on the following equation:

$$EE = - 0.58 + 0.28 \times MEn - 1.02 \times CP \quad (2.7)$$

where, EE is effective energy in Mcal/kg, MEn is the measured or estimated ME value at zero N retention, and CP is the ingredient CP.

With this equation, the EE values of ingredients can be calculated from data available in feed tables and adapted to growing animals, but is adaptable to pregnant, and lactating animals taking adequate measure to quantify the heat increment associated with those processes.

This system was developed from 43 diets fed to hen (Hartel, 1977) and appears to disregard the physiological differences among monogastric species and physiological stages within species. In addition, the MEn discussed previously (section 2.8.3.1), is a point of controversy.

2.8.6 Feed Units: Danish System

The energy evaluation system of the Scandinavian feed units (FU; an energy value equal to approximately one kg of barley) is based on the physiological energy value of an ingredient or on its ATP equivalents. In 2002, a new system that requires analysis of enzyme digestible ileal dry matter (EDDM) replaced the old feed unit for pig (FUp).

The system is based on the following equation:

FUgp per kg DM = [9.9 × RDCP + 31.7 × RDCF + factor × IDC + 7.0 × FC - 28 × EUDMi]/7375 (2.8)

FUgs per kg DM = [9.9 × RDCP + 26.1 × RDCF + factor × IDC + 9.0 × FC - 28 × EUDMi]/7540 (2.9)

where FUgp is feed unit for growing pig; FUgs is feed unit for gestating sow, RDCF is ideal digestible crude fat, IDC is ileal digestible carbohydrate, FC is fermentable carbohydrate and EUDMi is enzyme undigested ileal dry matter, all g/kg DM.

Compared to the old system, the new system has separate units for growing pigs and gestating sows (FUgp and FUgs, respectively; Table 2.7). With the new system, the energy value of grains has increased, while that of protein supplements has decreased (Table 2.8).

Table 2.7. Comparison of the fundamental changes in the old and new Danish feed evaluation system

	Feed evaluation system		
Relative energy value	Old FUp	New FUgp	New FUgs
Starch	1.0	1.0	1.0
Fermentable carbohydrates	1.0	0.6	0.77
Crude protein	1.24	0.85	0.85
Crude fat	2.20	2.71	2.23
Amino acid digestibility	Faecal	Ileal	Ileal
Amino acid digestibility	Crude protein	Per amino acid	Per amino acid

Source: New feed evaluation system in The National Committee for Pig Production. Annual report (2002).

Table 2.8. Changes in the energy content of barley, wheat, soybean and complete diet in the new FUgp compared to old FUp

Feed type	FUp/kg	FUgp/kg
Barley	0.98	1.05
Wheat	1.10	1.16
Soybean	1.14	0.88
Complete diet, 115 g digestible crude protein	1.04	1.06
Complete diet, 130 g digestible crude protein	1.04	1.04
Complete diet, 145 g digestible crude protein	1.04	1.02

Source: New feed evaluation system in The National Committee for Pig Production. Annual report (2002).

In general, the FU system has the same implication on the energy value of feed ingredients as the NE system and is in fact, a NE system where barley is considered the base unit. In this regard, feed formulation increasingly results in diets

with low crude protein but with an increased supplementation of synthetic aminoacids for finishing pigs and sows. Also, because of the amino acid digestibilities, the new FU system provides a more correct amino acid:energy ratio, and it becomes easier to produce weaned pigs' diets with optimum amino acid composition.

2.8.7 Modelling Approaches to Energy System

The application of models in animal nutrition originated in the last century from the methods developed to evaluate foods and feeds based on their carbohydrate, fat and protein content (Lusk, 1926). In one of the original models, Atwater and Bryant (1900) described the physiological fuel value system in which the energy value of foods was estimated by multiplying the carbohydrate, fat, and protein content by 4.0, 9.0, and 4.0 kcal/g, respectively.

Models represent a link between all the factors that influence performance from which the response to feed intake and economic return can be predicted (Close, 1996). It is becoming increasing clear that mathematical modelling of biological processes is the most efficient means to determine the nutrient requirements of animals and predict the impact of feed intake on growth at a given time or interval (Halas, 2004). Thus, modelling represents the best approach to apply current information to increase the profitability of production.

The main purpose of a model is to show the direction and scope of the response and sensitivity of the production system to a tactical or strategic change (Whittemore, 1993). Its strength lies in its ability to present options in decision-making and guidance to the likely outcome of those decisions rather than giving a single optimum solution.

Existing models are classified as static or dynamic, deterministic or stochastic, empirical or mechanical (Black, 1995). A static model represents the state of a system for just one point in time (e.g. Black, 1971) as opposed to dynamic model that describes time explicitly, typical of computer simulation models. Deterministic models produce only one outcome while stochastic models have a range of possible outcomes indicative of natural variability. Empirical models describe the response of an animal to a given sets of circumstances and usually attempt to develop predictive equations from experimental data using biometric procedures (Close, 1996). Usually, the underlying mechanisms are not considered in empirical models, while mechanistic models deal with the metabolic processes within the animal either at tissue, cellular or molecular levels. As a result, mechanistic models are flexible and adapted to predicting responses and requirements over a wide range of conditions.

Model development requires (and inspires) a great deal of research to generate information about the system to be modeled both on the physiology of growth and the responses of different genotypes and gender to diet and environmental factors (Baldwin and Sainz, 1995; Black, 1995).

Birkett and de Lange (2001) presented a mechanistic model that included a deterministic and static representation of nutrient and metabolite flow at the whole animal level. It incorporate the biochemical and biological processes involved in nutrient transformation and the generation of ATP. It is suggested to improve the accuracy of predicting the energetic efficiency of utilizing nutrient intake and useful to generate predicted values for the NE value of a diet at a defined metabolic state. Finally, the model is suggested to overcome the limitations of empirical NE systems.

Noblet and van Milgen (2004) in their review on the effect of pig body weight and energy evaluation systems concluded that improvements in feed evaluation systems would require more mechanistic approaches based on ATP generating nutrients used to meet the animal's requirement for protein and lipid synthesis. Consequently, modelling approaches are crucial for describing both the digestive and metabolic utilization of nutrients with absolute energy values of feed becoming an auxiliary variable of the model.

2.9 Relationship between Dietary Energy Concentration and Daily Energy Intake

When other constraints (e.g. environmental, social and animal) discussed in detail by Nyachoti et al. (2004) are absent, energy concentration represents the greatest determinant of voluntary feed intake (NRC, 1987; Lewis, 2001). Because the pig will often eat to meet its energy requirement, the response of ad libitum fed growing pigs to dietary energy concentration is adjustment in feed consumption (Campbell and Taverner, 1986b; Kyriazakis and Emmans, 1995). However, recent

studies suggest that at low energy densities, energy intake, subsequent growth performance and carcass quality may be influenced (Chadd and Cole, 1999; Smith et al., 1999b; De la Llata et al., 2001). The magnitude of the reduction in feed intake will ultimately determine the effect on energy intake.

As indicated by Henry (1985) and Kyriazakis and Emmans (1999), when energy is not the first limiting resource, feed intake will be modulated to meet the first limiting nutrient. For instance, the amino acid:energy ratio around the optimum level for growth will influence feed intake. A high supply of protein produces a self-limitation of feed intake, resulting in carcass leanness while a marginal deficiency in the limiting amino acid or protein supply results in a compensatory increase in feed intake to meet the requirement and a consequential increase in carcass fatness (Henry, 1985). Kyriazakis and Emmans (1992b) demonstrated that pigs would consume extra energy when given access to a diet that is low in protein and consume extra protein in diets relatively low in energy. In the first instance, the extra energy is deposited as fat, while the extra protein is deaminated and urea is eliminated in the urine.

2.9.1 Physical Limitations in Feed intake in Weaned Pigs

Before the steady genetic improvement for lean growth, excessive LD in pig carcass was the result of excessive feed intake (Henry, 1987). Approaches aimed at reducing excessive feed intake used energy dilution by the incorporation of fiber to reduce energy intake. It may be possible that at a certain dietary dilution (e.g. Campbell et al., 1975; Whittemore et al., 2001), as energy concentration decreases, energy intake declines, attributable to a possible progressive limitation of gut capacity

before the energy requirement is achieved. In this context, it is generally assumed that the young pig up to about 70 kg BW exhibits a limited physical capacity to ingest nutrients (Quiniou et al., 2000), and will respond to increases in dietary energy concentration with increase in growth rate during an “energy-dependent” phase of growth. This phase is believed to extend up to 90 kg BW; however the greatest limitation to ingest nutrients occurs in weaned pigs up to about 25 kg BW (Campbell and Dunkin, 1983a; Campbell, 1987; Whittemore, 1993). Such a limitation has been suggested to prevent the weaned pig from achieving its genetic capacity for growth, especially PD (Van Lunen and Cole, 1998).

2.9.2 Linear Increase in Energy Intake with Increasing Energy Concentration in Weaned Pigs

Unfortunately, there is little data available on the actual energy intake in studies conducted to evaluate the response of the weaned pig to dietary energy concentration (e.g. Van Lunen and Cole, 1998). This would involve using determined as opposed to formulated energy concentration. In one such study, Levesque (2002) found a linear increase in DE intake in weaned pigs growing from 7 to 20 kg BW when fed diets containing 3.18 to 3.59 Mcal DE/kg. Reis de Souza et al. (2000) evaluated the effect of increasing dietary GE content from 3.84 to 4.27 Mcal/kg on the growth and energy utilization of weaned pigs from 7 to 25 kg BW. The determined DE concentration increased from 3.24 to 3.50 Mcal/kg but had no effect on feed intake, whereas DE intake increased approximately 5% from 2.22 to 2.34 Mcal/d. Nam and Aherne (1994) investigated the performance of pigs from 9 to 26 kg

BW to increasing lysine:DE ratio at three energy densities (3.18 to 3.51 Mcal DE/kg). When calculated based on the reported feed intake and determined DE concentrations, a linear increase in DE intake was observed.

These results are in agreement with the suggestion by the NRC (1987) that weaned pigs may respond to increasing dietary energy concentration with an increase in energy intake due to the inability to fully regulate intake to match the requirement for tissue growth.

Whittemore et al. (2001) studied the dilution of diets from 3.20 to 2.56 Mcal DE/kg by incremental addition of sugar beet pulp (SBP) at 0, 50 and 70%. Diets were fed to pigs from 12 to 18 kg BW over a two wk period. Feed intake of pigs fed the 70% SBP diet compared to the control declined by 58% in the first wk of the trial, but intake was equalized in the last wk with all diets. The calculated energy intake declined by 66% in the first wk (0 vs. 70% SBP diet) and 19% in the second wk. This indicates that weaned pigs become adapted to diets with low energy concentration over time. The adaptation is believed to be the result of an enlargement of some of the sections of the GIT with time to adjust to diets with low energy density (Kyriazakis and Emmans, 1995). However, the adaptation in feed intake is not sufficient to achieve optimal energy intake for growth. Nevertheless, only at extreme energy dilutions such as that reported by Campbell et al. (1975) and Whittemore et al. (2001), would young pigs fail to achieve energy intake to match their requirement for maintenance and growth.

In the studies by Van Lunen and Cole (1998), Reis de Souza et al. (2000) and Levesque (2002), growth rate was not improved by increasing dietary energy concentration and would suggest that energy intake was not limiting in the low energy diets fed in those studies.

2.10 Conclusions and Implications

Digestive and metabolic utilization of feed ingredients yield a continuous supply of energy to the pig for maintenance and productive purposes. Different systems have been used to quantitatively describe the energy values of feed ingredients and the hierarchy between feed ingredients is influenced by energy systems. Irrespective of the energy system, due to the effects of BW on energy utilization, it is important that values are adapted to the physiological stage from which it was determined. Energy intake is linearly related to growth, protein and lipid deposition. Although there is an increased need to deposit lipid with increasing BW, there is no evidence of an intrinsic limitation to PD in selected modern genotypes. In the weaned pigs, dietary energy dilution reduces energy intake due to the inability to fully compensate for the dilution, whereas benefits of increased energy intake associated with increased energy concentration on growth are unclear. There is a great need to adequately predict the growth and nutrient deposition of pigs in response to dietary energy supply. In the long run, mathematical modelling approaches that describe both the digestive and metabolic utilization of nutrients are essential. This requires further development to accurately characterize feed and feed ingredients and transformations within the body to yield energy.

3. THE EFFECT OF DIETARY ENERGY CONCENTRATION AND TOTAL LYSINE/DIGESTIBLE ENERGY RATIO ON THE GROWTH PERFORMANCE OF WEANED PIGS

3.1 Introduction

Advances within the last decade in swine genetics and management, combined with higher expectations of animal performance, emphasize the need to carefully scrutinize existing feeding and management programs to ensure they are, in fact, optimal. From a nutritional perspective, the increased lean growth rate of hybrid pigs (Van Lunen and Cole, 1998) and/or reduced voluntary feed intake (Van Lunen and Cole, 2001) suggests that nutrient requirements defined previously under different management systems may no longer suffice.

It is generally accepted that growth performance in young pigs is limited by feed (energy) intake (Van Lunen and Cole, 1998). Expressing amino acid requirements as a ratio to energy will ensure that requirements are met irrespective of changing dietary energy concentration (Smith et al., 1999a). In addition, the relationship between energy intake and protein deposition is linear in pigs weighing less than 90 kg (Campbell and Taverner, 1988; Rao and McCracken, 1991; Bikker, 1994). It is therefore essential that lysine requirements for this category of pigs be

expressed in relation to dietary energy concentration (Nam and Aherne, 1994; Van Lunen and Cole, 1998).

Several investigations (e.g. Gatel et al., 1992; Nam and Aherne, 1994; Van Lunen and Cole, 1998) on the lysine requirement and the optimum total lysine:DE ratio for weaned pigs have yielded variable results. Existing recommendations range from 3.14 (Campbell and Taverner, 1986a) to 5.02 g/Mcal DE (Van Lunen and Cole, 1998) for weaned pigs up to 25 kg BW. These discrepancies warrant careful re-evaluation of the optimum dietary lysine:DE ratio. The objective of the present study was to determine the optimum total lysine:DE ratio for the weaned pig from 7.5 to 23 kg, in terms of growth performance and plasma urea nitrogen concentration. Two levels of DE were used to determine if there was an interaction between DE and the determined lysine requirement.

3.2 Materials and Methods

Animal and Procedures

A growth experiment was conducted with the offspring of C-22 females × 337 sires (PIC Canada Ltd, Airdrie, AB). At weaning, pigs were placed in all-in-all-out nursery rooms containing 24 pens (1.27 × 1.04 m) with fully-slatted floors. Each pen was equipped with a nipple drinker and an adjustable multiple-space dry feeder. Each room had automatic light timers (12-light:12-dark cycle) and integrated controllers (Model PEC; Phason, Winnipeg, MB) regulating heating and ventilation systems. Room temperature was initially set at 30ºC and gradually decreased by 1.5ºC/wk.

The experiment was conducted in three replicates of 20 pens and 80 pigs each per nursery room for a total of 60 pens and 240 pigs. At weaning (20.0 ± 1.7 d and 6.5 ± 0.9 kg; mean ± SD; age and weaning weight, respectively), all pigs were transferred to nursery rooms and allowed 7 days to acclimatize to weaning, the environment and feed. Piglets were given ad libitum access to a pelleted commercial phase-1 starter diet (Appendix A; Ultrawean 21, Co-op Feeds, Saskatoon, SK) for the first 4 days post-weaning followed by a pelleted phase-2 starter diet (Appendix B; GI MAX 21, Co-op Feeds, Saskatoon, SK) for the next 3 days. Selected pigs were blocked according to body weight and gender, and were randomly assigned to pen within each weight block of 4 pigs each (2 barrows and 2 gilts). Within rooms, a 5-pen block was assigned to either the low DE (LDE) or high DE (HDE) diets and pens were randomly assigned to treatments (Appendix C). Piglets were given ad libitum access to one of the dry mash experimental diets starting on d 8 postweaning when they were 28 days of age and remained on test for the 28-day experimental period.

The University Committee on Animal Care and Supply at the University of Saskatchewan (UCACS) approved the animal care protocol (#19960029) for adherence to guidelines of the Canadian Council of Animal Care (1993).

Treatments and Diets

The experiment utilized a total of 10 dietary treatments arranged in a 2 × 5 factorial with two levels of DE (3.4 and 3.6 Mcal/kg; LDE and HDE, respectively) and five levels of total lysine:DE ratio (3.7, 4.0, 4.3, 4.6, and 4.9 g/Mcal). Diets were formulated based on total lysine due to the uncertainty of the digestible amino acid contents of specialized starter diet ingredients.

The experimental diets were formulated with wheat, barley, fish meal, soybean meal, soy protein concentrate, spray dried plasma, spray dried whey and canola oil (Table 3.1). Fish meal, soybean meal, soy protein concentrate, spray dried plasma, and spray dried whey were assayed for protein and amino acid composition prior to diet formulation (Degussa Corporation, Amino acid Lab, Allendale, NJ). Diets were formulated to achieve a similar proportion of lysine and other amino acids coming from high lysine ingredients, such that soybean meal, fish meal, soy protein concentrate and spray dried plasma increased proportionately as the dietary lysine concentration increased (Table 3.1). Crystalline amino acids were then supplemented as required. All diets met the NRC (1998) requirements for this category of pig with the exception of lysine; the amino acid profile of each diet was adjusted based on ideal amino acid ratio (Table 3.2; NRC, 1998).

Table 3.1. Ingredient composition of the experimental diets, as-fed basis[a]

DE, Mcal/kg	3.4					3.6				
Lysine:DE, g/Mcal	3.7	4.0	4.3	4.6	4.9	3.7	4.0	4.3	4.6	4.9
Wheat	60.30	58.58	53.93	48.86	43.93	55.81	54.70	53.28	51.75	49.98
Barley	1.68	1.89	4.98	8.44	11.72	-	-	-	-	-
Soybean meal	7.30	7.90	8.50	9.10	9.85	8.60	9.30	9.90	10.60	11.30
Menhaden fish meal	6.80	7.40	7.90	8.50	9.00	7.50	8.10	8.70	9.30	9.80
Soy protein concentrate[b]	3.30	3.50	3.80	4.10	4.30	3.60	3.90	4.20	4.50	4.80
Spray dried whey	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
Lactose	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00	10.00
Spray dried plasma[c]	2.20	2.40	2.60	2.80	3.00	2.40	2.60	2.80	3.00	3.20
Canola oil	0.50	0.50	0.50	0.50	0.50	4.26	3.68	3.42	3.26	3.35
Dicalcium phosphate	0.85	0.74	0.64	0.53	0.43	0.78	0.65	0.54	0.42	0.32
Limestone	0.49	0.46	0.43	0.39	0.36	0.44	0.41	0.38	0.34	0.32
Salt	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30	0.30
Mineral premix[d]	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Vitamin premix[e]	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Choline chloride	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.00	0.05	0.00
l-lysine HCl	0.134	0.176	0.219	0.256	0.311	0.158	0.189	0.225	0.271	0.311
l-threonine	-	0.013	0.038	0.061	0.093	0.010	0.029	0.051	0.077	0.101
dl-methionine	-	-	0.0006	0.018	0.042	-	0.0023	0.013	0.026	0.053
l-tryptophan	-	-	-	0.004	0.015	-	-	0.0006	0.0096	0.018
LS-20[f]	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10

[a]Formulated DE concentration were based on NRC (1998) value of each ingredient.
[b]Soy protein concenetrate, PROFINE E.
[c]Spray dried plasma, AP 920.
[d]Provided per kg of diet: Zn, 100 mg as zinc sulfate; Fe, 80 mg as ferrous sulfate; Cu, 50 mg as copper sulfate; Mn, 25 mg as manganous sulphate; I, 0.50 mg as calcium iodate; Se, 0.10 mg as sodium selenite.
[e]Provided per kg of diet: vitamin A, 8,250 IU; vitamin D_3, 825 IU; vitamin E, 40 IU; niacin, 35 mg; D-pantothenic acid, 15 mg; riboflavin, 5 mg; menadione, 4 mg; folic acid, 2 mg; thiamine, 1 mg; D-biotin, 0.2 mg; vitamin B_{12}, 25 µg.
[f]Includes lincomycin at 22 g/kg and spectomycin at 22 g/kg product (BioAgrimix, Mitchell, ON).

Table 3.2. Calculated and analyzed nutrient contents of the experimental diets, as-fed basis[a]

DE, Mcal/kg[b]	3.4					3.6				
Lysine:DE, g/Mcal	3.7	4.0	4.3	4.6	4.9	3.7	4.0	4.3	4.6	4.9
Calculated										
ME, Mcal/kg[b]	3.20	3.20	3.20	3.19	3.19	3.40	3.38	3.38	3.37	3.38
Crude protein, %	20.72	21.51	22.22	22.99	23.74	21.37	22.33	23.21	24.15	25.00
Total lysine, %	1.25	1.35	1.45	1.55	1.66	1.35	1.45	1.55	1.66	1.76
Crude fat, %	2.25	2.28	2.29	2.32	2.34	5.95	5.41	5.23	5.04	5.15
Analyzed[c]										
GE, Mcal/kg	3.95	3.95	3.97	3.94	3.97	4.16	4.15	4.10	4.17	4.15
Crude protein, %	20.75	21.88	23.00	23.88	24.44	22.25	22.88	23.75	25.06	25.63
Crude fat, %	2.49	2.87	2.96	2.71	2.78	5.61	6.05	5.81	5.74	5.71
Total lysine, %	1.18	1.34	1.47	1.59	1.66	1.35	1.43	1.52	1.66	1.68
Total methionine, %	0.37	0.40	0.42	0.46	0.49	0.41	0.43	0.46	0.49	0.48
Total sulphur amino acid, %	0.78	0.83	0.89	0.93	0.97	0.84	0.87	0.91	0.97	0.93
Total threonine, %	0.79	0.86	0.94	1.00	1.08	0.88	0.95	0.99	1.08	1.08
Total isoleucine, %	0.78	0.84	0.88	0.95	0.95	0.88	0.90	0.90	0.98	0.93
Total leucine, %	1.46	1.56	1.65	1.73	1.76	1.59	1.64	1.68	1.82	1.76
Total valine, %	0.98	1.06	1.11	1.19	1.19	1.10	1.14	1.10	1.23	1.14

[a]Calculated crude protein and lysine content were based on pre-assayed value of fish meal, soybean meal, soy protein concentrate, spray dried plasma, and spray dried whey.
[b]Formulated DE and ME concentration were based on NRC (1998) value of each ingredient.
[c]Diets were analyzed for crude protein and amino acid content according to Llames and Fontaine (1994) (Degussa Corporation, Amino acid Lab, Allendale, NJ).

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Data and Sample Collection

Pigs were individually weighed on d 0 (27.0 ± 1.7 d and 7.5 ± 1.1 kg (mean ± SD; age and initial weight, respectively) and weekly thereafter (d 7, 14, 21, and 28). On each weigh day, feed consumption was also measured. These data were used to calculate the average daily gain (ADG), average daily feed intake (ADFI), and feed efficiency.

Feed samples were taken at the time of feeding, pooled per diet and kept frozen at -20°C until required for analysis. Freshly voided faeces were collected from each pen using the grab method over three days (d 21 to 23) and pooled per pen. Samples collected were kept frozen at -20°C until freeze-drying to a constant weight and analyzed for DM, nitrogen and energy content. Blood samples were collected on d 28 from one randomly selected gilt and barrow per pen via cranial vena cava venipuncture into vacutainer tubes containing 143 USP units of sodium heparin. Plasma was harvested after spinning at 700 × *g* for 15 minutes (Model Centrific 228; Fisher, Nepean, Ontario) and stored at –20ºC for later assay of plasma urea nitrogen (PUN) concentration.

Chemical Analyses

Feed and freeze-dried faecal samples were prepared for chemical analyses by grinding through a 1-mm screen in a Retsch mill (Retsch Model ZM1; Brinkman Instrument of Canada Ltd., Rexdale, ON).

The acid insoluble ash content of the diet was used as an indigestible marker and measured in feed and faeces (McCarthy et al., 1974) to determine the apparent faecal digestibility of DM, energy and crude protein. Pure celite standard samples were assayed to confirm the accuracy of the analytical procedure, and a recovery of 99.9 ± 0.01% was attained.

The moisture content of feed and freeze-dried faecal samples was determined by drying at 135ºC in an airflow-type oven for 2 h (Method 930.15; AOAC, 1990). Nitrogen in feed and faecal samples was measured by combustion (Method 968.06; AOAC, 1990) using a Leco protein/nitrogen determinator (Model FP-528, Leco Corp., St. Joseph, MI). Calibration was conducted with an EDTA standard (nitrogen content 9.57 ± 0.02%; Leco Corp., St. Joseph, MI). On analysis, the nitrogen content of the EDTA standard was 9.57 ± 0.01%. Crude protein was expressed as nitrogen × 6.25. Gross energy was measured in an adiabatic bomb calorimeter (Model 1281; Parr Instruments, Moline, IL). Benzoic acid (6318 kcal/kg; Parr Instruments, Moline, IL) was used as the standard for calibration and was determined to be 6319 ± 1 kcal/kg at assay. Plasma urea nitrogen (PUN) concentration was determined using a commercial enzyme kit (Sigma-Aldrich, Oakville, ON) as described by Fawcett and Scott (1960). Diets were analyzed for crude protein and amino acid content by a commercial laboratory (Degussa Corporation, Amino acid Lab, Allendale, NJ) according to Llames and Fontaine (1994).

Calculations and Statistical Analyses

Apparent digestibility coefficients of crude protein and energy were determined using the following equation:

$$D_{ADN}\% = 100\% - [(I_D \times A_F)/(A_D \times I_F) \times 100] \quad (3.1)$$

where D_{ADN} is apparent digestibility coefficient of crude protein and energy, I_D is percent index marker concentration in the assay diet, A_F is percent nutrient concentration in faeces, A_D is percent nutrient concentration in the assay diet, I_F is percent index marker concentration in faeces, all on DM basis.

The apparent digestibility coefficient of DM was determined using the following equation:

$$D_{ADM}\% = 100\% - [(I_D/I_F) \times 100] \quad (3.2)$$

where D_{ADM} is apparent digestibility coefficient of DM.

Digestible energy intake was calculated from the determined DE concentration as fed (Mcal/kg) × ADFI (kg/d).

Energy efficiency was calculated as DE intake/ADG

where DE intake is in Mcal/d and ADG is in kg/d.

Data were analyzed using the MIXED procedure of SAS (SAS Institute Inc., 1996) with pen as the experimental unit. Performance data were analyzed using repeated measures with weekly data and appropriate covariance structures (Littell et al., 1998; Wang and Goonewardene, 2004). The statistical model included the main effect of DE, lysine:DE ratio, day, and the following interactions: DE × lysine:DE ratio, day × DE, and day × lysine:DE ratio. Initial BW on d 0 of the experiment was used as a covariate for performance data. Orthogonal polynomial contrasts (linear and

quadratic) were used to partition variation associated with lysine:DE ratio (Steel and Torrie, 1980). Also, PUN and performance data were analyzed with ADG, ADFI and gain:feed ratio for periods (d 0 to 14, d 15 to 28, and d 0 to 28) as discrete dependent variables. Upon detecting a significant linear and quadratic response ($P < 0.10$) for a dependent variable without interaction between DE and lysine:DE ratio ($P > 0.10$), a solution statement was used to generate parameters estimate. When appropriate, the optimum lysine:DE ratio was calculated from the inflection point using the following equation:

$$x = -b/2c \qquad (3.3)$$

where x is the optimum lysine:DE ratio, b and c are the parameter estimate of the linear and quadratic effect of increasing lysine:DE ratios.

Since breakpoints are not a component of curvilinear response lines, an arbitrary point (e.g. 90 or 95% of the upper or lower asymptotic value) has to be selected. The present optimum values were determined using 95% of the upper asymptotic values (Coma et al. 1995).

In addition, non-linear regressions (exponential and linear-plateau models) were fitted to the experimental data using PROC NLIN procedure within SAS (SAS Institute Inc., 1996). The model with the minimum residual sum of square and the highest r-square statistics were selected to determine the optimum level. Significance was defined as $P < 0.05$ unless otherwise noted.

3.3 Results

Diets

Chemical analyses confirmed that the dietary lysine content was within analytical tolerance of formulated values (Table 3.2); therefore statistical analyses were based on formulated values.

Performance Parameters

The effect of lysine and the lysine:DE ratio on final body weight as well as on ADG, ADFI and gain:feed for the entire experimental period are shown in Table 3.3. Body weight was not affected by DE concentration ($P > 0.05$) but was increased quadratically with increasing lysine:DE ratios ($P < 0.05$). Average daily gain was not affected by DE concentration but was increased with increasing lysine:DE ratios (linear, $P < 0.05$). The ADFI was lower with HDE ($P < 0.05$), but was not affected by lysine:DE ratio ($P > 0.05$). Gain:feed ratio was increased with HDE ($P < 0.05$), as well as lysine:DE ratio (linear, $P < 0.05$). There was no interaction between lysine:DE ratio and DE concentration on ADG, ADFI and gain:feed ratio ($P > 0.05$).

The results for ADG, ADFI and gain:feed ratio by period (d 0 to 14 and d 15 to 28) are shown in Table 3.4. Average daily gain was not affected by DE concentration on d 0 to 14 ($P > 0.05$) but tended to be greater in HDE for d 15 to 28 ($P < 0.10$). Average daily gain was increased with increasing lysine:DE ratios on d 0 to 14 (quadratic, $P < 0.05$) but not on d 15 to 28 ($P > 0.10$). Average daily feed intake was decreased with DE concentration on d 0 to 14 ($P < 0.05$) but not on d 15 to 28. In addition, ADFI was not affected by lysine:DE ratios for either period ($P >$

0.05). Gain:feed ratio was not affected by DE concentration on d 0 to 14 ($P > 0.05$) but was on d 15 to 28 ($P < 0.05$). Gain:feed ratio increased linearly ($P < 0.05$) with increased lysine:DE ratios on d 0 to 14 but was not affected on d 15 to 28 ($P > 0.05$). There was no interaction between lysine:DE ratio and DE concentration on ADG, ADFI and gain:feed ratio for both periods ($P > 0.05$).

Table 3.3. The effects of digestible energy concentration and lysine:DE ratio on final body weight, growth rate, feed intake and feed efficiency of weaned pigs (d 0 to 28)[a]

		Initial Body weight, kg	Final Body weight, kg	ADG, g/d	ADFI, g/d	Gain/ feed ratio, g/g
DE, Mcal/kg						
3.4		7.48	22.43	538	857	0.649
3.6		7.46	22.57	540	825	0.673
SEM		0.10	0.19	7	9	0.008
Lysine:DE ratio, g/Mcal						
3.7		7.47	21.87	515	842	0.619
4.0		7.47	22.15	529	857	0.625
4.3		7.46	22.80	548	850	0.668
4.6		7.49	22.99	554	839	0.695
4.9		7.48	22.68	545	817	0.697
SEM		0.15	0.31	11	14	0.012
DE × Lysine:DE ratio						
3.4	3.7	7.47	21.74	510	866	0.606
	4.0	7.47	22.02	529	862	0.609
	4.3	7.48	22.71	544	880	0.644
	4.6	7.49	22.73	544	831	0.687
	4.9	7.49	22.94	556	847	0.701
3.6	3.7	7.46	22.01	519	817	0.633
	4.0	7.46	22.28	529	852	0.642
	4.3	7.43	22.89	551	819	0.693
	4.6	7.49	23.26	563	847	0.702
	4.9	7.46	22.43	534	787	0.693
SEM		0.07	0.43	16	20	0.017
P values						
Day			0.0001	0.0001	0.0001	0.0001
DE			0.7973	0.7572	0.0111	0.0338
Lysine:DE ratio			0.0003	0.0548	0.3534	0.0001
Linear			0.0002	0.0065	0.1391	0.0001
Quadratic			0.0146	0.1597	0.1476	0.5955
DE × Lysine:DE ratio			0.2088	0.7688	0.2234	0.5537
DE × Day			0.7886	0.1668	0.7446	0.2150
Lysine:DE ratio × Day			0.9914	0.5315	0.9145	0.0209

[a]The experiment included a total of 60 pens and 240 pigs, from 27 to 55 days of age. Thus, there were 30 pens per DE level, 12 pens per lysine:DE ratio and 6 pens per DE × lysine:DE ratio combination. Data were analyzed with repeated measures. All data were analyzed with initial BW as a covariate. The covariate was significant ($P < 0.05$) for final body weight, ADG, and ADFI but not for gain:feed ratio ($P > 0.05$).

Table 3.4. The effects of digestible energy concentration and lysine:DE ratio on growth rate, feed intake and feed efficiency of weaned pigs on d 0 to 14 and d 15 to 28[a]

		ADG, g/d		ADFI, g/d		Gain/ feed ratio, g/g	
		d 0 to 14	d 15 to 28	d 0 to 14	d 15 to 28	d 0 to 14	d 15 to 28
DE, Mcal/kg							
3.4		390	684	556	1158	0.706	0.594
3.6		376	703	513	1137	0.726	0.621
SEM		36	8	47	26	0.010	0.012
Lysine:DE ratio, g/Mcal							
3.7		342	687	533	1150	0.635	0.600
4.0		375	687	549	1165	0.681	0.592
4.3		396	700	548	1152	0.726	0.609
4.6		419	689	544	1134	0.769	0.608
4.9		386	705	499	1136	0.769	0.629
SEM		37	13	48	30	0.016	0.016
DE × Lysine:DE ratio							
3.4	3.7	360	660	568	1165	0.637	0.567
	4.0	370	695	569	1155	0.648	0.606
	4.3	391	696	567	1194	0.695	0.584
	4.6	409	679	545	1116	0.751	0.609
	4.9	422	689	533	1161	0.797	0.605
3.6	3.7	324	715	499	1135	0.632	0.634
	4.0	379	679	529	1176	0.715	0.578
	4.3	401	703	528	1111	0.757	0.634
	4.6	428	698	543	1151	0.786	0.608
	4.9	349	720	465	1110	0.742	0.653
SEM		40	18	51	35	0.023	0.022
P values							
DE		0.2610	0.0929	0.0035	0.1952	0.1689	0.0412
Lysine:DE ratio		0.0062	0.7981	0.1533	0.7421	0.0001	0.4675
Linear		0.0047	0.3673	0.1428	0.3094	0.0001	0.1121
Quadratic		0.0162	0.8455	0.0414	0.6456	0.1353	0.4483
DE × Lysine:DE ratio		0.1175	0.3416	0.5728	0.1479	0.0635	0.1271

[a]The experiment included a total of 60 pens and 240 pigs, from 27 to 55 days of age. Thus, there were 30 pens per DE level, 12 pens per lysine:DE ratio and 6 pens per DE × lysine:DE ratio combination. Data were analyzed with performance data of each period as a discrete dependent variable with initial BW as a covariate. The covariate was significant ($P < 0.05$) for ADG and ADFI on d 0 to 14 and d 15 to 28 but not significant ($P > 0.05$) for gain:feed ratio, both periods.

The effect of treatment on total lysine and digestible energy intake, energy efficiency for the entire experimental period as well as PUN concentration are shown in Table 3.5. Total lysine intake was not affected by DE concentration ($P > 0.05$) but tended to increase quadratically ($P < 0.10$) with increased lysine:DE ratios. Digestible energy intake was greater in the HDE diets ($P < 0.05$). However, a significant interaction ($P < 0.05$) was detected between DE concentration and lysine:DE ratios for DE intake.

The energy cost of BW gain (calculated as Mcal DE intake/kg weight gain) was greater with HDE ($P < 0.05$) and decreased quadratically with increased lysine:DE ratios. Plasma urea nitrogen concentrations were not affected by DE concentration but increased with increased lysine:DE ratios (linear, $P < 0.01$; Table 3.5). There was no effect of gender on PUN concentration ($P > 0.10$).

Apparent digestibility of DM, crude protein and energy were greater in the HDE diets ($P < 0.05$; Table 3.6). However, significant DE concentration × lysine:DE ratio interactions ($P < 0.01$) were observed for digestibility of DM, crude protein and energy ($P < 0.05$). The HDE resulted in lower apparent DM, crude protein and energy digestibility at the lowest lysine:DE ratio than the LDE. This trend was reversed at the higher lysine:DE ratios. Apparent energy and CP digestibility coefficients ranged from 80.9 to 87.9 and 79.7 to 85.8%, respectively. Overall, the average determined DE concentrations were 3.31 and 3.56 Mcal/kg in LDE and HDE, respectively (Table 3.6), and thus were quite close to expected.

Table 3.5. The effects of digestible energy concentration and lysine:DE ratio on lysine, energy intake, energy efficiency (d 0 to 28) and plasma urea nitrogen (PUN) concentrations in weaned pigs[a]

		Total lysine intake, g/d[b]	DE intake, Mcal/d[c]	Energy efficiency, Mcal/kg[d]	PUN, mg/dl[e]
DE, Mcal/kg					
3.4		12.41	3.47	6.40	10.53
3.6		12.58	3.53	6.59	11.41
SEM		0.21	0.04	0.08	0.93
Lysine:DE ratio, g/Mcal					
3.7		10.62	3.51	6.88	9.81
4.0		11.86	3.65	6.99	8.37
4.3		12.68	3.45	6.21	10.80
4.6		13.65	3.44	6.06	11.93
4.9		13.65	3.44	6.34	12.93
SEM		0.33	0.06	0.13	1.06
DE × Lysine:DE ratio					
3.4	3.7	10.22	3.63	7.04	9.68
	4.0	11.55	3.58	6.95	8.89
	4.3	12.95	3.37	6.07	10.07
	4.6	13.23	3.24	5.78	12.47
	4.9	14.08	3.52	6.17	11.54
3.6	3.7	11.02	3.39	6.72	9.93
	4.0	12.18	3.71	7.02	9.85
	4.3	12.42	3.53	6.35	11.53
	4.6	14.08	3.64	6.33	11.38
	4.9	13.22	3.35	6.51	14.33
SEM		0.47	0.08	0.19	1.25
P values					
Day		0.0001	0.0001	0.0001	-
DE		0.5637	0.0268	0.0172	0.1477
Lysine:DE ratio		0.0001	0.0799	0.0001	0.0011
Linear		0.0001	0.0327	0.0001	0.0001
Quadratic		0.0701	0.8023	0.0378	0.3097
DE × lysine:DE ratio		0.2328	0.0190	0.3389	0.3112
DE × Day		0.0253	0.0230	0.0222	-
Lysine:DE ratio × Day		0.0001	0.8153	0.0973	-

[a]The experiment included a total of 60 pens and 240 pigs, from 27 to 55 days of age. Thus, there were 30 pens per DE level, 12 pens per lysine:DE ratio and 6 pens per DE × lysine:DE ratio combination. Data were analyzed with repeated measures, except for PUN.
[b]Total lysine intake was calculated from assayed dietary lysine content (g/kg) and weekly ADFI.
[c]DE intake was calculated from the determined DE concentration as fed and weekly ADFI.
[d]Energy efficiency was calculated as DE intake/ADG.
[e]Blood samples were collected on d 28, n = 6 gilts and 6 barrows per DE × lysine:DE ratio combination.

Table 3.6. The effects of digestible energy concentration and lysine:DE ratio on apparent nutrient digestibility and determined DE concentration of experimental diets fed to weaned pigs[a]

		Apparent digestibility coefficients, %[b]			DE,
		DM	CP	Energy	Mcal/kg[c]
DE, Mcal/kg					
3.4		85.1	82.6	83.7	3.31
3.6		86.8	84.6	85.9	3.56
SEM		0.5	0.5	0.5	0.02
Lysine:DE ratio, g/Mcal					
3.7		86.7	84.2	85.6	3.47
4.0		87.2	84.6	86.3	3.50
4.3		84.5	81.8	83.1	3.36
4.6		84.9	82.9	83.7	3.39
4.9		86.5	84.6	85.4	3.47
SEM		0.6	0.6	0.6	0.02
DE × Lysine:DE ratio					
3.4	3.7	87.3	85.2	86.3	3.41
	4.0	86.4	83.4	85.3	3.37
	4.3	82.6	79.7	80.9	3.22
	4.6	83.4	81.0	81.7	3.22
	4.9	85.6	83.7	84.5	3.36
3.6	3.7	86.0	83.1	85.0	3.53
	4.0	87.9	85.8	87.2	3.62
	4.3	86.3	83.9	85.3	3.50
	4.6	86.4	84.9	85.7	3.57
	4.9	87.5	85.5	86.4	3.59
SEM		0.7	0.9	0.8	0.03
P values					
DE		0.0001	0.0003	0.0001	0.0001
Lysine:DE ratio		0.0001	0.0044	0.0001	0.0001
Linear		0.0829	0.6514	0.0488	0.0993
Quadratic		0.0023	0.0053	0.0015	0.0004
DE × lysine:DE ratio		0.0040	0.0027	0.0007	0.0031

[a]The experiment included a total of 60 pens and 240 pigs, from 27 to 55 days of age. Thus, there were 30 pens per DE level, 12 pens per lysine:DE ratio and 6 pens per DE × lysine:DE ratio combination.

[b]Apparent digestibility coefficients were based on analyses conducted on individual pen's faecal grab samples collected over three consecutive days (d 13 to 15). Acid insoluble ash in feed (mean = 0.21% as fed, in the 10 diets) and faeces was used as index marker.

[c]Determined DE concentration as fed.

3.4 Discussion

Improvements in genetic growth potential, health status and management suggest that existing recommendations for lysine:DE ratio may no longer suffice for optimal performance. In addition, a large disparity exists in the optimum lysine:DE ratio for weaned pigs presented in the literature. An accurate definition of the optimal amino acid/energy ratio is important as body lipid content increases and the efficiency of nitrogen utilization diminishes rapidly below the optimum level (Bikker, 1994).

The growth rate (mean = 538 g/d) observed in the present study was within the range of 410 to 640 g/d reported by Van Lunen and Cole (1998) in weaned pigs growing from 9.1 to 25.4 kg BW when fed diets formulated at two levels of DE concentration (3.4 and 3.9 Mcal/kg) and five levels of increasing total lysine:DE ratios from 2.5 to 5.9 g/Mcal. The feed intake in the present study (mean, 841 g/d) and Van Lunen and Cole (1998) were comparable (mean = 836 g/d). Nam and Aherne (1994) reported ADG that ranged from 550 to 621 g/d with pigs between 9.1 to 25.7 kg BW when fed diets formulated at 3 levels of DE concentration (3.18, 3.35 and 3.51 Mcal/kg) and four levels of increasing total lysine:DE ratios from 2.9 to 4.2 g/Mcal. Their study reported a greater feed intake (mean = 1045 g/d) than observed in the present study. The greater feed intake observed by Nam and Aherne (1994) may be related to the lower levels of DE utilized in the study, and conforms to the established relationship between increased DE concentration and voluntary feed intake (NRC, 1987). It has also been suggested that genetic selection has resulted in pigs with reduced voluntary feed intake capacity (Van Lunen and Cole, 2001); this may explain some of the differences in feed intake observed in the present study

compare to Nam and Aherne (1994). This further demonstrates the need for re-evaluation of amino acid requirements for optimal performance.

Effect of DE Concentration

In the present study, ADG was unaffected by DE concentration. In contrast, Nam and Aherne (1994) obtained a linear increase in ADG in weaned pigs fed diets formulated at 3.18 to 3.51 Mcal DE/kg. This may be expected due to the inclusion of lower DE concentrations than that used in the present study. Van Lunen and Cole (1998) observed faster growth rate in weaned pigs fed diets formulated at 3.9 compared with 3.4 Mcal DE/kg. Similar to the present study, Smith et al. (1999a) observed no effect of increasing ME concentration from 3.25 to 3.51 Mcal/kg on the growth performance of pigs between 10 to 20 kg BW. Also, Tokach et al. (1995) found no effect of increasing dietary formulated ME concentration from 3.25 to 3.74 Mcal/kg on the growth rate of pigs between 6.1 to 10 kg BW. Levesque (2002) who investigated the performance of weaned pigs from 6.8 to 20.1 kg BW, fed diets with determined DE concentration increasing from 3.18 to 3.59 Mcal/kg reported no improvement in growth rate. In the present study, we observed a 12% lower ADG in the first week in pigs fed HDE diets ($P < 0.05$). This may be partly due to a limited fat utilization in weaned pigs before 35 d of age (Leibbrandt et al., 1975; Cera et al., 1988; Tokach et al., 1996).

The lack of improvement in growth with increasing dietary energy concentration may suggest that at lower levels of DE concentration, pigs were able to achieve sufficient feed intake for growth. Since pigs fed diets formulated to contain lower levels of DE could achieve energy intake adequate for optimal growth performance, those offered diets with greater levels of DE would not be expected to grow faster.

It was postulated that increasing dietary energy density may be beneficial to growth in stressful situations (e.g. environmental stressors - including group size and space allowance, or immune challenge) when reduced feed consumption is limiting the animal's capacity for growth (van Heugten et al., 1996). However, Levesque (2002) observed no benefit of feeding a higher DE concentration at two levels of group size/space allowance (16 pigs per pen:0.32 m^2 per pig or 24 pigs per pen:0.26 m^2 per pig). Van Heugten et al. (1996) compared the effect of increasing dietary energy density by using fat or starch supplementation in pigs that were immune challenged with *Escherichia coli* lipopolysaccharide injections. It was found that increasing dietary energy density neither compensated for the reduction in feed intake nor alleviated the growth depression observed in the immune challenged pigs.

Alternatively, it is possible that when pigs are exposed to diets with a higher level of DE concentration, energy is supplied in excess of what is required for the maximum rate of body protein deposition. The 'excessive' energy thus ingested is not utilized for lean growth but used to support lipid deposition (Schinckel and de Lange, 1996). Indeed, previous work has shown an increase in carcass fatness when weaned pigs were fed diets with elevated DE (Endres et al., 1988). A 14% increase in carcass

fatness was reported in weaned pigs fed high fat diets (3.70 Mcal/kg DE) for one week after weaning compared to those fed 3.37 Mcal DE/kg (Endres et al., 1988). Nam and Aherne (1994) reported a linear increase in backfat thickness with increasing dietary DE concentration. Since carcass composition was not determined in the present study, it can only be speculated that differences may have occurred in lean growth and lipid accretion due to the increase in DE concentration. Taken together, the effects of increasing energy concentration on the rate of gain, composition of gain and profitability all warrant further investigation.

The 4% reduction in daily feed intake that we observed on the high DE diets is in agreement with the results of previous authors (Nam and Aherne, 1994; Van Lunen and Cole, 1998; Smith et al., 1999a). It is well documented that changes in dietary energy concentration can have a great impact on feed intake (NRC, 1987). Decreasing feed intake in response to increasing dietary DE concentration may be hormonally mediated. Cholecystokinin is a local and peripheral satiety hormone secreted in the duodenum (Konturek et al., 2004) and released in response to long chain fatty acids (Gregory et al., 1989; Matzinger et al., 2000). The HDE diets were formulated with a higher fat content; and thus, higher long chain fatty acids contents may influence cholecystokinin secretion and satiety and thus decrease feed intake.

Decreasing feed intake may also be produced by a decrease in the passage rate of digesta due to an increase in dietary fat content (Azain, 2001). Traditionally, increasing DE concentration has been achieved by increasing dietary fat content. It may be postulated that increasing DE concentration with starch may result in greater feed intake and a different outcome than the current observation. This was not

supported by the results of van Heugten et al. (1996). However, apart from its use to increase dietary DE concentration, fat is also added to diets to increase pellet quality and improve palatability (Tokach et al., 1995; Albin et al., 2001). Moreover, due to its low heat increment, increasing dietary fat content is recommended as a way to ensure adequate energy intake when pigs are exposed to heat stress (Schoenherr et al., 1986; Azain, 2001; Renaudeau et al., 2001).

The increase in feed efficiency with increasing DE concentration in the present study is consistent with that reported by Levesque (2002) who found a linear increase in feed efficiency in weaned pigs fed diets containing 3.18 to 3.59 Mcal DE/kg. Although feed intake was reduced with increased DE concentration, growth rate was unaffected. The increase in feed efficiency is thus not related to growth rate. The increase in feed efficiency observed herein is probably due to increases in the apparent digestibility of nutrients. Apparent dry matter, energy and crude protein digestibility were all increased by approximately 2% with increased DE concentration. We observed an overall 3.7% increase in feed efficiency when diet DE was increased by 5.9%.

To further examine if there is any benefit of increased DE concentration, energy efficiency (Mcal DE/kg weight gain) was computed. Energy efficiency declined 4.5% with increased DE concentration in the present study. Reis de Souza et al. (2000) reported poorer energy efficiency by increasing DE concentration from 2.94 to 3.21 Mcal/kg in weaned pigs from 7 to 25 kg BW. This was found to be associated with greater body lipid content in pigs fed diets with the higher DE content.

Effect of Lysine:DE Ratio

The increase in growth rate with increasing lysine:DE ratio was consistent with those reported in the literature (Gatel et al., 1992; Nam and Aherne, 1994; Van Lunen and Cole, 1998; Smith et al., 1999a). In the present study, no DE × lysine:DE ratio interaction on growth rate and other performance parameters was detected. This is consistent with the findings of Urynek and Buraczewska (2003) who did not detect a ME × lysine/ME ratio on growth rate in weaned pigs between 13 and 20 kg BW. Also, Nam and Aherne (1994) did not detect a DE × lysine:DE ratio interaction on growth rate in weaned pigs from 9.1 to 25.7 kg BW. Moreover, in growing pigs, Roth et al. (2000) who investigated ileal digestible lysine/ME ratios from 1.84 to 2.93 g/Mcal at 3.11 and 3.35 Mcal ME/kg did not detect a ME × lysine/ME ratio interaction in pigs between 28 to 58 kg BW. It was concluded that the optimum ratio for weight gain (2.76 g/Mcal ME) is independent of dietary energy concentration. As well, Lawrence et al. (1994) concluded that lean growth and protein deposition rates in pigs between 20 and 50 kg BW improved in response to increased lysine:DE ratio regardless of DE concentration. The optimum ratio was estimated at 3.0 g total lysine/Mcal DE.

However, Smith et al. (1999a) detected a ME × lysine/ME ratio interaction on growth rate in weaned pigs from 10 to 25 kg BW. Similarly, Van Lunen and Cole (1998) found a DE × lysine:DE ratio interaction on growth and nitrogen deposition rates in weaned pigs from 9.1 to 25.4 kg BW. The interaction suggests that energy intake in the low energy diets in these studies may be limiting growth. To supply the additional energy required for optimum growth, some amino acids would be

catabolized and deaminated, with increased urea production and reduced net energy (Van Lunen and Cole, 1998). In contrast, energy intake using diets high in energy concentration was adequate but amino acid supply was limiting growth. As dietary lysine:DE ratio increased, amino acid supply increased and reached the level required for optimum growth. In the present study, we can conclude that pigs were in a lysine-dependent, as opposed to energy-dependent circumstance.

As a result of the lack of DE × lysine:DE ratio interaction in the present study, the optimum total lysine:DE ratio for the weaned pig was calculated based on growth rate with the data pooled across energy concentration. Although the performance data were fitted to an exponential and linear-plateau regression models to determine the optimum lysine:DE ratio, the exponential model failed to reach convergence and the residual sum of square was greater with the linear-plateau compared with the quadratic model (Appendix D). It was determined based on the quadratic model that 4.46 g total lysine/Mcal DE is optimum for d 0 to 14, corresponding to 7.5 to 12.8 kg BW, and 4.27 g total lysine/Mcal DE for d 0 to 28 (7.5 to 22.5 kg BW; Table 3.7). However, because there was no response to increasing lysine:DE ratio on growth during d 15 to 28 (i.e 12.8 to 22.5 kg BW), it can be concluded that the requirement was met at the lowest level investigated (3.70 g total lysine/Mcal DE). These estimates of lysine:DE ratio are much higher than 3.4 g total lysine/Mcal DE for weaned pigs between 10 to 20 kg BW recommended by the NRC (1998) and 3.97 g/Mcal determined by Nam and Aherne (1994) for pigs from 9.1 to 25.7 kg BW. However, the present estimates are lower than those determined by Gatel et al. (1992) for weaned pigs between 8 to 17 and 8 to 25 kg BW (4.69 and 4.52 g/Mcal,

respectively) and 5.02 g/Mcal for young hybrid pigs between 9.1 to 25.4 kg BW estimated by Van Lunen and Cole (1998).

Table 3.7. Estimated optimum lysine:DE ratios using intended lysine:DE ratios[a]

Criteria	Lysine:DE ratio, g/Mcal[b]	Body weight, kg	*P* value[c]
ADG d 0 to 14[d]	4.46	7.5 to 12.8	L, 0.0141; Q, 0.0189
ADG d 0 to 28[e]	4.27	7.5 to 22.5	L, 0.0449; Q, 0.0588

[a]The regression analyses were conducted with the ADG data of periods as the dependent variable. Model selection was based on the residual sum of square (see Appendix D). The exponential model failed to reach convergence. The linear-plateau model generated the following equation: ADG d 0 to 14 = -1.18 + *b*(0.68) – *c*(0.07); (n = 60; *P* = 0.0689; R^2 = 0.09); estimated optimum lysine:DE ratio = 4.53 g/Mcal; ADG plateau = 0.407 kg/d. ADG d 0 to 28 = -0.34 + *b*(0.38) – *c*(0.04); (n = 60; *P* = 0.0936; R^2 = 0.08); estimated optimum lysine:DE ratio = 4.66 g/Mcal; ADG plateau = 0.553 kg/d.
[b]Optimum values were determined using the 95% of the upper asymptotic values [c]L = linear; Q = quadratic response to lysine:DE ratio.
[d]Estimated as –*b*/2*c*; parameter estimates were *b* = 0.94(SE = 0.37), *c* = -0.10(SE = 0.04).
[e]Estimated as –*b*/2*c*; parameter estimates were *b* = 0.45(SE = 0.22), *c* = -0.05(SE = 0.03).

As demonstrated in the factorial estimates of lysine requirement (Appendix E), the estimates in the present study would support a phase-feeding program for weaned pigs in the 7.5 to 22.5 kg BW range. The 4.46 g total lysine/Mcal DE ratio may be applied to the early phase while a lower ratio is applied to the late phase. In the absence of a phase-feeding program, 4.27 g total lysine/Mcal DE would be required for optimal performance for pig between 7.5 to 22.5 kg BW.

Plasma urea nitrogen is an estimate of protein utilization and has been suggested as a valuable criterion to establish amino acid requirements. A decrease in PUN concentration is an indirect index of changes in protein synthesis and

degradation (NRC, 1994) and is indicative of the extent to which amino acids are broken down (Eggum, 1970). Increasing amino acid utilization decreases urea synthesis, and thus PUN concentration (Coma et al., 1995). The underlying assumption is that at sub-optimal lysine intake, PUN concentration would be expected to rise due to a high rate of catabolism of other amino acids. PUN concentration should decrease as a limiting amino acid reaches the requirement and plateau or increase after the requirement has been met (Parr et al., 2003). Nam and Aherne (1994) and Smith et al. (1999a) detected a quadratic relationship between PUN concentration and lysine/energy ratio.

In the present study, only a linear but not quadratic increase in PUN concentration with increased lysine:DE ratio was detected. This is likely to be related to first, the time of blood sampling (wk 4) during when effects of DE and lysine:DE ratio on performance criteria were not detected. Second, it is possible that PUN concentration may be a rather poor index at the much higher ratios investigated in the present study compared to the aforementioned studies. Third, an inflection may require that energy intake is limiting at lower lysine:DE ratios. When energy supply from non-protein sources is inadequate to achieve intake level to support body protein deposition and growth, amino acid catabolism will increase (Kyriazakis and Emmans, 1995; Van Lunen and Cole, 1998) and clearly when amino acid intake is in excess of that required to achieve the maximum rate of body protein accretion, increments of amino acid intake are quantitatively catabolized (Fuller and Wang, 1987). Consequently, an increase in PUN concentration may be associated at first with inadequate energy intake and eventually to an elevated intake of amino acids above

levels required for maximal protein accretion and growth. This is supported by a linear increase in PUN reported by Levesque (2002) with increasing DE concentration that would suggest that energy intake was limiting in diets with lower DE concentration. In the present study, energy intake was greater at lower compared with higher lysine:DE ratios (interaction, DE × lysine:DE ratio, $P < 0.05$).

Cameron et al. (2003) did not detect a nonlinear response in serum urea nitrogen (SUN) in growing pigs fed diets with graded levels of lysine:DE ratios from 2.42 to 5.15 g/Mcal and were unable to estimate the optimum lysine:DE ratio with SUN concentration. The authors speculated that the lack of a nonlinear response in SUN to increasing lysine:DE ratio was the result of urinary elimination of excess amino acids rather than being catabolized for gluconeogenesis, or an insufficient dietary protein intake that resulted in amino acids recycling rather than being catabolized.

Nevertheless, given careful control of sampling times, as reported by Coma et al. (1995), PUN concentration responded to changes in dietary lysine content within 24 h with a new equilibria reached within 3 d. This may allow PUN concentrations to be used as a criterion in short-term trials. Since maximum protein accretion requires a greater intake of amino acids than maximal rate of BW gain (NRC, 1988) estimates assessed with PUN concentrations may be greater than that observed for rate of BW gain (Coma et al., 1995).

In conclusion, increasing DE concentration reduced feed intake, increased DE intake but failed to improve growth rate in weaned pigs. There was a minor improvement in feed efficiency. There was no interaction between DE and lysine:DE

ratio on the estimated lysine requirement for growth. Based on non-linear regression analysis, growth rate improved with increased total lysine:DE ratio up to 4.46 and 4.27 g/Mcal, over the 7.5 to 12.5 kg and 7.5 to 22.5 kg BW range, respectively.

3.5 Implications

These results suggest that for optimal growth of high performing weaned pigs growing from 7.5 to 12.5 kg BW, diets should contain a total lysine:DE ratio equal to 4.46 g/Mcal. The lack of response to increasing lysine:DE ratio in the later stage of the present study supports a phase feeding program for weaned pigs. Therefore, a lower total lysine:DE ratio (3.70 g/Mcal) should be applied to the later stage (i.e. 12.5 to 22.5 kg BW), whereas diets should contain a total lysine:DE ratio equal to 4.27 g/Mcal in a single phase feeding program for pigs between 7.5 to 22.5 kg BW.

4. GROWTH PERFORMANCE, BODY COMPOSITION AND NUTRIENT DEPOSITION RATES IN WEANED PIGS FED DIETS WITH SIMILAR DIGESTIBLE BUT DIFFERENT ESTIMATED NET ENERGY CONCENTRATION

4.1 Introduction

For the swine industry, a major prerequisite for maximizing net income and producing a high quality carcass is predictability of production. Successful diet formulation is a major contributor to the achievement of predictable animal performance. Energy and amino acids in combination account for more than 80% of feed cost (de Lange et al., 2001a), although energy is the greatest single cost-factor in pork production (de Lange and Birkett, 2004). Thus, approaches aimed at maximizing net income or reducing cost must include an adequate and accurate understanding of energy metabolism.

In terms of energy systems, there is widespread belief that the net energy (NE) system is the most accurate basis for predicting the quantity of energy actually available to the pig as all energy lost in the conversion of dietary to productive energy is accounted for (Galloway and Ewan, 1989; Noblet, 2000). Noblet and van Milgen (2004) indicated that NE is the only system where energy requirements and dietary energy values are expressed on the same basis, and should in theory be independent of the feed. Thus, NE would be expected to result in a more predictable animal

performance than would be expected from the more common (in North America) digestible (DE) or metabolizable energy (ME). However, empirical results supporting this theoretical advantage of NE over DE and ME in practice are very difficult to find.

When formulating diets using the DE system, increasing DE concentration with a coincidental increase in dietary CP content will result in constant NE. This could explain the lack of growth response to increased DE concentration previously reported in the weanling pig (Levesque, 2002). Our hypothesis is that diet formulation with NE will provide for more predictable performance than the traditional DE. Therefore, the main objective of this study was to determine if more predictable growth, nutrient deposition and energy utilization is achieved in the weaned pig with NE or with DE, to develop a better understanding of the relative merits of DE vs. NE in diet formulation. Additionally, the experiment investigated the influence of method of increasing NE on growth and energy metabolism.

4.2 Materials and Methods

Animal and Housing

A growth and comparative slaughter trial was conducted with the offspring of C 22 females × 337 sires (PIC Canada Ltd, Airdrie, AB) weaned at 20.3 ± 1.0 d and 6.8 ± 1.0 kg (mean ± SD; age and weaning weight, respectively). At weaning, pigs were placed in one of three nursery rooms, each containing 24 experimental pens (1.27 × 1.04 m) housing four pigs per pen; pigs were allowed 8 days to acclimatize to weaning, the environment and feed. All pens were equipped with fully-slatted floors, a nipple drinker and an adjustable multiple-space dry feeder. Each room had

automatic light timers (12-light:12-dark cycle) and integrated controllers (Model PEC; Phason, Winnipeg, MB) regulating heating and ventilation systems. Room temperature was initially set at 30ºC, and gradually decreased by 1.5ºC/wk. The feeders were checked daily for proper feed flow and to prevent wastage and the drinkers for adequate water flow.

Experimental Design

The experiment was conducted in three replicates of 80 pigs each plus the initial slaughter group (ISG; n = 8) which was included only in replicates 1 and 2. This provided a total of 256 pigs used in this experiment. Within gender, pigs were blocked by weaning weight and randomly allotted to pens of 4 pigs/pen. Within each room, pens were allocated to one of 4 locations of 5 pens each, to eliminate possible confounding of the experiment due to location. Treatments were randomly assigned to pens within location.

Piglets were given ad libitum access to a pelleted commercial phase-1 starter diet (Appendix A; Ultrawean 21, Co-op Feeds, Saskatoon, SK) for the first 4d post-weaning followed by a pelleted phase-2 starter diet (Appendix B; GI MAX 21, Co-op Feeds, Saskatoon, SK) for the next 4 days. Piglets were then given ad libitum access to one of the pelleted experimental diets throughout the entire 28-day test period (d 0 to 28).

The University Committee on Animal Care and Supply at the University of Saskatchewan (UCACS) approved the animal care protocol (#20020093) for adherence to the guidelines of the Canadian Council of Animal Care (1993).

Experimental Diets

Experimental diets were formulated to contain 1.40 % apparent digestible lysine which was based on the optimum total lysine:DE ratio derived in a previous experiment (Chapter 3). Essential amino acids were formulated to achieve the ideal amino acid ratio to lysine as defined by the NRC (1998).

Diets were formulated with ingredients suitable for complex diets for the weaned pig (Table 4.1). The levels of each ingredient reflected those used in commercial feed for the weaned pig or from research elsewhere (e.g. Kim et al., 1999; Piao et al., 2000; Woodworth et al., 2001; Webster et al., 2003). All diets were formulated to contain similar levels of DE (3.53 Mcal/kg) but with increasing levels of NE (2.24 to 2.40 Mcal/kg) based on the reported NE values of ingredients (CVB, 1998).

The formulated NE concentration was increased from 2.24 Mcal/kg in the control diet to 2.40 Mcal/kg in diet 3 (LoCP HiNE) by a gradual reduction of CP content from 27.0 to 19.9% while maintaining similar fat content. Diets 4 (MedFat MedNE) and 5 (HiFat HiNE) were formulated with similar CP content as the control diet but with increasing fat content. The formulated and analyzed nutrient composition of diets are shown in Table 4.2.

One major concern with most published research on energy metabolism is the acceptance of book values, as compared to determined DE values, of experimental diets. In order to elevate the precision of the experiment and accurate interpretation of results, dietary DE concentrations were determined and the NE concentrations were estimated from digestible nutrients as described below.

Table 4.1. Ingredient composition of experimental diets, as-fed basis[a]

	Diet				
	1	2	3	4	5
	Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE
	Formulated NE, Mcal/kg				
Ingredients, %	2.24	2.32	2.40	2.32	2.40
Barley	30.03	22.54	15.90	30.05	30.01
Wheat	16.00	15.50	13.25	8.00	-
Corn	2.50	20.50	38.65	7.75	13.00
Soybean meal	27.75	16.72	5.70	17.07	6.40
Full-fat soybean[b]	-	-	-	14.00	28.00
Menhaden fish meal	5.50	6.37	7.25	6.85	8.20
Spray dried whey	7.50	7.50	7.50	7.50	7.50
Spray dried whole blood	2.50	2.50	2.50	2.50	2.50
Canola oil	4.54	4.08	3.63	2.90	1.33
Dicalcium phosphate	0.69	0.69	0.69	0.55	0.41
Limestone	0.77	0.74	0.70	0.65	0.54
Salt	0.30	0.30	0.30	0.30	0.30
Mineral premix[c]	0.50	0.50	0.50	0.50	0.50
Vitamin premix[d]	0.50	0.50	0.50	0.50	0.50
Choline chloride	0.05	0.05	0.05	0.05	0.05
l-lysine HCl	0.063	0.359	0.656	0.032	-
dl-methionine	0.125	0.198	0.270	0.116	0.107
l-threonine	0.066	0.188	0.311	0.051	0.036
l-tryptophan	0.025	0.069	0.115	0.023	0.021
l- isoleucine	-	0.096	0.251	-	-
l-phenyalanine	-	-	0.165	-	-
l-valine	-	-	0.158	-	-
l-leucine	-	-	0.044	-	-
Celite[e]	0.50	0.50	0.50	0.50	0.50
$NaHCO_3$[f]	-	-	0.30	-	-
LS-20[g]	0.10	0.10	0.10	0.10	0.10

[a]Diets were formulated to similar levels of DE concentration using NRC (1998) value of each ingredient; formulated NE concentrations were based on NE value of ingredients (CVB, 1998; NRC, 1998).

[b]Extruded (Extra-Pro Feeds, Dent, MN).

[c]Provided per kg of diet: Zn, 100 mg as zinc sulfate; Fe, 80 mg as ferrous sulfate; Cu, 50 mg as copper sulfate; Mn, 25 mg as manganous sulphate; I, 0.50 mg as calcium iodate; Se, 0.10 mg as sodium selenite.

[d]Provided per kg of diet: vitamin A, 8,250 IU; vitamin D_3, 825 IU; vitamin E, 40 IU; niacin, 35 mg; D-pantothenic acid, 15 mg; riboflavin, 5 mg; menadione, 4 mg; folic acid, 2 mg; thiamine, 1 mg; D-biotin, 0.2 mg; vitamin B_{12}, 25 µg.

[e]Celite (Celite Corporation, Lompoc, CA) was added as a source of acid insoluble ash. Typical % physical composition: moisture, 0.8; SiO_2, 89.4; Na_2O, 3.8; Al_2O_3, 3.4; Fe_2O_3, 1.3; MgO, 0.6; CaO, 0.5; TiO_2, 0.2 (Megazyme International Ireland Ltd, Bray, Co. Wicklow, Ireland).

[f]Added to achieve approximately 200 mEq/kg dietary electrolyte balance (dEB) (Patience et al., 1987).

[g]Includes lincomycin at 22 g/kg and spectomycin at 22 g/kg product (BioAgrimix, Mitchell, ON).

Table 4.2. Calculated and analyzed nutrient composition of experimental diets, as-fed basis[a]

	Diet				
	1	2	3	4	5
	Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE
	Formulated NE, Mcal/kg				
Item	2.24	2.32	2.40	2.32	2.40
Calculated					
DE, Mcal/kg	3.53	3.53	3.53	3.53	3.54
ME, Mcal/kg	3.24	3.29	3.33	3.24	3.25
CP, %	25.67	22.11	18.84	25.68	25.68
Crude fat, %	6.35	6.35	6.35	7.29	8.30
Crude fiber, %	3.02	2.67	2.32	3.14	3.24
NDF, %	12.57	11.19	9.73	12.45	12.31
ADF, %	5.62	4.45	3.28	5.54	5.45
Digestible lysine, %[b]	1.40	1.40	1.40	1.40	1.40
dEB, mEq/kg[c]	291	226	196	299	307
Analyzed					
GE, Mcal/kg	4.26	4.19	4.17	4.33	4.40
NE, Mcal/kg[d]	2.29	2.39	2.55	2.45	2.44
DE, Mcal/kg[e]	3.47	3.47	3.57	3.58	3.59
CP, %	26.96	23.12	19.93	26.64	26.42
Starch, %[f]	20.38	30.88	34.86	22.42	19.40
Sugars, %[g]	17.32	13.85	17.03	15.74	16.82
Crude fat, %	6.39	6.53	6.34	7.91	9.12
Crude fiber, %	3.11	2.64	2.13	2.85	3.33
NDF, %	8.38	7.29	6.42	7.48	8.04
ADF, %	4.91	3.92	2.84	4.17	4.38
Ash, %	7.12	6.56	5.98	6.93	6.82

[a]Diets were formulated to similar levels of DE and calculated ME concentration using NRC (1998) of each ingredient; formulated NE concentrations were based on NE value of ingredients (CVB, 1998).
[b]Calculated based on apparent digestible lysine content of ingredients (NRC, 1998).
[c]Dietary electrolyte balance, Na + K - Cl (Patience et al., 1987).
[d]Estimated from analyzed digestible nutrient contents according to the CVB (1994) equation (see Table 4.4).
[e]Calculated based on the apparent digestibility coefficient of GE (see Table 4.4).
[f]Determined enzymatically (AOAC, 2002).
[g]Sugars were calculated as total carbohydrates – (starch + total NSP + free sugars).

Data and Sample Collection

Piglets were individually weighed on d 0 (28.3 ± 1.0 d and 8.4 ± 1.1 kg (mean ± SD; age and initial BW, respectively) and weekly thereafter (d 7, 14, 21, and 28). On each weigh day, feed consumption was measured. The data were used to calculate average daily gain (ADG), average daily feed intake (ADFI), and feed efficiency.

Feed samples were taken daily at the time of feeding and pooled per diet. Freshly voided faeces were collected from each pen using the grab method over three days (d 13 to 15) and pooled per pen. Faeces and feed samples were frozen at -20°C until required for data analysis.

Slaughter Procedure and Carcass Measurement

The 16 pigs assigned to the ISG were sacrificed on d 0 to determine initial body composition of experimental pigs. All other pigs remained on the experimental treatments for a 4-wk period, at which time one pig/pen (closest to pen average) was sacrificed to determine body composition (n = 60).

Pigs were euthanized by CO_2 asphyxiation followed by ex-sanguination (Hoenderken, 1983; Gregory et al., 1987). The carcass was split down the midline from the groin to the chest cavity. The entire viscera were removed from the carcass. The gastrointestinal tract (GIT) was separated from the viscera and weighed, emptied of all digesta, patted dry and reweighed. The liver, kidneys, heart, lungs, and spleen were weighed individually. The weight of the organ fraction and blood were recorded as total organ weight and herein referred to as “organ.” The weight of the eviscerated carcass (including head and feet) was recorded and referred to as “carcass.” The

empty body weight of the pig was taken as the sum of the eviscerated carcass plus the pooled organ fraction and blood. The organ fraction and blood were pooled and stored separately from the carcass.

The carcass and organs were frozen at –20ºC until further processing. The frozen carcasses were cut into quartiles and passed through a 10-mm die four times in a commercial grinder (Model 801 GHP-25; Autio Company, Astoria, OR.). Several subsamples were placed in a previously weighed aluminum container following the fourth passage through the die. The organ fraction was passed through the die once and mixed thoroughly before several subsamples were placed in a previously weighed aluminum container. All samples were weighed immediately (approximately 250 g) after collection and kept frozen until freeze-drying to a constant weight.

Chemical Analyses

Feed and faecal samples were prepared for chemical analyses by air-equilibration and passed through a 1-mm screen (Retsch Model ZM1; Brinkman Instrument of Canada Ltd., Rexdale, ON).

The AIA content of the diet was used as an indigestible marker and measured in feed and faeces (McCarthy et al., 1974) to determine the apparent faecal digestibility of DM and other nutrients. Pure celite standard samples were assayed to confirm the accuracy of the analytical procedure, and a recovery of 99.9 ± 0.01% was attained.

The moisture content of feed and freeze-dried faecal samples was determined by drying at 135ºC in an airflow-type oven for 2 h (Method 930.15; AOAC, 1990). Nitrogen in feed and faecal samples was measured by combustion (Method 968.06; AOAC, 1990) using a Leco protein/nitrogen apparatus (Model FP-528, Leco Corp., St. Joseph, MI). Calibration was conducted with an EDTA standard (nitrogen content 9.57 ± 0.02%; Leco Corp., St. Joseph, MI). On analysis, nitrogen content of the EDTA standard was 9.56 ± 0.01%. Crude protein was expressed as nitrogen × 6.25.

Gross energy was measured in an adiabatic bomb calorimeter (Model 1281; Parr Instruments, Moline, IL). Benzoic acid was used as the standard for calibration (6318 kcal/kg) and was determined to be 6317 ± 3 kcal/kg at assay. Crude fat in feed samples was determined after ether extraction (Serial # 263220, Labconco Corp., Kansas city, MO) (Method 920.39; AOAC, 1990) and in faecal samples after acidification with 9 N HCl, followed by ether extraction. Feed and faecal samples were analyzed for NDF, ADF and CF using an Ankom^{200} fiber analyzer (Ankom Technology Co., Fairport, MI). Ash was determined by incineration in a muffle furnace at 600ºC for 12 h. Feed samples were passed through a 0.5-mm screen and analyzed for starch enzymatically using a total starch assay kit (Megazyme International Ireland Ltd, Bray, Co. Wicklow, Ireland) (Method 996.11; AOAC, 2002).

Feed samples were analyzed for total carbohydrates, total nonstarch polysaccharides (NSP) and free sugars based on the method of Englyst and Hudson (1987) and Englyst (1989). Sugars were calculated as total carbohydrates – (starch + total NSP + free sugars). According to Graham et al. (1986) and Bach Knudsen and

Hansen (1991), faecal digestibility of starch and sugar was assumed to be 100%; therefore starch and sugar were not determined in the faecal samples (Noblet et al., 1994; Schrama et al., 1998; Le Goff and Noblet, 2001).

Freeze-dried carcass and organ samples were prepared for chemical analyses by blending in a grinder (Retsch Grindomix, Model GM200; F.Kurt Retsch GmbH & Co.KG, Haan, Germany). Samples were analyzed for DM, GE, crude fat and ash as described above. Nitrogen was measured with the Leco apparatus (Method 992.15; AOAC, 2002) and crude protein was expressed as nitrogen × 6.25.

All chemical analyses were carried out in duplicate and were repeated when intra-duplicate CV exceeded 3%.

Calculations and Statistical Analyses

Apparent digestibility coefficients of N, energy and other nutrients were determined using the following equation:

$$D_{ADN}\% = 100\% - [(I_D \times A_F)/(A_D \times I_F) \times 100] \quad (4.1)$$

where D_{ADN} is apparent digestibility of a nutrient in the assay diet, I_D is percent index marker concentration in the assay diet, A_F is percent nutrient concentration in faeces, A_D is percent nutrient concentration in the assay diet, I_F is percent index marker concentration in faeces, all on DM basis.

Apparent digestibility coefficient of DM was determined using the following equation:

$$D_{ADM}\% = 100\% - [(I_D/I_F) \times 100] \quad (4.2)$$

where D_{ADM} is apparent digestibility of DM in the assay diet.

NE was estimated from digestible nutrients according to CVB (1994).

$$NE = 2.58 \times DCP + 8.63 \times DEE + 3.23 \times ST + 3.04 \times SG + 2.27 \times DRES \quad (4.3)$$

where NE is expressed in kcal/kg as is, DCP is digestible CP, DEE is digestible ether extract, ST is starch, SG is sugar, and DRES is digestible residuals, calculated as digestible organic matter - (DCP + DEE + ST + SG + digestible crude fiber).

Digestible energy intake (DE*i*) was calculated from the actual DE concentration × ADFI. Similarly, NE*i* was calculated from the determined NE concentration (Eq. 4.3) × ADFI.

Energy efficiency was calculated as DE*i* or NE*i*/ADG

where DE*i* and NE*i* are in Mcal/d, and ADG is the average daily gain in kg/d.

Data from the body composition of the ISG were used to estimate the initial body composition of the 60 pigs of the same gender sacrificed on d 28. The relationship between live weight and empty BW at slaughter was calculated and used with the carcass and organ analysis data of the ISG. The gain of protein, lipid, ash, water and energy was estimated as:

[(Final content, g or Mcal) – (initial content, g or Mcal)]/28 d (4.4)

Empty body GE content was estimated in two ways: by bomb calorimeter analysis conducted on carcass and organ and by calculation based on the analyzed protein and lipid content and using the factors 5.66 and 9.46 Mcal/kg for protein and lipid, respectively (Ewan, 2001).

Growth performance data were analyzed using the MIXED procedure of SAS (SAS Institute Inc., 1996) with pen as the experimental unit and initial weight as a covariate. Data for final weight, ADG, ADFI, gain:feed ratio, energy intake, and energy efficiency were analyzed using repeated measures with weekly data and appropriate covariance structures (Littell et al., 1998; Wang and Goonewardene, 2004). The statistical model included the effect of week, diet, gender and the following interactions: diet × day, diet × gender and diet × gender × day. The data for apparent digestibility of nutrients, carcass, organ, empty body composition and nutrient deposition rates were analyzed using a model with diet, gender and diet × gender interaction. Differences in least square means were determined using the PDIFF option of SAS and considered statistically significant at $P < 0.05$. In addition, trends ($0.05 < P < 0.10$) were reported and $P > 0.10$ was considered non-significant.

Data on ADG, protein and lipid deposition rates were related to energy intake (DE*i* and NE*i*) using linear and non-linear regression procedures of SAS (SAS Institute Inc., 1996).

The degree to which performance and carcass variables were related to actual DE, determined NE concentration and respective intake was determined with Pearson correlation coefficients using the correlation procedure of SAS (SAS Institute, Inc., 1996).

4.3 Results

Overall, ADG was greatest in pigs fed the MedCP MedNE diet, but was similar to those fed the control diet, and was lowest in pigs fed the HiFat HiNE diet (Table 4.3; $P < 0.05$). The ADFI on the control diet was greater than the LoCP HiNE, the MedFat MedNE and the HiFat HiNE diets ($P > 0.05$). In addition, ADFI was greater in barrows than gilts ($P < 0.05$). The ADFI was on average 85.3% of the estimated ad libitum intake calculated with the NRC (1998) equation. Gain:feed ratio was similar among dietary treatments ($P > 0.05$). Due to the faster rate of gain with the pigs fed the MedCP MedNE diet, pigs were heaviest on d 28 ($P < 0.05$; Table 4.3), and similar to those fed the control diet. Pigs fed the HiFat HiNE diet had the lightest body weight on d 28 ($P < 0.05$).

The apparent digestibility of GE and DM was greatest in the LoCP HiNE diet, while the MedCP MedNE and the MedFat MedNE diets were similar and intermediate to those in the LoCP HiNE diet and the lower values in the control and the HiFat HiNE diets ($P < 0.001$; Table 4.4). The apparent digestibility of CP was greatest in the LoCP HiNE diet and was lowest in the HiFat HiNE diet ($P < 0.001$). Conversely, the apparent digestibility of crude fat was greatest in the HiFat HiNE diet, and was lowest in the control diet ($P < 0.001$). The apparent digestibility of NDF and CF were greater in the MedFat MedNE and the HiFat HiNE diets compared with the other diets ($P < 0.001$). The apparent digestibility of ADF in the LoCP HiNE diet was lower in comparison with the other diets except the HiFat HiNE diet ($P < 0.05$). The apparent digestibility of ash was greatest in the MedFat MedNE diet but was similar to that in the LoCP HiNE diet and lowest in the MedCP MedNE diet ($P <$

Table 4.3. Effects of diets formulated at similar DE but increasing NE concentration on the final weight and performance of weaned pigs from 8 to 25 kg BW[a]

		Diets					
		1	2	3	4	5	
		Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE	
	DE, Mcal/kg[b]	3.47	3.47	3.57	3.58	3.59	
Item	NE, Mcal/kg[c]	2.29	2.39	2.55	2.45	2.44	SEM
Number of pens		12	12	12	12	12	
Start weight, kg		8.37	8.39	8.30	8.36	8.39	0.13
Final weight, kg		24.84^{wx}	25.34^{w}	24.45^{xyz}	24.59^{xy}	23.88^{z}	0.23
ADG, g/d		589^{wx}	607^{w}	575^{xz}	580^{x}	554^{yz}	9
ADFI, g/d		854^{y}	833^{yz}	803^{z}	820^{z}	800^{z}	13
ADFI, % NRC[d]		86.7	83.7	84.3	86.3	85.3	2.1
Gain:feed ratio, g/g		0.690	0.728	0.711	0.704	0.680	0.006
P values		Final weight	ADG	ADFI	Gain:feed ratio		
Day		0.0001	0.0001	0.0001	0.0001		
Diet		0.0001	0.0033	0.0217	0.1706		
Gender[e]		0.4464	0.3353	0.0254	0.4908		
Diet × Day		0.5989	0.4560	0.8748	0.4503		
Diet × Gender		0.9361	0.9948	0.9122	0.6989		
Diet × Gender × Day		1.0000	0.9538	0.9767	0.6515		

[a]Data are least square means. The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. There were 6 pens per diet × gender, for a total of 12 pens per diet. Weekly data were analyzed with repeated measure. All data were analyzed with initial BW as a covariate. The covariate was significant ($P < 0.05$) for final body weight and ADG, but not significant ($P > 0.05$) for ADFI and gain:feed ratio.

[b]Determined digestible energy concentration.

[c]Estimated from analyzed digestible nutrient content according to CVB (1994) equation.

[d]ADFI as a percentage of estimate was based on DE intake from determined dietary DE concentration and estimated DE intake using the equation: DE intake (Mcal/d) = -1.531 + (0.4555 × BW) - (0.00946 × BW^2) in NRC (1998).

[e]Barrows consumed 26 g/d more feed than gilts.

[w,x,y,z]Means within a row lacking a common superscript letter differ ($P < 0.05$).

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Table 4.4. Effects of diets formulated at similar DE but increasing NE concentration on apparent digestibility of energy, and nutrients in weaned pigs from 8 to 25 kg BW[a]

		Diets						
		1	2	3	4	5		
		Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE		
	DE, Mcal/kg[b]	3.47	3.47	3.57	3.58	3.59		*P* values[c]
Item	NE, Mcal/kg[d]	2.29	2.39	2.55	2.45	2.44	SEM	Diet	Gender
Apparent digestibility, %									
Gross energy		81.6^{z}	82.9^{y}	85.7^{x}	82.7^{y}	81.5^{z}	0.4	0.0001	0.4483
Dry matter		81.9^{z}	83.3^{y}	86.4^{x}	83.5^{y}	82.0^{z}	0.3	0.0001	0.2833
Crude protein		81.8^{xy}	80.9^{y}	83.1^{x}	81.3^{y}	78.1^{z}	0.7	0.0001	0.9271
Crude fat		74.9^{z}	76.6^{yz}	79.2^{xy}	81.2^{wx}	82.7^{w}	1.3	0.0001	0.7458
NDF		40.7^{z}	39.2^{z}	39.3^{z}	46.3^{y}	47.9^{y}	1.1	0.0001	0.9320
ADF		41.2^{y}	39.8^{y}	27.1^{z}	40.4^{y}	36.0^{yz}	3.3	0.0249	0.1916
Crude fiber		32.8^{z}	34.7^{z}	34.6^{z}	40.0^{y}	43.7^{y}	2.1	0.0001	0.7513
Ash		57.7^{z}	56.6^{z}	61.0^{xy}	61.3^{x}	59.6^{y}	0.8	0.0001	0.0206
Energy content and ratios									
DE, Mcal/kg		3.47^{z}	3.47^{z}	3.57^{y}	3.58^{y}	3.59^{y}	0.02	0.0001	0.4119
NE, Mcal/kg		2.29^{z}	2.39^{y}	2.55^{w}	2.45^{x}	2.44^{x}	0.01	0.0001	0.4885
NE/DE		66.1^{z}	68.9^{w}	71.3^{v}	68.5^{x}	68.1^{y}	0.2	0.0001	0.7297
NE/GE		53.9^{z}	57.1^{x}	61.1^{w}	56.6^{x}	55.5^{y}	0.2	0.0001	0.5074

[a]Data are least square means. The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. There were 6 pens per diet × gender, for a total of 12 pens per diet. Apparent digestibility coefficients were based on analyses conducted on individual pen's faecal grab samples collected over three consecutive days (d 13 to 15). Acid insoluble ash in feed (0.82, 0.78, 0.67, 0.75 and 0.77% as fed in diets 1 to 5, respectively) and faeces was used as index marker.

[b]Determined digestible energy concentration.

[c]Effect: diet × gender, $P > 0.05$ for all variables except for apparent ash digestibility ($P < 0.05$); greater apparent ash digestibility with barrows than gilts.

[d]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation.

[v,w,x,y,z]Means within a row lacking a common superscript letter differ ($P < 0.05$).

0.001). In addition, apparent digestibility of ash was greater with barrows than gilts ($P < 0.05$).

Actual DE concentrations were similar in the control and the MedCP MedNE diets, but were lower compared with the LoCP HiNE, the MedFat MedNE and the HiFat HiNE diets (Table 4.4; $P < 0.001$). Actual DE values were lower than formulated (3.53 Mcal/kg) in the control and the MedCP MedNE diets, but greater than formulated in the LoCP HiNE, the MedFat MedNE and the HiFat HiNE diets. All actual DE concentrations were within 98% of the formulated value. As expected, the determined NE concentration increased from the control diet to the LoCP HiNE diet ($P < 0.001$). The determined NE values with the MedFat MedNE and the HiFat HiNE diets were similar ($P > 0.05$) but lower than the LoCP HiNE diet ($P < 0.05$).

Energy intake (DE*i* and NE*i*; Table 4.5) was not affected by dietary treatments ($P > 0.05$) but was greater in barrows than gilts ($P < 0.05$). The efficiency of DE utilization for weight gain was poorer in the HiFat HiNE diet compared to other diets (Table 4.5; $P < 0.05$). Additionally, the efficiency of NE utilization for weight gain tended to be poorer in the HiFat HiNE diet compared to the other diets ($P < 0.10$). The efficiency of energy utilization for PD and LD was not affected by dietary treatments ($P > 0.05$)

Among individual pigs, the DE*i* ranged from 2.84 to 4.08 Mcal DE/d. A significant linear and quadratic ($P < 0.0001$) relationship was detected between ADG and DE*i* within the observed range (n = 60; Figure 4.1).

$$ADG = -1.15 + 0.92DEi - 0.12DEi^2;\ R^2 = 0.49 \qquad (4.5)$$

where ADG is in kg/d, and DE*i* is in Mcal/d.

Table 4.5. Effects of diets formulated at similar DE but increasing NE concentration on energy intake and energy efficiency in weaned pigs from 8 to 25 kg BW[a]

		Diets					
		1	2	3	4	5	
		Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE	
	DE, Mcal/kg[b]	3.47	3.47	3.57	3.58	3.59	
Item	NE, Mcal/kg[c]	2.29	2.39	2.55	2.45	2.44	SEM
Energy intake, Mcal/d							
DE[d]		3.50	3.50	3.36	3.39	3.40	0.05
NE[d]		2.32	2.41	2.40	2.32	2.32	0.04
Energy utilization							
Mcal DE/kg BW gain[e]		6.14[z]	6.00[z]	5.99[z]	6.08[z]	6.90[y]	0.24
Mcal DE/Mcal RE[f]		4.03	3.50	3.44	3.76	3.92	0.18
Mcal DE/kg PD[f,g]		36.7	34.9	35.9	34.4	38.5	1.5
Mcal DE/kg LD[f,g]		92.9	74.6	68.6	86.5	81.2	7.3
Mcal NE/kg BW gain[e]		4.06	4.13	4.27	4.17	4.70	0.17
Mcal NE/Mcal RE[f]		2.66	2.41	2.46	2.57	2.67	0.12
Mcal NE/kg PD[f,g]		24.2	24.0	25.6	23.5	26.2	1.0
Mcal NE/kg LD[f,g]		61.4	51.4	48.9	59.2	55.3	5.0

P values	DE intake	NE intake	Mcal DE/ kg BW gain	Mcal NE/ kg BW gain	Mcal DE/ Mcal RE	Mcal NE/ Mcal RE
Day	0.0001	0.0001	0.0001	0.0001	-	-
Diet	0.1992	0.1647	0.0443	0.0564	0.1137	0.4603
Gender[h]	0.0153	0.0141	0.8720	0.8754	0.6822	0.6711
Diet × Day	0.8714	0.6489	0.1136	0.1171	-	-
Diet × Gender	0.9438	0.9394	0.3559	0.3369	0.5323	0.5145
Diet × Gender × Day	0.9794	0.9800	0.2912	0.2866	-	-

[a]The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. Six pens per diet × gender, 12 pens per diet. RE = retained energy; PD = protein deposition; LD = lipid deposition.
[b]Determined digestible energy concentration.
[c]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation.
[d]Analyzed data were calculated from dietary actual DE concentration (or determined NE concentration) and weekly ADFI.
[e]Analyzed data were calculated from weekly estimated DE (or NE) intake/weekly ADG.
[f]Analyzed data were calculated from average DE (or NE intake) of individual pen/determined RE (PD or LD) of corresponding sacrificed pen mate.
[g]Effect: Diet, gender, diet × gender; $P > 0.05$.
[h]Barrows consumed 121 and 84 kcal/d more DE and NE, respectively, than gilts.
[y,z]Means within a row lacking a common superscript letter differ ($P < 0.05$).

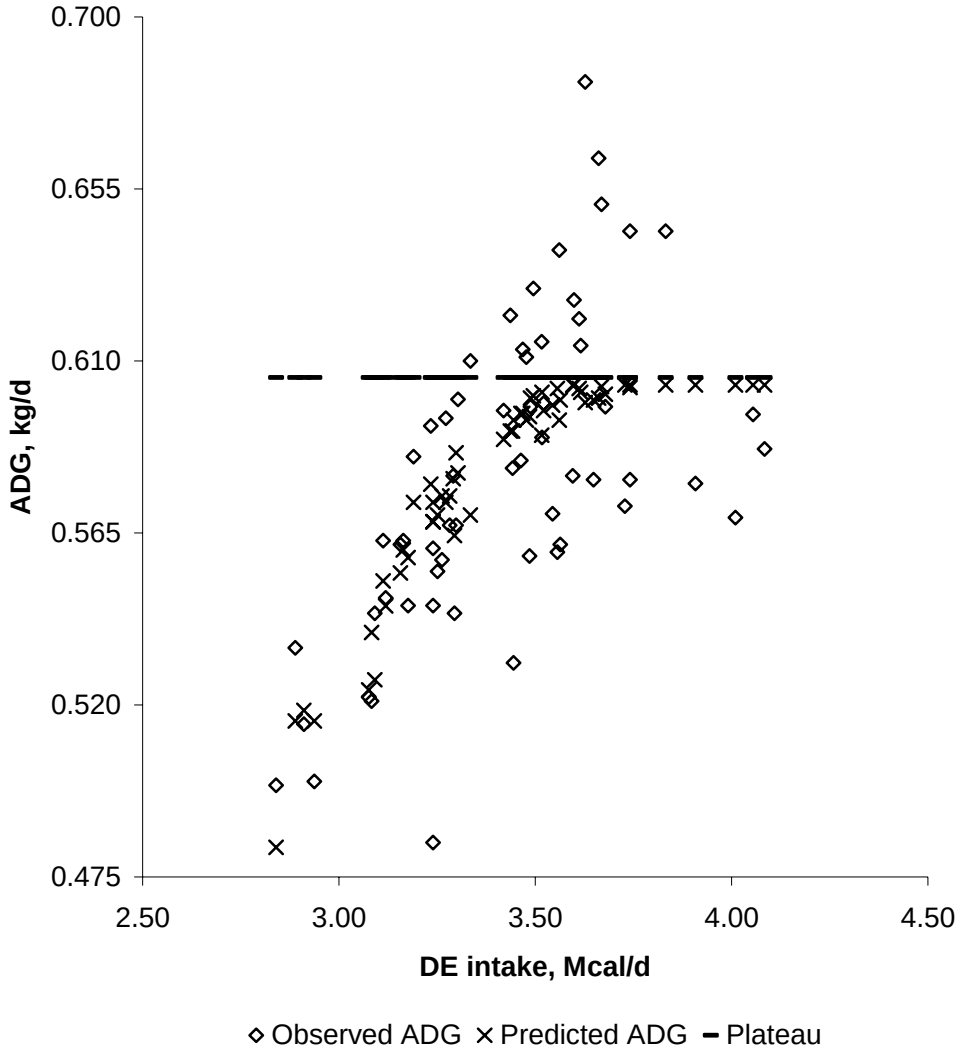

Figure 4.1. The relationship between ADG and DE intake in weaned pigs fed diets formulated at similar DE but increasing NE concentration (Linear-plateau model). ADG = -1.15 + 0.92DE*i* - 0.12DE*i*^{2} (n = 60; R^2 = 0.49; *P* < 0.001). DE*i* optimum = 3.77 kcal/d; ADG plateau = 0.607 kg/d. DE*i* optimum for PD and plateau = 3.86 Mcal/d and 101 g/d, respectively, while DE*i* optimum for LD and plateau = 4.05 Mcal/d and 52 g/d, respectively.

Among individual pigs, the NE*i* ranged from 1.95 to 2.72 Mcal NE/d. A significant linear and quadratic ($P < 0.0001$) relationship detected between ADG and NE*i* is summarized in the following equation (n = 60; Figure 4.2):

$$ADG = -1.13 + 1.33NEi - 0.26NEi^2; R^2 = 0.45 \quad (4.6)$$

where ADG is in kg/d, and DE*i* is in Mcal/d.

Carcass weight was greatest in pigs fed the MedCP MedNE diet, and similar to the LoCP HiNE and the MedFat MedNE diets but not the control and the HiFat HiNE diets ($P < 0.05$; Table 4.6). However, carcass weight (g/kg liveweight) was greater in pigs fed the LoCP HiNE diet compared to the control, the MedFat MedNE and the HiFat HiNE diets. Organ weight was greater in pigs fed the MedFat MedNE diet relative to other diets ($P < 0.05$). The same result was obtained with organ weight (g/kg liveweight) except that it was similar to those fed the HiFat HiNE diet. There was a relatively lower EBW in pigs fed the HiFat HiNE diet compared to those fed the MedCP MedNE and the MedFat MedNE diets ($P < 0.05$). The weight of individual organs remained fairly similar across treatments except for a greater blood weight in pigs fed the MedFat MedNE diet relative to those fed the control, the LoCP HiNE and the HiFat HiNE diets ($P < 0.05$). In contrast, spleen weight and in g/kg liveweight in pigs fed the LoCP HiNE diet was greater than those fed control, the MedFat MedNE and the HiFat HiNE diets ($P < 0.05$).

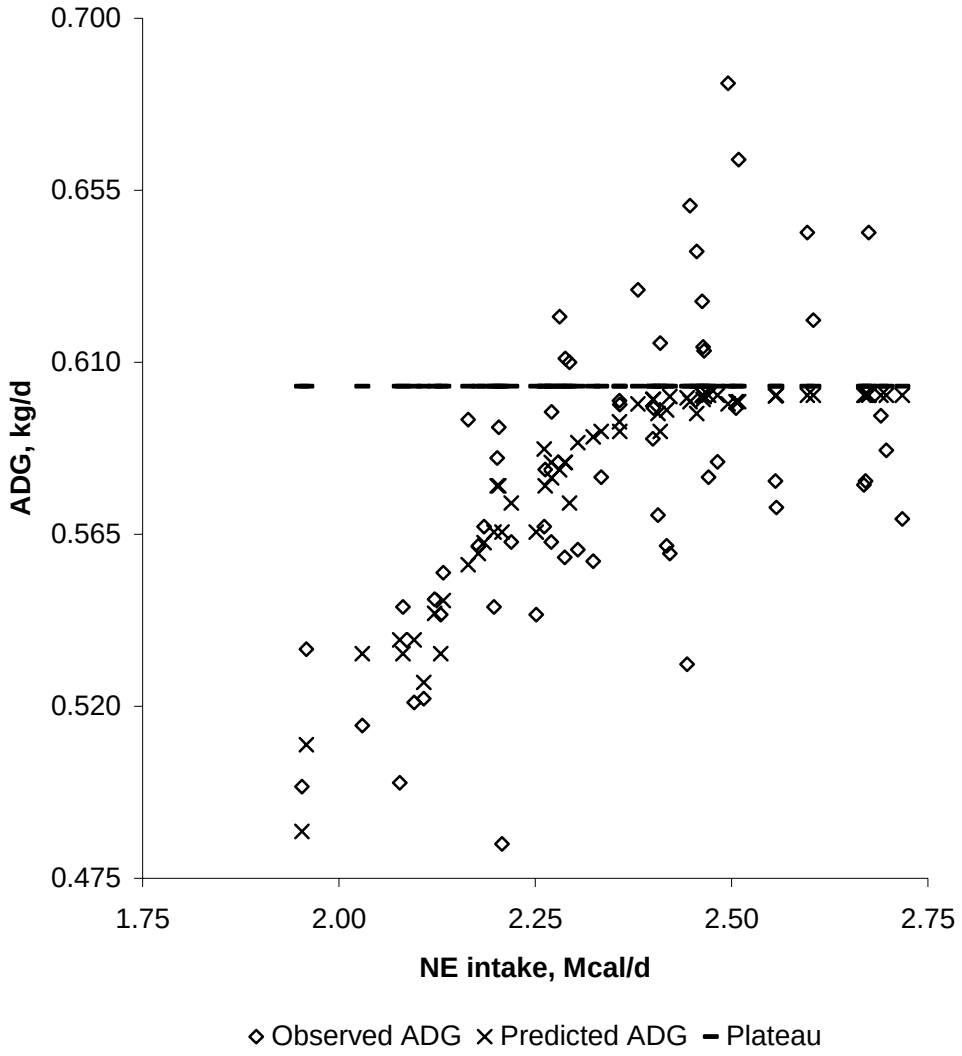

Figure 4.2. The relationship between ADG and NE intake in weaned pigs fed diets formulated at similar DE but increasing NE concentration (Linear-plateau model). ADG = -1.13 + 1.33NE*i* - 0.26NE*i*^{2} (n = 60; R^2 = 0.45; *P* < 0.001). NE*i* optimum = 2.57 Mcal/d; ADG plateau = 0.605 kg/d. NE*i* optimum for PD and plateau = 2.65 Mcal/d and 101 g/d, respectively, while NE*i* optimum for LD and plateau = 2.72 Mcal/d and 53 g/d, respectively.

Table 4.6. Effects of diets formulated at similar DE but increasing NE concentration on the physical body composition of weaned pigs at 25 kg BW[a]

	Diets								
	1	2	3	4	5				
	Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE				
DE, Mcal/kg[b]	3.47	3.47	3.57	3.58	3.59			*P* values[c]	
Item NE, Mcal/kg[d]	2.29	2.39	2.55	2.45	2.44	ISG[e]	SEM	Diet	Gender
Number of pigs	12	12	12	12	12	16			
Weight, kg									
Carcass	18.7^{y}	19.5^{x}	18.8^{xy}	18.6^{xy}	17.5^{y}	6.5	0.2	0.0089	0.6142
Organ	4.2^{y}	4.2^{y}	4.0^{y}	4.5^{x}	4.1^{y}	1.4	0.1	0.0227	0.4876
Empty body (EBW)	23.0^{xy}	23.6^{x}	22.9^{xy}	23.2^{x}	21.7^{y}	8.0	0.2	0.0233	0.5396
Weight, g/kg liveweight									
Carcass	753^{y}	764^{xy}	782^{x}	752^{y}	748^{y}	771	3	0.0031	0.4202
Organ	170^{yz}	164^{y}	168^{yz}	183^{x}	177^{xy}	170	2	0.0078	0.9854
Empty body (EBW)	923	928	950	935	925	941	3	0.0681	0.4783
Organ weight, g									
Empty digestive tract	1914	1830	1810	1921	1851	641	28	0.5548	0.7500
Blood	900^{y}	986^{xy}	855^{y}	1089^{x}	853^{y}	343	29	0.0453	0.9089
Liver	737	738	717	792	775	225	12	0.1964	0.0757
Heart	147	154	141	152	145	54	2	0.1574	0.0559
Lung	317	334	319	374	308	98	10	0.2331	0.9320
Kidneys	153	155	143	152	150	54	2	0.3737	0.6221
Spleen	54^{y}	59^{xy}	67^{x}	58^{xy}	51^{y}	19	2	0.0158	0.9670
g/kg EBW									
Empty digestive tract	83.7	77.7	79.1	82.9	85.7	80.9	1.2	0.2191	0.5587
Blood	39.2	42.0	37.2	46.8	39.4	42.8	1.2	0.0877	0.6608
Liver	32.1^{yz}	31.3^{z}	31.3^{z}	34.2^{xy}	35.6^{x}	28.3	0.4	0.0016	0.0602
Heart	6.4	6.5	6.2	6.6	6.7	6.7	0.1	0.2451	0.1292
Lung	13.8	14.1	13.9	16.2	14.2	12.4	0.4	0.3768	0.9892
Kidneys	6.7	6.6	6.2	6.6	6.7	6.8	0.1	0.0972	0.9172
Spleen	2.3^{y}	2.5^{xy}	2.9^{x}	2.4^{y}	2.3^{y}	2.4	0.1	0.0429	0.9282

[a]Data are least square means. The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. There were 6 pens per diet × gender, for a total of 12 pens per diet. One pig/pen closest to pen average final BW was selected for slaughter. Carcass is the eviscerated body including the head and feet; organ is the pooled individual organ including emptied GIT and blood; empty body is the sum of the two components. EBW = empty body weight.
[b]Determined digestible energy concentration.

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[c]Effect: diet × gender, $P > 0.05$; except organ wt, heart wt, heart g/kg EBW and spleen wt ($P < 0.05$).
[d]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation.
[e]Data of the initial slaughter group (ISG) were not included in the statistical analysis; n = 8 gilts and 8 barrows, average BW at slaughter = 8.5 ± 1.0 kg (mean ± SD).
[x,y,z]Means within a row lacking a common superscript letter differ (P < 0.05).

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Carcass and empty body protein content was similar in pigs fed the control, the MedCP MedNE and the MedFat MedNE diets (Table 4.7), and was lowest in those fed the LoCP HiNE diet ($P < 0.05$). A 2.5% reduction in protein and 17% increase in lipid content in the LoCP HiNE diet compared with the control diet were observed ($P < 0.05$). Organ and empty body lipid content was greatest in pigs fed the LoCP HiNE diet ($P < 0.05$).

Carcass water deposition rate was lower in pigs fed the HiFat HiNE diet compared to the others ($P < 0.05$; Table 4.8). Similarly, carcass PD was lower in pigs fed the HiFat HiNE diet compared to those fed the control, the MedCP MedNE and the MedFat MedNE diets ($P < 0.05$). Carcass LD tended to be greater in pigs fed the MedCP MedNE and the LoCP HiNE diets compared to the others ($P = 0.0686$) while LD:PD ratio was greater in pigs fed the LoCP HiNE diet compared to the control and the MedFat MedNE diets ($P < 0.05$). Carcass ash deposition rate, protein:water and ash:protein ratios were similar across treatments ($P > 0.05$). Pigs fed the MedFat MedNE diet had a greater organ water and ash deposition rates compared to the others ($P < 0.05$).

Table 4.7. Effects of diets formulated at similar DE but increasing NE concentration on the chemical composition of carcass, organ and empty body of weaned pigs at 25 kg BW[a]

			Diets							
			1	2	3	4	5			
			Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE			
	DE, Mcal/kg[b]		3.47	3.47	3.57	3.58	3.59		P values[c]	
Item, g/kg	NE, Mcal/kg[d]	ISG[e]	2.29	2.39	2.55	2.45	2.44	SEM	Diet	Gender
Number of pigs		16	12	12	12	12	12			
Carcass										
Water		696	696	689	685	696	691	2	0.3282	0.6042
Protein		154	176^{x}	173^{xy}	170^{z}	175^{x}	172^{yz}	1	0.0014	0.4775
Lipid		111	96	105	111	98	107	2	0.0715	0.6332
Ash		31	31	30	31	31	31	0.2	0.6830	0.3437
GE, Mcal/kg		1.90	1.83	1.93	1.95	1.83	1.90	0.19	0.1127	0.6735
Organ										
Water		821	797	797	790	800	792	1	0.0873	0.9959
Protein		133	156	155	157	155	155	1	0.9047	0.1996
Lipid		21	27^{y}	27^{y}	31^{x}	24^{y}	27^{xy}	1	0.0109	0.2216
Ash		12	12	12	12	12	12	0.5	0.2285	0.0353
GE, Mcal/kg		0.99	1.16	1.16	1.20	1.13	1.18	0.01	0.1089	0.9887
Empty body										
Water		721	715	708	704	716	710	2	0.1765	0.6272
Protein		150	172^{x}	170^{xyz}	168^{z}	171^{xy}	169^{yz}	1	0.0073	0.8583
Lipid		95	83^{y}	92^{xy}	97^{x}	83^{y}	92^{xy}	2	0.0417	0.5861
Ash		28	28	27	28	28	28	0.18	0.8109	0.2504
GE, Mcal/kg[f]		1.73	1.71	1.79	1.82	1.70	1.76	0.02	0.0919	0.6849
GE, Mcal/kg[g]		1.75	1.76	1.83	1.87	1.75	1.82	0.02	0.1655	0.5904

[a]Data are least square means. The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. There were 6 pens per diet × gender, for a total of 12 pens per diet. One pig/pen closest to pen average final BW was selected for slaughter. Carcass is the eviscerated body including the head and feet; organ is the pooled individual organ including emptied GIT and blood; empty body is the sum of the two components.

[b]Determined digestible energy concentration.

[c]Effect: diet × gender, $P > 0.05$; greater organ ash content in gilts than barrows.

[d]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation.

[e]Data of the initial slaughter group were used to estimate the initial body composition of the experimental pigs and were not included in the statistical analysis. BW at slaughter was 8.5 ± 1.0 kg (mean ± SD).
[f]Bomb calorimeter analysis.
[g]Calculated from analyzed protein and lipid content as 5.66 and 9.46 kcal/kg for protein and lipid, respectively (Ewan, 2001).
[x,y,z]Means within a row lacking a common superscript letter differ ($P < 0.05$).

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Table 4.8. Effects of diets formulated at similar DE but increasing NE concentration on deposition rates of water, protein, lipid, ash and energy retention in carcass and organ of weaned pigs between 8 and 25 kg BW[a]

	Diets							
	1	2	3	4	5			
	Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE			
DE, Mcal/kg[b]	3.47	3.47	3.57	3.58	3.59		*P* values[c]	
Item, g/d NE, Mcal/kg[d]	2.29	2.39	2.55	2.45	2.44	SEM	Diet	Gender
Number of pigs	12	12	12	12	12			
Carcass								
Water	296^{y}	317^{y}	296^{y}	300^{y}	276^{z}	9	0.0029	0.6039
Protein	80^{y}	85^{y}	78^{yz}	81^{y}	74^{z}	3	0.0028	0.7081
Lipid	37	48	48	39	42	4	0.0686	0.7557
Ash	13.6	14.0	13.6	13.6	12.4	0.8	0.0890	0.8312
Lipid:protein ratio	0.47^{z}	0.56^{xyz}	0.62^{x}	0.49^{yz}	0.57^{xy}	0.06	0.0278	0.5658
Protein:water ratio	0.27	0.27	0.26	0.27	0.27	0.01	0.7621	0.6102
Ash:protein ratio	0.16	0.16	0.17	0.17	0.17	0.01	0.5035	0.6240
RE, Mcal/d	0.77^{z}	0.90^{y}	0.86^{yz}	0.78^{z}	0.77^{z}	0.05	0.0233	0.9823
Organ								
Water	79^{z}	77^{z}	74^{z}	87^{y}	76^{z}	3	0.0148	0.5461
Protein	16.9	16.3	16.0	18.3	16.2	0.7	0.0736	0.1397
Lipid	2.9	3.0	3.4	2.8	3.0	0.2	0.4853	0.9923
Ash	1.2^{z}	1.1^{z}	1.1^{z}	1.4^{y}	1.2^{z}	0.1	0.0097	0.6698
Lipid:protein ratio	0.17^{yz}	0.18^{yz}	0.21^{x}	0.16^{z}	0.19^{xy}	0.01	0.0207	0.2903
Protein:water ratio	0.212	0.212	0.216	0.209	0.212	0.004	0.8773	0.1307
Ash:protein ratio	0.071	0.069	0.073	0.073	0.074	0.005	0.4552	0.0303
RE, Mcal/d	0.124	0.122	0.123	0.132	0.123	0.005	0.5766	0.3268

[a]Data are least square means. The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. There were 6 pens per diet × gender, for a total of 12 pens per diet. One pig/pen closest to pen average final BW was selected for slaughter. Carcass is the eviscerated body including the head and feed and organ is the pooled individual organ including emptied GIT and blood.

[b]Determined digestible energy concentration.

[c]Effect: diet × gender interaction, $P > 0.05$ for all variables except for organ protein and ash deposition rates ($P < 0.05$); greater organ Ash:protein ratio in gilts than barrows (0.074 vs. 0.070; $P < 0.05$).

[d]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation.

[x,y,z]Means within a row lacking a common superscript letter differ ($P < 0.05$).

Empty body water and protein deposition rates were lower in pigs fed the HiFat HiNE diet compared to those fed the control, the MedCP MedNE and the MedFat MedNE diets ($P < 0.05$; Table 4.9). There was a tendency for greater LD in pigs fed the LoCP HiNE diet ($P = 0.0744$) and the LD:PD ratio was increased in pigs fed the LoCP HiNE diet compared to those fed the control and the MedFat MedNE diets ($P < 0.05$; Table 4.9). Empty body RE:DE ratio in pigs fed the LoCP HiNE diet was 15% greater than those fed the control diet ($P < 0.05$) whereas RE:ME and RE:NE were not affected by diets ($P > 0.05$).

There was no correlation between actual DE concentration, performance variables and empty body nutrient content and deposition rates ($P > 0.05$; Table 4.10). Empty body CP content was weakly negatively correlated with determined NE concentration ($r = -0.32$; $P < 0.05$). Actual DE concentration was strongly positively correlated with determined NE concentration ($r = 0.73$; $P < 0.0001$).

Average daily feed intake was strongly positively correlated with DE and NE intake ($r = 0.96$ and 0.90, respectively; $P < 0.0001$; Table 4.10). Average daily gain was moderately positively correlated with DE and NE intake ($r = 0.50$ to 0.60; $P < 0.0001$) whereas gain:feed ratio was negatively correlated with DE and NE intake ($r = -0.50$ to -0.60; $P < 0.0001$). Empty body lipid content and the LD:PD ratio were weakly positively correlated with NE intake ($r = 0.25$ to 0.30; $P < 0.05$) but were not correlated with DE intake ($P > 0.05$). Empty body PD and LD were weakly positively correlated with DE and NE intake ($r = 0.30$ to 0.45; $P < 0.05$). Furthermore, DE intake was strongly positively correlated with NE intake ($r = 0.95$; $P < 0.0001$).

Table 4.9. Effects of diets formulated at similar DE but increasing NE concentration on deposition rates of water, protein, lipid, ash and energy retention in the empty body of weaned pigs between 8 and 25 kg BW[a]

	Diets							
	1	2	3	4	5			
	Control	MedCP MedNE	LoCP HiNE	MedFat MedNE	HiFat HiNE			
DE, Mcal/kg[b]	3.47	3.47	3.57	3.58	3.59		*P* values[c]	
Item, g/d NE, Mcal/kg[d]	2.29	2.39	2.55	2.45	2.44	SEM	Diet	Gender
Number of pigs	12	12	12	12	12			
Water	383^{y}	396^{y}	373^{yz}	390^{y}	348^{z}	11	0.0070	0.5219
Protein	99^{y}	101^{y}	95^{yz}	99^{y}	89^{z}	3	0.0069	0.4852
Lipid	42	51	52	42	44	5	0.0744	0.7658
Ash	14.8	15.1	14.7	14.9	13.6	0.6	0.0953	0.7990
Lipid:protein ratio	0.42^{z}	0.50^{yz}	0.55^{y}	0.43^{z}	0.50^{yz}	0.05	0.0197	0.5047
Protein:water ratio	0.26	0.26	0.25	0.25	0.25	0.01	0.9286	0.8300
Ash:protein ratio	0.15	0.15	0.15	0.15	0.15	0.01	0.5416	0.4325
RE, Mcal/d[e]	0.91	1.03	1.00	0.92	0.88	0.05	0.1141	0.7349
RE, Mcal/d[f]	0.93	1.05	1.02	0.96	0.94	0.05	0.3160	0.7902
RE:GE intake	0.21^{x}	0.24^{yz}	0.26^{z}	0.23^{xy}	0.21^{x}	0.01	0.0029	0.6927
RE:DE intake	0.26^{xy}	0.29^{yz}	0.30^{z}	0.27^{xyz}	0.26^{xy}	0.01	0.0399	0.6293
RE:ME intake	0.27	0.31	0.36	0.29	0.27	0.01	0.0941	0.5257
RE:NE intake	0.40	0.42	0.42	0.40	0.38	0.02	0.3457	0.6435

[a]Data are least square means. The experiment included a total of 60 pens and 240 pigs, from 28 to 56 days of age. There were 6 pens per diet × gender, for a total of 12 pens per diet. One pig/pen closest to pen average final BW was selected for slaughter. Empty body is the sum of the carcass and organ.

[b]Determined digestible energy concentration.

[c]Effect: diet × gender interaction, $P > 0.05$ for all variables.

[d]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation.

[e]Determined from bomb calorimeter analysis.

[f]Calculated from daily protein and lipid deposition rate using 5.66 and 9.46 kcal/kg for protein and lipid, respectively (Ewan, 2001).

[y,z]Means within a row lacking a common superscript letter differ ($P < 0.05$).

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Table 4.10. Correlations among actual DE, determined NE concentration and performance and empty body nutrient content and deposition rates in weaned pigs between 8 and 25 kg BW[a]

Variables	Correlation coefficient	*P* values
Actual DE concentration and,		
ADG	-0.2125	0.1031
ADFI	-0.1705	0.1928
Gain:feed ratio	-0.0232	0.8604
Empty body CP content	-0.2386	0.0663
Empty body lipid content	0.0042	0.9747
Empty body PD	-0.1330	0.3109
Empty body LD	-0.0335	0.7995
Empty body LD:PD ratio	0.0287	0.8276
Determined NE concentration	0.7333	0.0001
Determined NE concentration and,		
ADG	-0.1488	0.2564
ADFI	-0.2330	0.0731
Gain:feed ratio	0.1086	0.4088
Empty body CP content	-0.3188	0.0130
Empty body lipid content	0.2185	0.0935
Empty body PD	-0.0644	0.6247
Empty body LD	0.1931	0.1394
Empty body LD:PD ratio	0.2493	0.0548
DE intake, and		
ADG	0.5593	0.0001
ADFI	0.9638	0.0001
Gain:feed ratio	-0.5753	0.0001
Actual DE concentration	0.0969	0.4613
Empty body CP content	0.1196	0.3629
Empty body lipid content	0.2053	0.1156
Empty body PD	0.3552	0.0053
Empty body LD	0.3254	0.0112
Empty body LD:PD ratio	0.1937	0.1380
NE intake	0.9503	0.0001
NE intake, and		
ADG	0.5493	0.0001
ADFI	0.8971	0.0001
Gain:feed ratio	-0.5115	0.0001
Determined NE concentration	0.2186	0.0933
Empty body CP content	0.0408	0.7568
Empty body lipid content	0.2978	0.0208
Empty body PD	0.3635	0.0043
Empty body LD	0.4180	0.0009
Empty body LD:PD ratio	0.2937	0.0227

[a]Correlation coefficients were computed using individual pen's actual DE and determined NE concentration (see Table 4.4); n = 60.

4.4 Discussion

This experiment was conducted to determine if more predictable growth, nutrient deposition and energy utilization is achieved when diets are formulated using the NE as compared to the DE system. Diets were therefore formulated to a theoretically similar DE concentration but with varied NE concentration to allow the expected superiority of NE over DE to be identified.

Previous research has demonstrated that formulated DE and actual DE values may differ, and that determination of actual values is essential (Levesque, 2002; Rijnen et al., 2004). In our experiment, while all diets were formulated to an equal DE content, diets 3, 4 and 5 (LoCP HiNE, MedFat MedNE and HiFat HiNE, respectively) contained about 3% more DE than diets 1 and 2 (control and MedCP MedNE, respectively) . Nonetheless, the variation in NE was much greater than in DE, with the LoCP HiNE containing 11% more NE than the control diet, and the MedFat MedNE and HiFat HiNE diets containing 7% more. These results confirm the essential nature of determining actual DE values in experimental diets, and further, present practical advantage of DE over NE. While DE can be measured directly and accurately, NE can only be estimated by applying prediction equations (e.g. CVB, 1994) using the actual digestibility of individual components of the diet.

With the gradual decline in dietary CP content (the control, MedCP MedNE and LoCP HiNE diets), determined NE concentration increased in a linear fashion through increased apparent digestibility of CP, crude fat and GE. On the other hand, diets formulated to increase NE with increased fat content (the MedFat MedNE and HiFat HiNE diets), were associated with increased apparent digestibility of crude fat,

NDF and GE at the intermediate level (the MedFat MedNE diet), but when dietary fat content was further increased in the HiFat HiNE diet, apparent digestibility of CP, ADF and GE declined, and in some cases was poorer than the control diet. Consequently, NE concentration did not increase further in the HiFat HiNE diet as compared to the MedFat MedNE diet.

The failure to increase the determined NE in the HiFat HiNE diet compared to the MedFat MedNE diet is likely due to a specific ingredient effect, most likely associated with full-fat soybeans (FFSB). Since the apparent CP digestibility was lower in the HiFat HiNE diet compared to the MedFat MedNE diet (78 vs. 81%), it is possible that the FFSB may not have received proper heat treatment to remove the high level of trypsin inhibitor (TI; e.g. Rudolph et al., 1983) present in raw soybeans. Therefore, FFSB may be involved in the poorer apparent CP digestibility reported herein and would explain some of the lack of increase in NE concentration in the HiFat HiNE diet as compared to the MedFat MedNE diet. This is further supported by the observation that liver weight, expressed as a portion of EBW, increased as the quantity of FFSB increased in the diet. Garthoff et al. (2002) found a 23% increase in relative liver weight in pigs fed partially purified TI extracted from soybeans compared to control pigs.

However, it is also possible that a 15% higher fat content in the HiFat HiNE diet compared to the MedFat MedNE diet (9.1 vs. 7.9%) was simply too high for this age of pigs. This speculation is not supported by the fact that up to 3.3 fold increase in dietary fat content from 2.5 to 13% in diets fed to weaned pigs did not affect apparent faecal CP digestibility (Lowrey et al., 1962; Li and Sauer, 1994; Reis de Souza et al., 2000). Therefore, the most likely explanation for the lower CP digestibility is the quality of FFSB.

The NE system has been widely portrayed as superior for diet formulation and delivery to the pig as compared to the DE or ME systems, because it accounts for metabolic utilization and partitioning of energy in body tissue. At present, diet formulation on a DE and ME basis is more common in the U.S. and Canada than NE. Any study of the relationship between an energy system and animal performance may be confounded by specific ingredient effects, or by deficiencies in other nutrients. In our instance, it was important, for example, to ensure that amino acids were not limiting performance; we are confident that this was not the case, since the total lysine:DE ratio of diets ranges between 4.5 to 4.7 g/Mcal, equivalent to or slightly greater than the requirement determined in a previous experiment (Chapter 3). Other amino acids were formulated on an ideal amino acid ratio basis according to NRC (1998), so should also be above requirement.

The response to dietary treatment by the pigs differed when measuring BW gain versus measuring the composition of that gain. Therefore, it is important to measure ADG and the body composition of that gain to effectively study energy metabolism in weaned pigs.

The effect of increasing NE concentration on physical and chemical body composition and nutrient deposition rates has not been well documented in the weaned pig. In the present study, in addition to an increase in gross carcass weight, there was also an increase in carcass weight as a portion of total body weight (g/kg) when the determined NE increased with declining CP content, but not when determined NE increased through added fat. There was an increase in organ weight in pigs fed the MedFat MedNE diet, but this appeared to be due to the quantity of "blood" and therefore is an artifact, since blood collection would not be complete.

In contrast to the dietary effects on carcass and organ weight described above, there were important changes in carcass and empty body chemical composition. There was a linear decrease in empty body protein content as NE increased with declining CP (the control, the MedCP MedNE and the LoCP HiNE diets), and this occurred concurrent with a linear increase in empty body lipid content. The linear decrease in protein and increase in lipid content in the empty body is not explained by excess energy intake since NE intake was similar across diets.

In the present study, increasing NE concentration did not increase ADG. Indeed, ADG remained fairly constant when NE increased with declining CP content, whereas, ADG declined when NE increased through increased dietary fat content. Other studies that evaluated the effect of increasing dietary energy concentration on the growth performance of weanling pigs have consistently reported no improvement in ADG (Smith et al., 1999a; Reis de Souza et al., 2000; Levesque, 2002).

The failure to improve growth performance with increased dietary DE concentration was suggested by Levesque (2002) to be due to a similar NE concentration, the result of increasing dietary CP content concurrent with increasing DE. To avoid this situation, the diets utilized in the present investigation were formulated to a similar DE concentration while NE concentration increased. This allowed for a determination of the response of weaned pigs to increasing NE concentration. NE concentration was increased from the control to the LoCP HiNE diet with as much as a 26% reduction in dietary CP content, but again there was no improvement in ADG. The results of the present study strongly suggest that a higher dietary CP content per se and the concomitant lower NE concentration would not explain the lack of improvement in ADG and in other studies (e.g. Reis de Souza et al., 2000; Levesque, 2002).

Carcass and empty body PD were constant when NE increased with declining CP content, while PD decreased when NE increased through increased fat content. Conversely, LD tended to increase when NE increased with declining CP content whereas it was unchanged when NE increased through increased dietary fat content. Consequently, the LD:PD ratio of pigs increased on diets with declining CP content and tended to increase in pigs fed the diets with increased fat content. Indeed, LD:PD ratio was 31% greater in pigs fed the LoCP HiNE diet compared to those fed the control diet (0.55 vs. 0.42).

There is little data available on the effect of energy concentration on the LD:PD ratio of weaned pigs. In one such study, Reis de Souza et al. (2000) observed a 20% increase in the LD:PD ratio from 0.65 to 0.78 in weaned pigs when actual DE

concentration was increased from 3.24 to 3.50 Mcal/kg. Studies with growing pigs consistently found that the LD:PD ratio increased with increasing energy intake (Campbell et al., 1985b; Bikker et al., 1995; Quiniou et al., 1996a). Since the LD:PD ratio is an indicator of the associated variations in the composition of BW gain (Whittemore and Fawcett, 1976) and of lean growth, the increase in LD:PD ratio signifies that the efficiency of energy utilization for lean growth becomes poorer with increasing energy intake. Although, NE intake across diets in the present study did not differ significantly, the result of the LD:PD ratio resembled that observed with increased energy intake in growing pigs and demonstrates that increasing dietary energy concentration produce a poorer lean growth in weaned pigs. The poorer lean growth thus explains some of the lack of improvement in growth with increased NE concentration observed in the present study as well as earlier studies.

In studies of this nature, it is useful to determine the ratios of various nutrients to each other. If certain ratios are constant, this information can be used in other studies where detail carcass chemical composition is not measured directly. In general, increasing NE concentration did not affect ash deposition rate and the effect of dietary NE concentration on water deposition rate in carcass, organ and empty body closely resembled the effect described for PD. Therefore, the empty body protein:water ratio was constant across diets (mean = 0.25). Likewise the ash:protein ratio was not influenced by dietary NE concentration (mean = 0.16). These results are not surprising, since according to Kotarbinska (1971) and de Greef (1992), there is a close association of empty body protein to water and ash content. Nonetheless, with

these ratios known in the young pig, ash and water content in the carcass can be estimated from determined protein and lipid content by difference.

The decline in ADFI with increase NE concentration in the present study agrees with others (Van Lunen and Cole, 1998; Smith et al., 1999a; Levesque, 2002) who increased formulated DE, ME and actual DE by 15, 8 and 13%, respectively, and reported up to a 7% decline in feed intake of nursery pigs. It is well established that dietary energy concentration is an important determinant of voluntary feed intake of pigs (NRC, 1987; Lewis, 2001). However, other factors such as ingredient type (Nyachoti et al., 2004) and specific nutrient effects cannot be overlooked. Because feed intake was lowest in pigs fed the HiFat HiNE diet in the present study, it is possible that a specific ingredient effect and/or a higher fat content associated with a high level of FFSB may have influenced feed intake. Furthermore, feed intake is hormonally modulated (Nyachoti et al., 2004). For example, cholecystokinin, a local and peripheral satiety hormone secreted in the duodenum (Konturek et al., 2004) released in response to long chain fatty acids, decreases feed intake (Gregory et al., 1989; Matzinger et al., 2000).

Interestingly, increasing NE with fat appeared to exert the greatest impact on reducing feed intake. The higher fat content in the HiFat HiNE diet, and thus higher long chain fatty acids concentration, may increase cholecystokinin secretion and satiety and thus decrease feed intake. As well, with increasing dietary fat content, feed intake may decrease due to a reduction in the passage rate of digesta (Azain, 2001) producing a ‘gut-fill’ or satiety effect. Nonetheless, since the dietary fat content

in the control and LoCP HiNE diets was similar, fat content alone cannot explain the lower feed intake observed in pigs on the LoCP HiNE diet.

Although feed intake declined with increased determined NE concentration, it appears that pigs were eating to a constant NE intake. This suggests strongly that the control diet was not limiting in NE, and did not possess dietary characteristics inimical to achieving a desirable energy intake (Whittemore et al., 2001). Therefore, since pigs on the control diet were able to achieve energy intake desirable for optimal growth, it is not surprising that growth performance of those pigs offered diets with increasing levels of NE did not improve.

Energy intake (NE*i* and DE*i*) across diets was related to ADG (Figures 4.1 and 4.2), PD and LD using non-linear regression procedures (Table 4.11). There was a similarity in the NE*i* that maximized ADG and PD (2.57 and 2.65 Mcal NE/d, respectively), whereas LD required a higher level of NE*i* (2.72 Mcal NE/d). Similarly, the DE*i* that maximized ADG and PD (3.77 and 3.86 Mcal DE/d, respectively) was lower than that for LD (4.05 Mcal DE/d). Although the young pig is said to be in the energy dependent phase of growth (Campbell and Dunkin, 1983a; Edwards and Campbell, 1993), these results indicate that energy intake represents a greater constraint to LD than ADG or PD in weaned pigs. Moreover, increasing energy intake beyond a certain level would produce an increase in LD without further improvement in PD or total BW in the weaned pig.

Table 4.11. The relationships between energy intake and average daily gain, protein and lipid deposition rates in the empty body of weaned pigs between 8 and 25 kg BW allowed ad libitum access to diets formulated at similar DE but increasing NE concentration[a,b,c,d]

No.	Equation	R^2	*P* values	
1	ADG = -1.15 + 0.92DE*i* - 0.12DEi^2	0.49	0.0001	DEi_0 = 3.77 Mcal/d; Plateau = 0.607 kg/d
2	PD = -146 + 125DE*i* - 66DEi^2	0.16	0.0064	DEi_0 = 3.86 Mcal/d; Plateau = 101 g/d
3	LD = -71 + 51DE*i* - 5DEi^2	0.12	0.0211	DEi_0 = 4.05 Mcal/d; Plateau = 52 g/d
4	ADG = -1.13 + 1.33NE*i* - 0.26NEi^2	0.45	0.0001	NEi_0 = 2.57 Mcal/d; Plateau = 0.605 kg/d
5	PD = -160 + 195NE*i* - 36NEi^2	0.16	0.0064	NEi_0 = 2.65 Mcal/d; Plateau = 101 g/d
6	LD = -105 + 97NE*i* - 14NEi^2	0.20	0.0016	NEi_0 = 2.72 Mcal/d; Plateau = 53 g/d

[a]DE*i* and NE*i* used in the analyses were calculated from dietary actual DE concentration and determined NE concentration, respectively, and weekly ADFI (see Table 4.4). DEi_0 and NEi_0 are optimum DE*i* and NE*i*, respectively (i.e. intake for maximum performance).

[b]Regression analyses were conducted using the linear-plateau model (Proc NLIN of SAS); where ADG (PD or LD) = a + b*DE*i* (or NE*i*), when DE*i* < DEi_0 (or NE*i* < NEi_0), and ADG (PD or LD) = constant, when DE*i* > DEi_0 (or NE*i* > NEi_0). The break point DEi_0 and NEi_0 were determined using the iteration (Marquardt) method until the residual mean square error was minimized.

[c]ADG is in kg/d, PD and LD are in g/d; DE*i* and NE*i* are in Mcal/d.

[d]n = 60 pens (4 pigs per pen). PD and LD were determined from the data of the sacrificed pigs (one pig/pen; Table 4.9).

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One of the objectives of the present study was to determine if a more predictable growth, nutrient deposition and energy utilization in the weaned pig is achieved with NE or with DE. While DE*i* and NE*i* were both significantly correlated with ADG, there was a stronger correlation between NE*i* and LD than between DE*i* and LD. In addition, both NE*i* and determined NE concentration were more strongly correlated with empty body nutrient content and deposition rates. Therefore, based on correlation analysis, NE gives a marginal advantage over DE on predictable body composition rather than overall growth performance.

The observed reduction in ADFI with increased NE concentration, combined with a growth rate that either remained unchanged or declined, resulted in no difference in feed efficiency, except for a numerical increase in feed efficiency when NE increased with declining CP content. The increased feed efficiency in other studies (e.g. Smith et al., 1999a; Levesque, 2002) was due to a reduced feed intake at constant growth rate. The absence of a change in feed efficiency in the present study is puzzling, since increased energy concentration should, as a minimum, cause a change in feed efficiency. The fact that we saw none brings into question the utilization of energy by the pigs fed the higher energy diets. Since the diet DE content was measured directly, and the NE values were determined from actual nutrient digestibility according to CVB (1994), we are confident that some diets contained elevated energy relative to the control diet. The efficiency of DE and NE utilization for BW gain declined when NE increased with increased fat but remained constant when NE increased with declining CP content.

In conclusion, growth rates in weaned pigs were not improved at higher levels of determined dietary NE concentration (> 2.29 Mcal NE/kg). Dietary formulation on a DE basis using an iso-energetic reduction in CP or an increase in fat content did not improve growth but increased body fat content and lipid deposition rate. The differences in growth, body composition and nutrient deposition rates when diets contained similar DE but different determined NE concentration showed that DE does not produce predictable performance. Inconsistencies with determined NE concentration and performance confound any benefit or advantage of NE. However, NE is marginally better than DE in describing the composition of gain and nutrient deposition rather than overall animal performance.

4.5 Implications

This present study showed that by lowering dietary CP, estimated dietary energy concentration (i.e. NE) was increased. However, the increase in energy concentration was not apparent on a DE basis. To take advantage of reducing dietary CP (e.g. favourable economics of synthetic AA vs. protein supplements in least-cost formulations, and or reduced nitrogen output), NE based formulation for the weaned pig is to be favoured. Furthermore, NE offered a slight advantage over DE in describing the composition of gain and nutrient deposition in weaned pigs.

5. THE EFFECT OF REDUCING ENERGY INTAKE ON THE PERFORMANCE OF WEANED BARROWS WHEN AMINO ACID INTAKE DECLINES EITHER IN DIRECT PROPORTION TO ENERGY OR AT A REDUCED RATE

5.1 Introduction

The response of pigs to daily energy intake has often been studied by controlling daily feed allowance as opposed to changing diet energy concentration (Rao and McCracken, 1991; de Greef and Verstegen, 1993; Bikker et al., 1995). However, reducing energy intake in this manner results in a parallel and proportional reduction in amino acid intake. This leads to questions about the adequacy of amino acid nutriture under such conditions, especially at very low feed intakes.

To overcome this issue, diets can be formulated to contain excess amino acids to theoretically ensure amino acid intake is not limiting the pig's response to energy (Quiniou et al., 1996a,b). However, both amino acids and energy intake still varies simultaneously, and the interpretation of results may be difficult. Alternatively, two basal diets may be formulated at similar energy content and ideal protein ratio, with one diet containing elevated levels of amino acids. The intake of the higher amino acid basal diet may then be increased as the feed intake declines, so that amino acid intake is either constant or declines at a rate that is less than that of energy. This

eliminates amino acid intake as a confounding factor in studies of differing energy intake.

The objective of the present study was to evaluate the response of weaned pigs to decreasing daily energy intake, with amino acid intake either declining at a constant proportion with energy or declining at a reduced rate. This experiment was conducted as a precursor to the following energy study in the thesis, to help determine how it should be designed.

5.2 Materials and Methods

General

A growth trial was carried out with the offspring of C-22 females × 337 sires (PIC Canada Ltd, Airdrie, AB). At weaning (21 d; 6.7 ± 1.3 kg; mean ± SD) all pigs were transferred to all-in-all-out nursery rooms equipped with automatic light timers (12-light:12-dark cycle) and an integrated controllers (Model PEC; Phason, Winnipeg, MB) regulating heating and ventilation systems. Room temperature was initially set at 29ºC at weaning and gradually decreased by 1.5ºC/wk.

Nursery rooms contained 32 pens each (1.27 × 1.04 m) with fully slatted floors. Each was equipped with a single nipple drinker and an adjustable multiple-space dry feeder. The feeders were checked daily for proper feed flow and to prevent wastage and the drinkers for adequate water flow.

The experiment was conducted in two replicates of 28 individually housed pigs each per nursery room for a total of 56 barrows (average weaning weight, 7.5 ± 0.9 kg; mean ± SD). Pigs were allowed 14 days to acclimatize to weaning, the

environment and feed. During the acclimatization period, pigs were fed a pelleted commercial phase-1 starter diet (Appendix A; Ultrawean 21, Co-op Feeds, Saskatoon, SK) for the first 6-d post weaning followed by a pelleted phase-2 starter diet (Appendix B; GI MAX 21, Co-op Feeds, Saskatoon, SK) for the next 8 d. Fourteen days after weaning (d 0), pigs were weighed and the most uniform pigs were selected for use in the experiment, based on absolute weight (10.2 ± 0.9 kg; mean ± SD) and weight per day of age (0.290 ± 0.026 kg; mean ± SD). Pigs were blocked according to body weight and the 7 pigs within each weight block were randomly assigned to pen; the allocation of pen within the room to treatment was also random. In this way, a total of 8 pigs per treatment were assigned.

The University Committee on Animal Care and Supply at the University of Saskatchewan approved the animal care protocol (# 20030103) for adherence to guidelines of the Canadian Council of Animal Care (1993).

Experimental Diets and Treatments

Two experimental diets based on wheat, corn and barley were formulated to contain the same level of DE (Table 5.1; 3.41 Mcal DE/kg). Diet 1 (D1) was formulated to meet the amino acid, mineral and vitamin requirements of pigs of this age, according to the NRC (1998) when fed ad libitum. Diet 2 (D2) was formulated with the concentration of amino acids, minerals and vitamins increased by about 40%, relative to D1 (Table 5.2).

Table 5.1. Ingredient composition of the experimental diets, as fed

Ingredients, %	Diet 1	Diet 2
Wheat	42.50	27.00
Corn	14.72	11.27
Barley	10.32	14.41
Soybean meal	17.73	25.80
Menhaden fish meal	7.70	11.00
Dried skimmed milk	4.13	5.90
Limestone/glass rock	0.42	0.61
Mono/dical phosphate	0.59	0.84
Salt	0.30	0.43
Mineral premix	0.50[a]	0.72[c]
Vitamin premix	0.50[b]	0.72[d]
Choline chloride	0.05	0.07
l-lysine HCl	0.28	0.49
l-threonine	0.10	0.25
dl-methionine	0.03	0.22
l-tryptophan	0.04	0.09
LS 20[e]	0.10	0.10

[a]Provided per kg of diet: Zn, 100 mg as zinc sulfate; Fe, 80 mg as ferrous sulfate; Cu, 50 mg as copper sulfate; Mn, 25 mg as manganous sulphate; I, 0.50 mg as calcium iodate; Se, 0.10 mg as sodium selenite.
[b]Provided per kg of diet: vitamin A, 8,250 IU; vitamin D_3, 825 IU; vitamin E, 40 IU; niacin, 35 mg; D-pantothenic acid, 15 mg; riboflavin, 5 mg; menadione, 4 mg; folic acid, 2 mg; thiamine, 1 mg; D-biotin, 0.2 mg; vitamin B_{12}, 25 µg.
[c]Provided per kg of diet: Zn, 144 mg as zinc sulfate; Fe, 115 mg as ferrous sulfate; Cu, 72 mg as copper sulfate; Mn, 36 mg as manganous sulphate; I, 0.72 mg as calcium iodate; Se, 0.144 mg as sodium selenite.
[d]Provided per kg of diet: vitamin A, 11,880 IU; vitamin D_3, 1,188 IU; vitamin E, 58 IU; niacin, 50 mg; D-pantothenic acid, 22 mg; riboflavin, 7.2 mg; menadione, 5.8 mg; folic acid, 2.9 mg; thiamine, 1.4 mg; D-biotin, 0.29 mg; vitamin B_{12}, 36 µg.
[e]Includes lincomycin at 22 g/kg and spectomycin at 22 g/kg product (BioAgrimix, Mitchell, ON).

Table 5.2. Calculated and analyzed nutrient contents of the experimental diets, as fed[a,b,c]

Nutrients	Diet 1	Diet 2
Calculated		
DE, Mcal/kg	3.41	3.41
ME, Mcal/kg	3.18	3.14
NE, Mcal/kg	2.24	2.17
Crude protein, %	25.28	30.11
Crude fat, %	2.60	2.66
Crude fiber, %	2.82	2.79
Total lysine, %	1.51	2.07
TID lysine, %[c]	1.37	1.90
Total threonine, %	1.01	1.36
TID threonine, %	0.88	1.20
Total methionine, %	0.50	0.77
TID methionine, %	0.46	0.73
Total sulphur amino acid, %	0.90	1.21
TID sulphur amino acid, %	0.80	1.10
Total tryptophan, %	0.29	0.39
TID tryptophan, %	0.26	0.35
Total phosphorus, %	0.72	0.90
Calcium, %	0.74	1.04
Sodium, %	0.24	0.32
Chlorine, %	0.26	0.39
Analyzed		
GE, Mcal/kg	3.92	3.94
CP, %	25.37	30.44
Crude fat, %	3.07	3.09
Crude fiber, %	2.52	2.67
Ash, %	7.04	8.72

[a]Diets were formulated to similar levels of DE concentration using NRC (1998) value of each ingredient. Calculated NE concentration was based on NE value of ingredients (CVB, 1998).

[b]Calculated crude protein and lysine content were based on pre-assayed value of wheat, corn, barley, soybean meal, fish meal and skimmed milk. Amino acid analysis was conducted according to Llames and Fontaine (1994) (Degussa Corporation, Amino acid Lab, Allendale, NJ).

[c]TID = true ileal digestible amino acid; calculated based on analyzed amino acid content and TID coefficient (NRC, 1998) of individual ingredients.

Prior to diet formulation, wheat, corn, barley, soybean meal, fish meal and skimmed milk were assayed for protein and amino acid composition (Degussa Corporation, Amino acid Lab, Allendale, NJ) to maximize diet accuracy.

The two diets were fed as follows to provide seven dietary treatments: 1, D1 fed ad libitum; 2, D1 fed at 70% of ad libitum; 3, D1 fed at 60% of ad libitum; 4, D1 fed at 50% of ad libitum; 5, 67% of D1 and 33% of D2 fed at 70% of ad libitum; 6, 33% of D1 and 67% of D2 fed at 60% of ad libitum; and 7, D2 fed at 50% of ad libitum.

As the daily feed allowance declined, two amino acid regimens were created. The amino acid intake of pigs on treatments 2 to 4 declined in constant proportion to energy (ConP). As the proportion of D2 increased, amino acid intake of pigs on treatments 5 to 7 was increased in proportion to energy (RedP). This allowed us to determine the impact of declining amino acid and energy intake concurrently.

The restricted treatments were based on the feed intake of ad libitum pigs on a BW basis. Prior to the first weigh period completed on d4 of the experiment, the ad libitum intake of the control pigs was obviously unavailable, so for this period alone, the restricted intakes were based on the estimated ad libitum intake; this in turn was taken from the ad libitum intake of pigs of a similar size and age in a previous experiment. The ad libitum intake was defined as 0.368 Mcal DE per kg $BW^{0.75}$ per day. Diets were offered to pigs in a single morning feeding.

Data Collection

The feeding of the experimental diets was initiated on d 0 (35 d and 10.1 ± 0.9 kg; age and initial BW, respectively; mean ± SD) and pigs were weighed twice weekly thereafter on Mondays and Thursdays, prior to feeding. On each weigh day, feed consumption was measured. The daily feed allowance of the restricted pigs was then determined on the basis of the feed consumption of the ad libitum pigs at the same BW.

The data were used to calculate the average daily gain (ADG), average daily feed intake (ADFI), gain:feed ratio, DE intake and energy efficiency.

Chemical Analyses

Feed samples were prepared for chemical analyses by grinding through a 1-mm screen in a Retsch mill (Retsch Model ZM1; Brinkman Instrument of Canada Ltd., Rexdale, ON).

Nitrogen in feed samples was measured by combustion (Method 968.06; AOAC, 1990) using a Leco protein/nitrogen determinator (Model FP-528, Leco Corp., St. Joseph, MI). Calibration was conducted with an EDTA standard (nitrogen content 9.57 ± 0.02%; Leco Corp., St. Joseph, MI). On analysis, the nitrogen content of the EDTA standard was 9.57 ± 0.01%. Crude protein was expressed as nitrogen × 6.25. Gross energy was measured in an adiabatic bomb calorimeter (Model 1281; Parr Instruments, Moline, IL). Crude fat in feed samples was determined after ether extraction (Serial # 263220, Labconco Corp., Kansas city, MO) (Method 920.39; AOAC, 1990). Feed samples were analyzed for CF using an Ankom^{200} fiber analyzer

(Ankom Technology Co., Fairport, MI). Ash was determined by incineration in a muffle furnace at 600ºC for 12 h. All analyses were carried out in duplicate.

Calculation and Statistical Analyses

Energy efficiency expressed as Mcal/kg was calculated as DE intake/ADG, where DE intake (Mcal/d) was calculated from the formulated DE concentration as fed (Mcal/kg) × ADFI (kg/d), and ADG is the average daily gain (kg/d).

Data were analyzed using the MIXED procedure of SAS (SAS Institute Inc., 1996) with the individual pig as the experimental unit. Data were analyzed using repeated measures with appropriate covariance structures (Littell et al., 1998; Wang and Goonewardene, 2004) in a model that included day, feeding level, amino acid intake, and the following interactions: feeding level × amino acid intake, feeding level × day and amino acid intake × day. Initial BW on d 0 of the experiment was used as the covariate. Orthogonal polynomial contrasts (linear and quadratic) were used to partition variation associated with feeding level. Least squares means are presented and differences are considered statistically significant at $P < 0.05$.

5.3 Results

Body weight increased linearly with feeding level (Table 5.3; $P < 0.0001$) but was not affected by amino acid intake regime ($P > 0.05$). Average daily gain and ADFI increased linearly with increased feeding level (Table 5.3; $P < 0.0001$) but were not affected by amino acid intake ($P < 0.05$). Gain:feed ratio was not affected by feeding level ($P > 0.05$); however, there was a feeding level × amino acid intake

Table 5.3. The effect of declining energy intake with amino acid intake maintained at constant proportion (ConP) or increasing proportion (RedP) to energy on body weight, growth rate, feed intake and feed efficiency of weaned barrows (entire period)[a]

	Treatments[b]							
		ConP			RedP			
	1	2	3	4	5	6	7	
Item	100	70	60	50	70	60	50	SEM
Number of pigs	8	8	8	8	8	8	8	
Body weight, kg								
Start weight	10.17	10.13	10.17	10.16	10.16	10.08	10.17	0.12
Day 7	13.95	11.96	11.44	11.07	11.99	11.82	11.42	0.23
Day 14	19.28	15.48	14.77	13.80	15.77	14.81	14.32	0.32
Day 21	24.92	20.54	18.76	17.23	20.47	19.09	18.16	0.38
Day 26	29.31	24.43	21.99	19.89	24.24	22.49	21.15	0.42
ADG, g/d	734	538	443	364	527	465	411	15
ADFI, g/d	1065	719	616	520	721	627	532	12
Gain:feed ratio, g/g	0.757	0.712	0.671	0.647	0.703	0.705	0.735	0.022

Effect	Body weight	ADG	ADFI	Gain:feed ratio
Day	0.0001	0.0001	0.0001	0.0001
Feeding level	0.0001	0.0001	0.0001	0.6321
Linear	0.0001	0.0001	0.0001	0.0335
Quadratic	0.9612	0.1386	0.8861	0.6977
AA intake regime	0.1671	0.1097	0.3852	0.0370
Feeding level × AA intake regime	0.6432	0.1546	0.9173	0.0077
Feeding level × Day	0.0001	0.6437	0.0001	0.1983
AA intake regime × Day	0.5635	0.8884	0.9396	0.1987

[a]The experiment included a total of 56 individually housed barrows from 35 to 61 days of age. Data were analyzed with repeated measure including initial BW as a covariate. The covariate was significant ($P < 0.05$) for ADG, ADFI and gain:feed ratio.
[b]AA = Amino acid; ConP = amino acid intake at constant proportion to energy; RedP = amino acid intake at increasing proportion to energy.

interaction for gain:feed ratio ($P < 0.01$). Pigs on the 50% feeding level with ConP had a lower gain:feed ratio compared to ad libitum fed pigs, whereas the gain:feed ratio of pigs with RedP was similar to ad libitum fed pigs. There was a feeding level × day interaction for BW and ADFI ($P < 0.01$).

Digestible energy intake increased quadratically with increased feeding level (Table 5.4; $P < 0.001$) but was not affected by amino acid intake ($P > 0.05$). The amino acid intake of pigs on the RedP regimen in treatments 5, 6 and 7 were 18, 25, and 38% greater than those on the ConP regimen in treatments 2, 3 and 4, respectively. Total and digestible lysine intake increased quadratically with increased feeding level ($P < 0.001$) and was greater with the RedP compared with ConP treatments ($P < 0.001$). The efficiency of energy utilization for growth (Mcal DE/kg weight gain) was not affected by feeding level and amino acid intake ($P > 0.05$). However, a feeding level × amino acid intake interaction ($P < 0.05$) revealed a better energy utilization in pigs on the 50% feeding level with RedP compared to ad libitum fed pigs, whereas the energy utilization of pigs with ConP was similar to ad libitum fed pigs. The efficiency of lysine utilization for growth (g/kg weight gain) decreased with increased feeding level ($P < 0.005$) and was poorer in pigs with RedP compared with ConP treatments ($P < 0.001$).

Table 5.4. The effect of declining energy intake with amino acid intake maintained at constant proportion (ConP) or increasing proportion (RedP) to energy on estimated energy and lysine intake and utilization in weaned barrows[a]

	Treatments[b]							
		ConP			RedP			
	1	2	3	4	5	6	7	
Item	100	70	60	50	70	60	50	SEM
Number of pigs	8	8	8	8	8	8	8	
DE intake, Mcal/d[c]	4.50	3.00	2.62	2.20	3.07	2.62	2.24	0.10
Total lysine intake, g/d	16.1	10.8	9.3	7.8	12.2	11.8	11.0	0.4
TID lysine intake, g/d[d]	14.6	9.7	8.5	7.2	11.3	10.7	10.1	0.3
Energy utilization, Mcal DE/kg gain	6.35	5.43	5.91	6.01	5.69	5.65	5.46	0.20
Total lysine utilization, g/kg gain	22.7	19.2	21.2	21.6	23.0	25.3	26.7	0.8
TID lysine utilization, g/kg gain	20.6	17.5	19.2	19.6	20.9	23.1	24.5	0.7

Effect	DE intake	Total lysine intake	TID lysine intake	Energy utiliz.	Total lysine utiliz.	TID utiliz.
Day	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Feeding level	0.0001	0.0001	0.0001	0.5583	0.0031	0.0023
Linear	0.0001	0.0001	0.0001	0.0168	0.4800	0.4345
Quadratic	0.6580	0.7560	0.6258	0.0764	0.0409	0.0423
AA intake regime	0.6915	0.0001	0.0001	0.3108	0.0001	0.0001
Feeding level × AA intake regime	0.9151	0.2386	0.2011	0.0252	0.4665	0.3831
Feeding level × Day	0.0001	0.0001	0.0001	0.2255	0.1626	0.1610
AA intake regime × Day	0.8115	0.0001	0.0001	0.3355	0.7774	0.7882

[a]The experiment included a total of 56 individually housed barrows from 35 to 61 days of age. Data were analyzed with repeated measures.
[b]AA = amino acid; ConP = amino acid intake at constant proportion to energy; RedP = amino acid intake at increasing proportion to energy.
[c]Analyzed data were calculated from formulated dietary DE concentration and weekly ADFI.
[d]Dietary true ileal digestible lysine (TID) content was estimated with lysine digestibility coefficient of individual ingredient used in diets (NRC, 1998). True ileal digestible lysine intake was calculated from ADFI and dietary TID content.

5.4 Discussion

The growth rate of weaned pigs declined progressively in response to reduced energy intake, irrespective of the amino acid intake regimen (i.e. constant proportion, ConP or increasing proportion to energy, RedP). In a study similar to the present one with growing-finishing pigs over two 30-kg BW ranges (30 to 60 and 80 to 110), Nyachoti et al. (2000) investigated the effects of energy restriction when amino acid intake declined at a constant proportional to energy or was maintained at a constant daily intake. Growth, protein and lipid deposition rates declined with decreasing energy intake irrespective of the amino acid intake regimen. Our results also agree with that of Quiniou et al. (1996a) who found that growth and protein deposition rates in growing pigs from 45 to 100 kg BW declined when fed at 90, 80 or 70% of ad libitum but with a constant daily intake of amino acids. We could find no other report in the literature of studies of this nature in weanling pigs.

Whilst there were no statistically significant effects of amino acid intake on BW or ADG, there were large numerical differences that approached significance, with $P = 0.17$ and 0.11, respectively. It is therefore possible that a larger experiment with greater statistical precision may have significant differences. Because this experiment was held as a preliminary investigation to the main experiment (Chapter 6), we viewed these numerical differences with concern.

In contrast to findings with growing pigs between 30 to 60 kg BW (Nyachoti et al., 2000), differences in gain:feed ratio to energy and amino acid regimen were observed in the present study. Relative to ad libitum, the gain:feed ratio was poorer in pigs fed at 50% on ConP regimen (treatment 4) but not those on the RedP regimen

(treatment 7). The reason for this difference is not clear. Amino acid and energy dependent phases of protein deposition have been described (Campbell and Dunkin, 1983a; Edwards and Campbell, 1993). The supply of amino acid limits protein deposition, initially independent of energy and animal factors such as sex or genotype. As protein intake progressively increases, energy becomes limiting and protein deposition improves only when additional energy is supplied. Therefore, it is possible that amino acid intake may be limiting growth in pigs on the ConP but not those on the RedP regime. This explanation is supported by a numerically greater ADG of pigs on the RedP regimen at 50 and 60% energy restriction compared to those on the ConP regime ($P = 0.11$).

Interestingly, lysine utilization, expressed as g/kg BW gain, was constant across all ConP treatments. Since energy and amino acid intake declined across these treatments, it appears that lysine and not energy may have limited pig performance. In contrast, amino acid utilization in the RedP treatments increased as feed intake declined, and energy utilization, expressed as Mcal/kg gain was more or less constant. This would suggest that energy and not amino acid was limiting pig performance in the RedP pigs.

Protein deposition and growth of the restricted fed pigs was limited by energy intake based on calculated energy intake:requirement ratio (Table 5.5). The limitation of energy appeared to be greater in the RedP pigs. Additionally, according to a factorial estimation of lysine requirement based on the NRC model within the stated assumptions, the TIDlysine intake:required ratio would suggest that amino acid intake may have exerted a greater restriction to protein deposition of pigs on the ConP

Table 5.5. Estimated lysine requirement in weaned barrows fed decreasing amount of energy with amino acid intake maintained at constant proportion (ConP) or increasing proportion (RedP) to energy[a]

	Treatments[b]							
		ConP			RedP			
	1	2	3	4	5	6	7	
Item	100	70	60	50	70	60	50	SEM
Number of pigs	8	8	8	8	8	8	8	
TID lysine requirement, g/d[c]	14.92	11.18	9.30	7.69	11.04	9.69	8.66	0.31
for maintenance, g/d[d]	0.339	0.304	0.289	0.275	0.305	0.293	0.285	0.004
for protein deposition, g/d[e]	14.59	10.88	9.01	7.42	10.73	9.40	8.38	0.31
Protein deposition, g/d[f]	118.0	87.7	72.7	59.7	86.7	75.7	68.0	2.5
TIDintake:Required[g]								
d 0 to 7	0.71	1.34	1.61	2.44	1.41	1.69	2.13	0.12
d 8 to 14	0.91	0.80	0.74	0.76	0.86	1.06	1.02	0.02
d 15 to 21	1.15	0.83	0.89	0.86	1.02	1.06	1.10	0.02
d 22 to 26	1.11	0.95	0.96	0.96	1.11	1.16	1.23	0.02
d 0 to 26	0.98	0.90	0.93	0.95	1.04	1.14	1.20	0.02
ME intake, Mcal/d[h]	3.46	2.37	2.04	1.71	2.38	2.04	1.75	0.08
ME required, Mcal/d[i]	3.01	2.40	2.10	1.83	2.38	2.16	1.99	0.05
MEintake:Required	1.14	0.99	0.97	0.93	1.00	0.95	0.88	0.01

[a]The experiment included a total of 56 individually housed barrows from 35 to 61 days of age.
[b]ConP = amino acid intake at constant proportion to energy; RedP = amino acid intake at increasing proportion to energy.
[c]TID = true ileal digestible lysine; calculated as the sum of lysine required for maintenance and for protein deposition for entire period (d 0 to 26).
[d]Estimated as 0.036g × kg $BW^{0.75}$ per day (NRC, 1998).
[e]Estimated as 0.12 × whole body protein gain (NRC, 1998).
[f]Estimated assuming 16.1% of daily weight gain is protein (Chapter 4).
[g]Weekly TID intake/required; calculated with weekly intake and growth data.
[h]Calculated dietary ME concentration and ADFI for entire period (d 0 to 26).
[i]The sum of ME required for maintenance, protein, and lipid gain: where ME maintenance = 0.106 Mcal × kg $BW^{0.75}$ per d; ME protein = 0.0106 Mcal/kg; ME lipid = 0.0125 Mcal/kg; and LD is assumed as 0.48PD (data from Chapter 4).

compared to the RedP regimen at 50 and 60% energy restriction (Table 5.5). This provides further support for the suggestion that amino acid intake, not energy was limiting growth in the ConP treatments.

Also, there is a possibility of differences in nutrient accretion rate and body composition as a factor in the gain:feed ratio observed in the present study. According to Close (1996), if protein and amino acids are supplied in excess, lipid gain in pigs may be reduced as a result of the energetic cost of deamination and a consequent reduction in net energy. Skiba et al. (2002) who compared the effect of 40% energy (E) and protein (P) restriction in pigs between 15 to 25 kg BW found that the P and E restricted pigs grew slower compared to the control (370, 247, and 513 g/d, respectively). Although protein deposition rate was similar in the P and E pigs (39 and 37 g/d, respectively), lipid deposition rate was greater in the P than E pigs (95 vs. 13 g/d).

In conclusion, growth rate of weaned pigs increased with increasing energy intake. Amino acid intake appeared to reduce the growth rate of pigs with constant amino acid intake in proportion to energy at the two lowest levels of energy restriction. The interaction between energy and amino acid intake produced a poorer feed and energy utilization in pigs with constant amino acid intake in proportion to energy compared to those with increasing amino acid intake in proportion to energy at 50% and 60% energy intake.

5.5 Implications

The results of the present study confirm that the response of weaned pigs to declining energy intake, achieved through limiting daily feed allowance, may be confounded by amino acid supply, particularly at very severe feed intake restriction. Consequently, studies of reduced energy intake, achieved through restriction of feed intake must be conducted at no greater than 30% restriction if a single diet is to be used.

6. THE INTERACTIVE EFFECTS OF CHANGING NET ENERGY CONCENTRATION AND DAILY FEED (ENERGY) INTAKE ON ENERGY METABOLISM IN WEANLING BARROWS

6.1 Introduction

The interactive effects of energy concentration and feed (energy) intake have rarely been studied simultaneously. In the weaned pig, an accurate understanding of energy metabolism requires a simultaneous and detailed evaluation of the impact of dietary energy concentration and daily energy intake on growth and body composition.

Limited physical gut capacity, and resulting limits on energy intake, restricts growth (Van Lunen and Cole, 1998) in the weaned pig. Presumably then, increasing dietary energy concentration should increase energy intake and growth. However, in recent studies (Smith et al., 1999a; Reis de Souza et al., 2000; Levesque, 2002), increasing dietary energy concentration failed to improve weanling pig growth performance. The reasons for this lack of response are not clear.

There is no available literature on the impact of changing energy intake through the control of daily feed intake in the weanling pig. However, we can infer from studies on the growing pig (e.g. Bikker et al., 1995; Quiniou et al., 1995) that both protein-dependent and energy-dependent phases of growth probably exist. The

study reported herein tested the hypothesis that increasing dietary NE concentration will increase growth performance, tissue gain, and nutrient deposition rates with no interaction with feed (energy) intake in weaned pigs.

The main objective of the present study was to define the interaction between daily energy intake and dietary net energy concentration on body weight gain and on tissue (protein, lipid, ash, water) accretion rates and ratios. Secondary objectives were to evaluate the accuracy of existing factorial estimates of the efficiency of energy utilization for protein and lipid deposition and to determine whether actual (measured) DE intake or determined NE intake (CVB-based) is more effective in predicting animal growth performance.

6.2 Materials and Methods

General

The experiment involved all-in-all-out nursery rooms equipped with automatic light timers (12-light:12-dark cycle) and integrated controllers (Model PEC; Phason, Winnipeg, MB) regulating heating and ventilation systems. Room temperature was initially set at 29ºC at weaning and gradually decreased by 1.5ºC/wk. All pens (1.27 × 1.04 m) were equipped with fully-slatted floors, a single nipple drinker and an adjustable multiple-space dry feeder. The feeders were checked daily for proper feed flow to prevent wastage and the drinkers for adequate water flow.

The University Committee on Animal Care and Supply at the University of Saskatchewan approved the animal care protocol (# 20030103) for adherence to guidelines of the Canadian Council of Animal Care (1993).

Experimental Treatments and Design

A growth and comparative slaughter trial was conducted with the castrated male offspring of C-22 females × 337 sires (PIC Canada Ltd, Airdrie, AB). Treatments were arranged as a 3 x 3 factorial, with three diets and three feed intake levels. Diets were formulated to contain 2.21, 2.32 and 2.42 Mcal NE/kg. Three feed intake levels were employed, corresponding to 100%, 80% or 70% of ad libitum. These levels of restriction, and the nature of the design, were validated in a previous experiment (Chapter 5).

Feed intake levels in the restricted pigs were based on the intake of the corresponding ad libitum fed pigs. Prior to the first weigh period completed on d 4 of the experiment, the ad libitum intake of the control pigs was obviously unavailable, so for this period alone, the restricted intakes were based on the estimated ad libitum intake derived from the ad libitum intake of pigs of a similar size and age in a previous experiment. Feed was offered to pigs in a single morning feeding.

The experiment was conducted in three replicates of 27 pigs each plus the initial slaughter group (ISG; n = 3/replicate) which was included only in replicates 1 and 2. This provided a total of 87 barrows used in this experiment. Prior to the start of the experiment, pigs were allowed ad libitum access to a pelleted commercial phase-1 starter diet (Appendix A; Ultrawean 21, Co-op Feeds, Saskatoon, SK) for the first 6-d post-weaning followed by a pelleted phase-2 starter diet (Appendix B; GI MAX 21, Co-op Feeds, Saskatoon, SK) for the next 4 d. All available pigs were weighed at 7 d postweaning and the most uniform animals, based on BW, weight per day of age and post-weaning average daily gain (8.5 ± 0.9 kg, 0.298 ± 0.041, 0.164 ± 0.080 kg,

respectively; mean ± SD) were selected. Pigs were blocked and randomly assigned to experimental treatments and the ISG based on BW.

Experimental Diets

Experimental diets (Table 6.1) were formulated to contain increasing levels of NE, based on CVB (1998) NE values of ingredients. The target NE concentration was 2.21 to 2.42 Mcal/kg; on analysis, the determined NE concentration was 2.15 (low), 2.26 (medium) and 2.37 (high) Mcal NE/kg. Differences in NE concentration were achieved by a gradual reduction of CP content from 29.0 to 24.7% and crude fiber from 3.0 to 2.4%. Fat content was increased from 3.5 to 5.4% in the low to high NE diet. The diets contained celite at 0.5% as a source of exogenous acid insoluble ash, to serve as indigestible marker. The calculated and analyzed nutrient composition of experimental diets is reported in Table 6.2.

The amino acid profile of each diet was adjusted based on apparent digestible ideal amino acids. The apparent digestible lysine level was calculated to be constant across diets based on the optimum total lysine/Mcal DE ratio derived in a previous experiment (Chapter 3), and applied to the high energy diet. Other amino acids were formulated to levels according to the ideal protein ratio for this age of pig (NRC, 1998). This ensured that amino acid supply was non-limiting for growth. Diet formulation was based on pre-assayed crude protein and amino acid composition of soybean meal, fish meal and skimmed milk powder (Degussa Corporation, Amino acid Lab, Allendale, NJ).

Table 6.1. Ingredient composition of the experimental diets, as-fed basis[a]

	NE concentration, Mcal/kg		
Ingredients, %	2.21	2.32	2.42
Wheat	51.89	57.70	63.24
Soybean meal	27.00	19.25	11.50
Menhaden fish meal	8.50	8.50	8.50
Soy protein concentrate[b]	2.25	2.25	2.25
Dried skim milk	2.50	2.50	2.50
Lactose[c]	5.00	5.00	5.00
Canola oil	0.50	1.75	3.00
Limestone/glass rock	0.34	0.42	0.50
Salt	0.30	0.30	0.30
Mineral premix[d]	0.50	0.50	0.50
Vitamin premix[e]	0.50	0.50	0.50
Choline chloride	0.05	0.05	0.05
Celite[f]	0.50	0.50	0.50
$NaHCO_3$[g]	-	-	0.28
l-lysine HCl	-	0.29	0.59
l-threonine	0.04	0.17	0.30
dl-methionine	0.04	0.13	0.22
l-tryptophan	-	0.03	0.07
l-valine	-	0.05	0.09
l-isoleucine	-	0.01	0.02
LS 20[h]	0.10	0.10	0.10

[a]Calculated NE concentrations were based on NE value of ingredients (CVB, 1998). Soybean meal, fish meal and skimmed milk powder were assayed for crude protein and amino acid composition prior to diet formulation. Amino acid analysis was conducted according to Llames and Fontaine (1994) (Degussa Corporation, Amino acid Lab, Allendale, NJ).

[b]Soy protein conc. PROFINE E.

[c]Prolac (83% lactose).

[d]Provided per kg of diet: Zn, 100 mg as zinc sulfate; Fe, 80 mg as ferrous sulfate; Cu, 50 mg as copper sulfate; Mn, 25 mg as manganous sulphate; I, 0.50 mg as calcium iodate; Se, 0.10 mg as sodium selenite.

[e]Provided per kg of diet: vitamin A, 8,250 IU; vitamin D_3, 825 IU; vitamin E, 40 IU; niacin, 35 mg; D-pantothenic acid, 15 mg; riboflavin, 5 mg; menadione, 4 mg; folic acid, 2 mg; thiamine, 1 mg; D-biotin, 0.2 mg; vitamin B_{12}, 25 µg.

[f]Celite (Celite Corporation, Lompoc, CA), provided as a source of acid insoluble ash. Typical % physical composition: moisture, 0.8; SiO_2, 89.4; Na_2O, 3.8; Al_2O_3, 3.4; Fe_2O_3, 1.3; MgO, 0.6; CaO, 0.5; TiO_2, 0.2 (Megazyme International Ireland Ltd, Bray, Co. Wicklow, Ireland).

[g]Added to maintain dietary electrolyte balance (dEB) above 225 mEq/kg across diets (Patience et al., 1987).

[h]Includes lincomycin at 22 g/kg and spectomycin at 22 g/kg product (BioAgrimix, Mitchell, ON).

Table 6.2. Calculated and analyzed nutrient content of the experimental diets, as-fed basis[a]

	Formulated NE concentration, Mcal/kg		
Nutrients	2.21	2.32	2.42
Calculated			
ME, Mcal/kg	3.26	3.32	3.37
DE, Mcal/kg	3.48	3.53	3.57
DM, %	89.42	89.51	89.63
CP, %[b]	28.29	25.94	23.55
Crude fat, %	2.17	3.97	5.22
Crude fiber, %	2.68	2.58	2.48
Total lysine, %[b]	1.63	1.65	1.67
TID lysine, %[c]	1.47	1.51	1.55
TEAAN, %[d]	1.90	1.76	1.62
TEAAN/TNEAAN[d]	0.72	0.74	0.76
dEB, mEq/kg[e]	303	254	238
Analyzed			
GE, Mcal/kg	4.03	4.07	4.11
NE, Mcal/kg[f]	2.15	2.26	2.37
DE, Mcal/kg[g]	3.35	3.45	3.49
CP, %	28.99	26.74	24.70
Starch, %[h]	30.31	34.84	38.62
Sugars, %[i]	10.33	9.76	6.26
NSP, %	9.62	8.88	9.37
Crude fat, %	3.54	3.93	5.41
Crude fiber, %	2.99	2.56	2.35
Ash, %	7.25	6.83	6.30

[a]Calculated DE and ME concentrations were based on NRC (1998) values of each ingredient; calculated NE concentrations were based on NE value of ingredients (CVB, 1998).
[b]Calculated levels based on pre-assayed crude protein or total lysine content of soybean meal, fish meal and skimmed milk; other ingredients were based on NRC (1998) total lysine content.
[c]TID = true ileal digestible; calculated based on analyzed amino acid content and TID coefficient (NRC, 1998) of individual ingredients.
[d]TEAAN, total essential amino acid nitrogen; TNEAAN, total non-essential amino acid nitrogen.
[e]Dietary electrolyte balance, Na + K - Cl (Patience et al., 1987).
[f]Estimated from analyzed digestible nutrient contents according to CVB (1994) equation (see Table 6.7).
[g]Calculated based on apparent digestibility coefficients of GE (see Table 6.7).
[h]Determined enzymatically (AOAC, 2002).
[i]Sugars were calculated as total carbohydrates – (starch + total NSP + free sugars).

Data and Sample Collection

Pigs were weighed at the initiation of feeding of the experimental diets (31.5 ± 0.3 d and 9.5 ± 1.0 kg; age and initial BW, respectively; mean ± SD) and twice weekly thereafter on Mondays and Thursdays, prior to feeding. Feed disappearance was measured at each weigh day in the ad libitum-fed pigs and the daily feed allowances for the limit-fed pigs were adjusted based on the ad libitum intake on each diet, calculated on a BW basis. Freshly voided faeces were collected from each pig using the grab method over 3 d (days 15 to 17) and pooled per pig, in order to determine DE and estimate NE concentration of diets from digestible nutrient content. Faecal samples were frozen at –20ºC prior to lyophilization. Feed samples was taken at the time of feeding and pooled per diet. All samples were kept frozen at –20ºC until required for analysis.

Each pig was bled at approximately 1100 h on d 7 and again on d 21. Blood samples were collected via venipuncture into vacutainer tubes containing 143 USP units of sodium heparin. Plasma was harvested after spinning at 700 × *g* for 15 minutes (Model Centrific 228; Fisher, Nepean, Ontario) and stored at –20ºC for later assay of insulin-like growth factor-I (IGF-I) concentration.

Slaughter Procedure and Carcass Measurement

The comparative slaughter procedure was applied to replicates 1 and 2. Replicate 3 was conducted to increase the number of pigs for the growth performance study only. Pigs assigned to the ISG (n = 6; BW at slaughter was 9.4 ± 1.0 kg, mean ± SD) were sacrificed at the commencement of the experiment (d 0). The rest of the

pigs remained on the experimental treatments until they reached 25 ± 1 kg BW, at which time they were sacrificed to determine body composition.

Pigs were euthanized by CO_2 asphyxiation followed by exsanguination (Hoenderken, 1983; Gregory et al., 1987). The carcass was split down the midline from the groin to the chest cavity and the entire viscera were removed from the carcass. The gastrointestinal tract (GIT) was separated from the viscera and weighed, emptied of all digesta, patted dry and reweighed. The liver, kidneys, heart, lungs, and spleen were weighed individually. The weight of the organ fraction and blood were recorded as total organ weight and herein referred to as "organ." The weight of the eviscerated carcass (including head and feet) was recorded and referred to as "carcass." The empty body weight of the pig was taken as the sum of the weight of the carcass and the organs. The organ fraction and blood were pooled and stored separately from the carcass.

The carcass and organs were frozen at –20ºC until further processing. The frozen carcasses were cut into quartiles and passed through a 10-mm die four times in a commercial grinder (Model 801 GHP-25; Autio Company, Astoria, OR). Approximately 250 g of ground sample were taken from several subsamples and placed in a previously weighed aluminum container following the fourth passage through the die. The organ fraction was passed through the die once and mixed thoroughly before several subsamples were placed in a previously weighed aluminum container. All samples were weighed immediately after collection and kept frozen until freeze-drying to a constant weight.

Chemical Analyses

Feed and faecal samples were prepared for chemical analyses by air-equilibration and passed through a 1-mm screen (Retsch Model ZM1; Brinkman Instrument of Canada Ltd., Rexdale, ON).

The acid insoluble ash content of the diet was used as an indigestible marker and measured in feed and faeces (McCarthy et al., 1974) to determine the apparent faecal digestibility of DM and other nutrients. Pure celite standard samples were assayed to confirm the accuracy of the analytical procedure, and a recovery of 99.9 ± 0.01% was attained.

The moisture content of feed and freeze-dried faecal samples was determined by drying at 135ºC in an airflow-type oven for 2 h (Method 930.15; AOAC, 1990). Nitrogen in feed and faecal samples was measured by combustion (Method 968.06; AOAC, 1990) using a Leco protein/nitrogen apparatus (Model FP-528, Leco Corp., St. Joseph, MI). Calibration was conducted with an EDTA standard (nitrogen content 9.57 ± 0.02%; Leco Corp., St. Joseph, MI). On analysis, the nitrogen content of EDTA was 9.56 ± 0.02%. Crude protein was expressed as nitrogen × 6.25.

Gross energy was measured in an adiabatic bomb calorimeter (Model 1281; Parr Instruments, Moline, IL). Benzoic acid (6318 kcal/kg; Parr Instruments, Moline, IL) was used as the standard for calibration and was determined to be 6317 ± 2 kcal/kg at assay. Crude fat in feed samples was determined after ether extraction (Method 920.39; AOAC, 1990) in an extractor apparatus (Serial # 263220, Labconco Corp., Kansas city, MO) and in faecal samples after acidification with 9 N HCl, followed by ether extraction. Feed and faecal samples were analyzed for crude fiber

using an Ankom^{200} fiber analyzer (Ankom Technology Co., Fairport, MI). Ash was determined by incineration in a muffle furnace at 600ºC for 12 h.

Feed samples were passed through a 0.5-mm screen and analyzed for starch enzymatically (Method 996.11; AOAC, 2002) using a total starch assay kit (AA/AMG; Megazyme International Ireland Ltd, Bray, Co. Wicklow, Ireland). Feed samples were analyzed for total carbohydrates, total nonstarch polysaccharides (NSP) and free sugars based on the method of Englyst and Hudson (1987) and Englyst (1989). Sugars were calculated as total carbohydrates – (starch + total NSP + free sugars). According to Graham et al. (1986) and Bach Knudsen and Hansen (1991), faecal digestibility of starch and sugar were assumed to be 100%; therefore starch and sugar were not determined in the faecal samples (Noblet et al., 1994; Schrama et al., 1998; Le Goff and Noblet, 2001).

Freeze-dried carcass and organ samples were prepared for chemical analyses by blending in a grinder (Retsch Grindomix, Model GM200; F.Kurt Retsch GmbH & Co.KG, Haan, Germany). Samples were analyzed for DM, GE, crude fat and ash as described above. Nitrogen was measured with the Leco apparatus (Method 992.15; AOAC, 2002) and crude protein was expressed as nitrogen × 6.25.

Plasma samples were analyzed for IGF-I by radioimmunoassay as described previously (Kerr et al., 1990).

All chemical analyses were carried out in duplicate and were repeated when intra duplicate CV exceeded 3%.

Calculations and Statistical Analyses

Apparent digestibility coefficients of N, energy and other nutrients were determined using the following equation:

$$D_{ADN}\% = 100\% - [(I_D \times A_F)/(A_D \times I_F) \times 100] \quad (6.1)$$

where D_{ADN} is apparent digestibility coefficient of a nutrient N, I_D is percent index marker concentration in the assay diet, A_F is percent nutrient concentration in faeces, A_D is percent nutrient concentration in the assay diet, I_F is percent index marker concentration in faeces, all on DM basis.

The apparent digestibility coefficient of DM was determined using the following equation:

$$D_{ADM}\% = 100\% - [(I_D/I_F) \times 100] \quad (6.2)$$

where D_{ADM} is apparent digestibility coefficient of DM.

Metabolizable energy (ME) was calculated according to Noblet and Perez (1993).

$$ME = 0.999 \times DE – (0.82 \times DCP) \quad (6.3)$$

NE was estimated from digestible nutrients according to CVB (1994).

$$NE = 2.58 \times DCP + 8.63 \times DEE + 3.23 \times ST + 3.04 \times SG + 2.27 \times DRES \quad (6.4)$$

where NE is expressed in kcal/kg as is, DCP is digestible CP, DEE is digestible ether extract, ST is starch, SG is sugar, and DRES is digestible residuals, calculated as digestible organic matter - (DCP + DEE + ST + SG + digestible crude fiber).

Digestible energy intake (DE*i*) was calculated from the actual DE concentration × ADFI. Similarly, metabolizable energy intake (ME*i*) was calculated

from the calculated ME concentration (Eq. 6.3) × ADFI, and net energy intake (NE*i*) was calculated from the determined NE concentration (Eq. 6.4) × ADFI. In all calculations, DE, ME and NE (Mcal/kg) and ADFI (kg/d) were on DM basis.

Digestible energy intake for maintenance (DE*i*m) was calculated as 0.110 Mcal per kg $BW^{0.75}$ per d (NRC, 1998) and net energy for maintenance (NE*i*m) was calculated as 0.078 Mcal per kg $BW^{0.75}$ per d (Just, 1982), both expressed in Mcal/d.

Digestible energy and NE available for growth (DE*i*g and NE*i*g, respectively) was calculated as DE*i* - DE*i*m or NE*i* - NE*i*m.

Energy efficiency for gain (expressed as Mcal/kg) was calculated as DE*i*g or NE*i*g/ADG, where DE*i*g or NE*i*g was expressed in Mcal/d and ADG was the average daily gain in kg/d. Energy efficiency for protein and lipid deposition (expressed as g/Mcal) was calculated as PD (or LD)/DE*i*g or PD (or LD)/NE*i*g, where PD and LD were the respective determined deposition rates (g/d) of the sacrificed experimental pigs calculated as described below.

Data from the body composition of the ISG were used to estimate the initial body composition of the experimental pigs. The relationship between live weight and empty BW at slaughter was calculated and used with the carcass and organ analysis data of the ISG. The gain of protein, lipid, ash, water and energy were estimated as:

[(Final content, g or Mcal) – (initial content, g or Mcal)]/number of days on trial (6.5)

Empty body GE content was estimated in two ways: by bomb calorimeter analysis conducted on carcass and organ and by calculation based on the analyzed protein and lipid content and using the factors 5.66 and 9.46 Mcal/kg for protein and

lipid, respectively (Ewan, 2001). Similarly, energy retained as protein (ERP) and energy retained as lipid (ERL) were calculated as PD (in g/d) × 5.66 kcal/g and LD (in g/d) × 9.46 kcal/g, respectively.

Statistical analyses. Data were analyzed using the MIXED procedure of SAS (SAS Institute Inc., 1996) with the individual pig as the experimental unit and initial BW as a covariate for performance data. The statistical model included the effect of diet, feeding level and diet × feeding level interaction. Plasma IGF-I concentration data were analyzed using repeated measures and appropriate covariance structures (Littell et al., 1998; Wang and Goonewardene, 2004). The statistical model included the effect of day, diet, feeding level and the following interactions: diet × day and diet × feeding level. Regression analyses within SAS were used to evaluate the efficiency of utilization of actual DE and determined NE within diets for growth and nutrient deposition. Differences in the slopes of regression lines were evaluated according to Zar (1984).

The degree to which performance and carcass variables were related to actual DE and determined NE intake was determined with Pearson correlation coefficients using the correlation procedure of SAS (SAS Institute, Inc., 1996).

Least squares means were reported and differences were considered statistically significant at $P < 0.05$. Trends ($0.05 < P < 0.10$) were reported and $P > 0.10$ was considered non-significant.

6.3 Results

Performance

The performance results are shown in Table 6.3 and Figure 6.1. Starting weight was similar across treatment and final weight remained unaffected by dietary NE concentration ($P > 0.05$) but was increased by feeding level ($P < 0.05$). Days on test were longest in pigs fed the intermediate dietary NE concentration ($P < 0.05$), but ADG, ADFI and feed efficiency were not affected by dietary NE concentration ($P > 0.05$). Final weight and ADFI increased ($P < 0.05$) while days on test declined ($P < 0.001$) with increasing feeding level. The concomitant ADG increased with increasing feeding level ($P < 0.001$). Neither dietary NE concentration nor feeding level affected gain:feed ratio ($P > 0.05$). However, a NE × feeding level interaction ($P < 0.05$) in gain:feed ratio was observed as pigs fed the intermediate NE concentration diet at the 80% feeding level exhibited a poorer gain:feed ratio compared with the other treatments (Table 6.4).

Table 6.3. Effect of dietary NE concentration and feeding level on the performance of barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a,b]

	NE, Mcal/kg[c]			Feeding level, %[d]				*P* values		
Item	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	27	27	27	27	27	27				
Start weight, kg	9.47	9.49	9.44	9.53	9.46	9.40	0.12			
Final weight, kg	24.76	24.98	24.92	24.63	24.85	25.17	0.17	0.5551	0.0445	0.6571
Days on test	27.1	28.4	27.3	31.0	29.0	22.8	0.6	0.0328	0.0001	0.7487
ADG, g/d	577	561	579	491	534	692	8	0.2282	0.0001	0.3420
ADFI, g/d	789	771	784	661	740	943	9	0.3451	0.0001	0.1484
Gain:feed ratio, g/g	0.733	0.727	0.740	0.743	0.724	0.733	0.009	0.5344	0.2828	0.0306

[a]Data are presented as least square means. The experiment included a total of 81 barrows, from on average 31 to 62 days of age. Thus, there were 27 pigs per NE level, 27 pigs per feeding level and 9 barrows per NE × feeding level combination.
[b]Data were analyzed with initial BW as a covariate. The covariate was significant ($P < 0.05$) for final weight, days on test, ADG, and ADFI but not significant ($P > 0.05$) for gain:feed ratio.
[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).
[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

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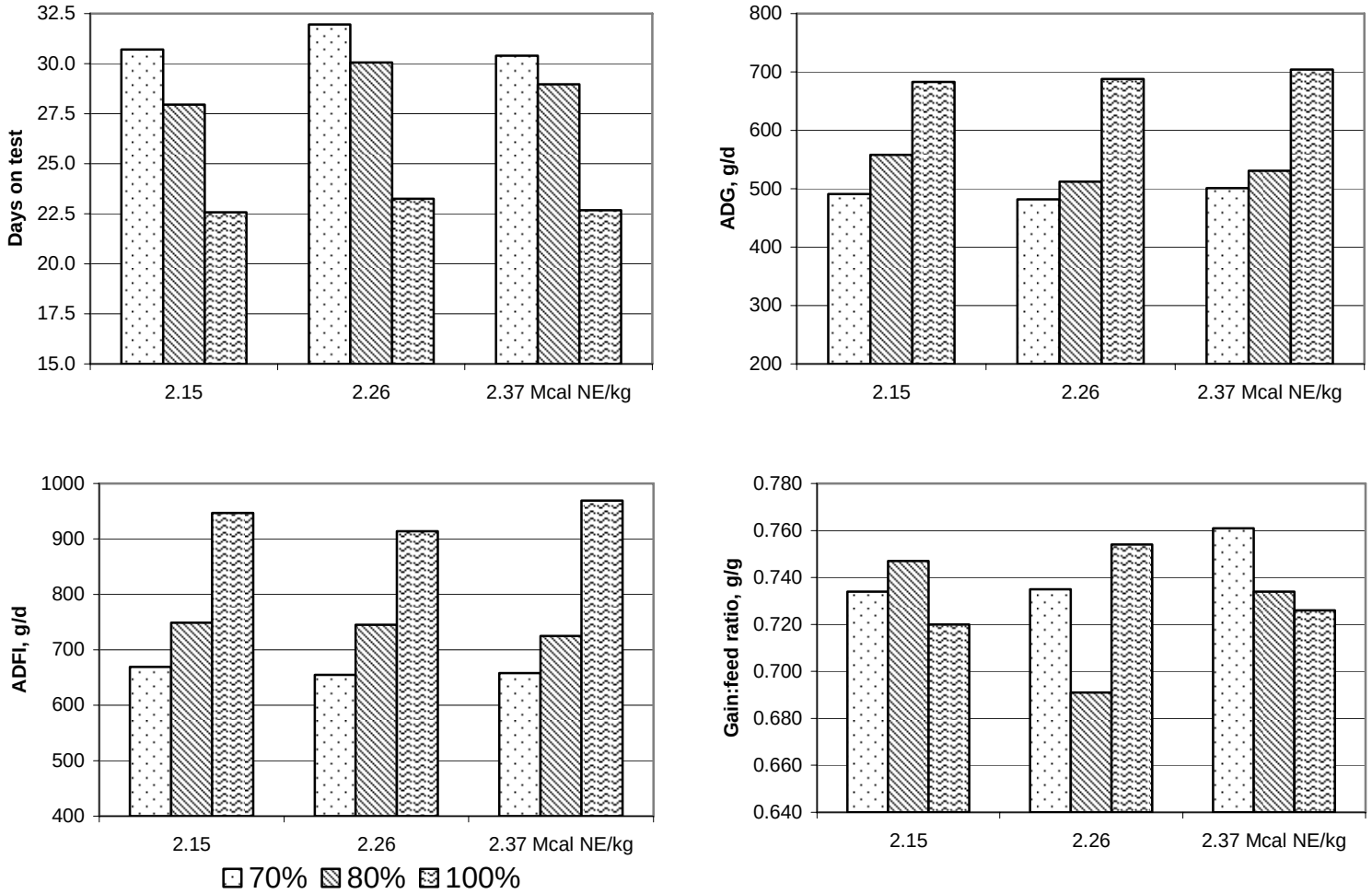

Figure 6.1. Days on test, daily gain, feed intake and feed efficiency of barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. SEM = 0.03, 8, 9 and 0.009 for days on test, ADG, ADFI and gain:feed ratio, respectively (see Table 6.3 for *P* values).

Table 6.4. Feed efficiency of barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a]

NE, Mcal/kg[b]	Feeding level, %[c]	Gain:feed ratio, g/g
2.15	70	0.734
	80	0.747
	100	0.720
2.26	70	0.735
	80	0.691
	100	0.754
2.37	70	0.761
	80	0.734
	100	0.726
SEM		0.015
P values		
NE		0.5344
Feeding level		0.2828
NE × Feeding level		0.0306

[a]Data are presented as least square means. The experiment included a total of 81 barrows, from on average 31 to 62 days of age. Thus, there were 9 barrows per NE × feeding level combination.
[b]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).
[c]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

Digestible energy intake (DE*i*), DE*i*g, DE*i*m and NE*i*m were similar across dietary NE concentration (Table 6.5; $P > 0.05$). In addition, DE*i*m and NE*i*m were of course not changed with increasing feeding level ($P > 0.05$). Net energy intake (NE*i*) and NE*i*g were increased with increased dietary NE concentration ($P < 0.001$). As expected, DE*i*, DE*i*g, NE*i*, and NE*i*g increased with increasing feeding level ($P < 0.001$).

Table 6.5. Effect of dietary NE concentration and feeding level on energy utilization in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a]

	NE, Mcal/kg[b]			Feeding level, %[c]				*P* values		
Item	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	27	27	27	27	27	27				
DE intake, Mcal/d[d]	3.22	3.23	3.32	2.83	3.11	3.83	0.04	0.2195	0.0001	0.6224
Maintenance (DE*i*m)[e]	0.92	0.93	0.93	0.92	0.93	0.93	0.01	0.8452	0.7161	0.6755
Growth (DE*i*g)[f]	2.29	2.30	2.39	1.90	2.18	2.90	0.04	0.1650	0.0001	0.5533
DE*g* efficiency										
Mcal DE/kg wt gain[g]	3.96	4.11	4.12	3.88	4.10	4.21	0.06	0.1130	0.0006	0.1792
g Protein/Mcal DE[h]	41.7	40.2	39.4	42.5	40.3	38.4	0.6	0.0517	0.0002	0.2204
g Lipid/McalDE[h]	15.4	17.4	21.3	16.9	16.5	20.7	0.8	0.0001	0.0014	0.0040
NE intake, Mcal/d[d]	2.07	2.12	2.26	1.86	2.04	2.54	0.03	0.0001	0.0001	0.4688
Maintenance (NE*i*m)[e]	0.66	0.66	0.66	0.66	0.66	0.66	0.01	0.8601	0.7281	0.6777
Growth (NE*i*g)[f]	1.41	1.46	1.60	1.20	1.39	1.88	0.03	0.0001	0.0001	0.3682
NE*g* efficiency										
Mcal NE/kg wt gain[g]	2.43	2.59	2.75	2.44	2.60	2.73	0.04	0.0001	0.0001	0.1357
g Protein/Mcal NE*ig*[h]	68.0	63.9	59.4	68.0	63.9	59.3	1.0	0.0001	0.0001	0.2387
g Lipid/Mcal NE*ig*[h]	25.0	27.7	32.2	27.2	26.0	31.7	1.3	0.0011	0.0081	0.0041

[a]Except when indicated, data are presented as least square means of 81 individually housed barrows. The experiment included a total of 81 pigs, from on average 31 to 62 days of age. Thus, there were 9 barrows per NE × feeding level combination.
[b]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).
[c]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.
[d]DE intake calculated from actual DE and ADFI. NE intake was calculated from NE concentration as estimated from digestible nutrients (CVB, 1994; Table 4).
[e]DE*i*m was calculated as 0.110 Mcal per kg $BW^{0.75}$ per d. NE*i*m was calculated as 0.078 Mcal per kg $BW^{0.75}$ per d.
[f]Calculated as DE or NE intake – DE*i*m or NE*i*m.
[g]Calculated as DE*i*g or NE*i*g/ADG.
[h]Calculated from the observed protein and lipid deposition of sacrificed pigs and (n = 54 pigs; 6 pigs per dietary NE concentration × feeding level combination).

The efficiency of energy utilization for growth (Mcal NE/kg) declined with increased dietary NE concentration and feeding level (Table 6.5; $P < 0.001$).The efficiency of DE*i*g and NE*i*g for PD (g/Mcal) tended to decline ($P = 0.052$) and declined ($P < 0.001$), respectively, as dietary NE concentration increased. In contrast, the efficiency of DE*i*g and NE*i*g for lipid deposition (g/Mcal) was increased with increased dietary NE concentration and feeding level ($P < 0.05$). However, a NE × feeding level interaction ($P < 0.05$) was observed the efficiency of DE*i*g and NE*i*g for lipid deposition. This was due to a greater lipid deposited per Mcal DE*i*g and NE*i*g in pigs allowed ad libitum access to the high NE concentration diet compared with the other treatments ($P < 0.05$).

Regression analyses within dietary NE concentration revealed differences in the slope of the linear relationship between ADG and NE*i*g ($P < 0.05$; Figure 6.2). Similar analyses revealed differences in the slope ($P < 0.05$) of the linear relationship between PD (Figure 6.3), LD (Figure 6.4), and LD:PD ratio (Figure 6.5) and NE*i*g.

Regression analyses were conducted to relate PD, LD, and LD:PD ratio with DE and NE intake. These relationships were described by equations that included a significant quadratic ($P < 0.001$) term of energy intake (Table 6.6).

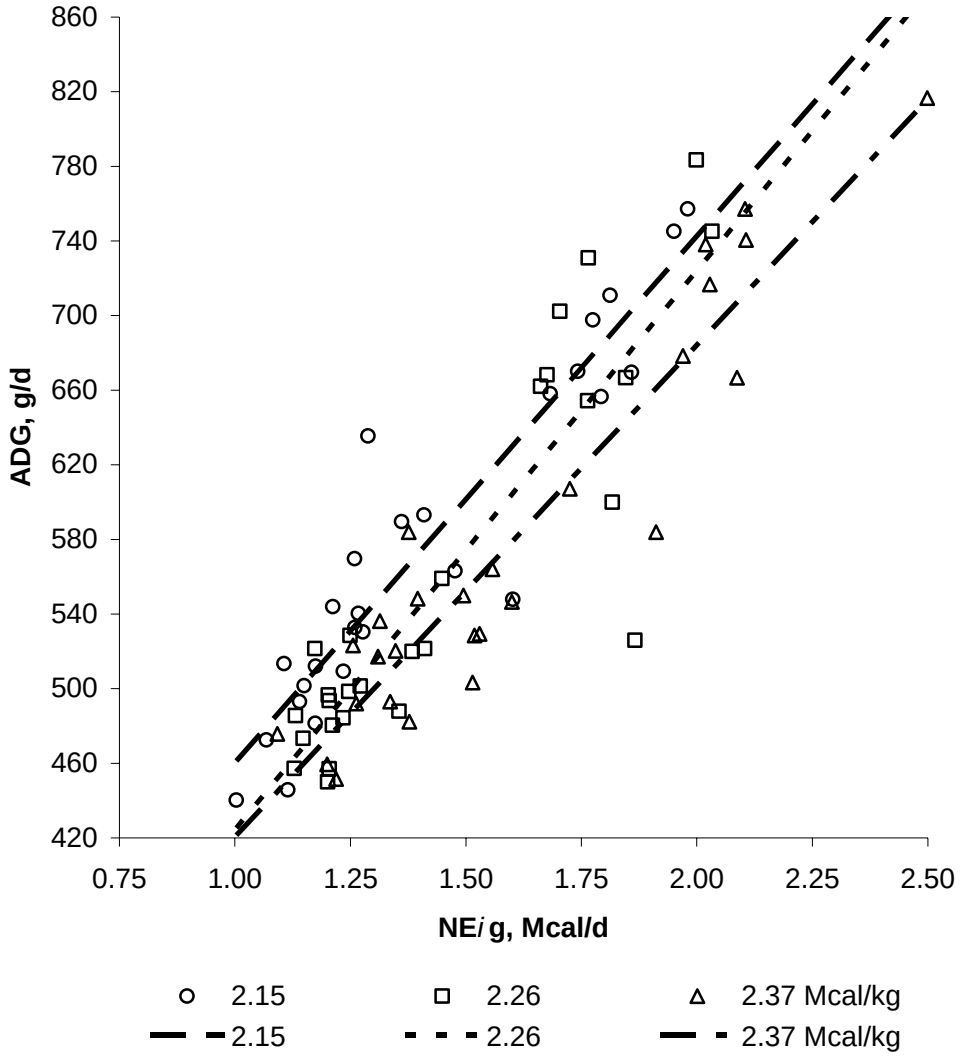

Figure 6.2. Effect of NE for growth on ADG in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations: [2.15, Mcal/kg]: ADG = 177 + 283NE*i*g, R^2 0.87; [2.26, Mcal/kg]: ADG = 124 + 300NE*i*g, R^2 0.79; [2.37, Mcal/kg]: ADG = 156 + 264NE*i*g, R^2 0.89. Slopes differed significantly ($P < 0.001$).

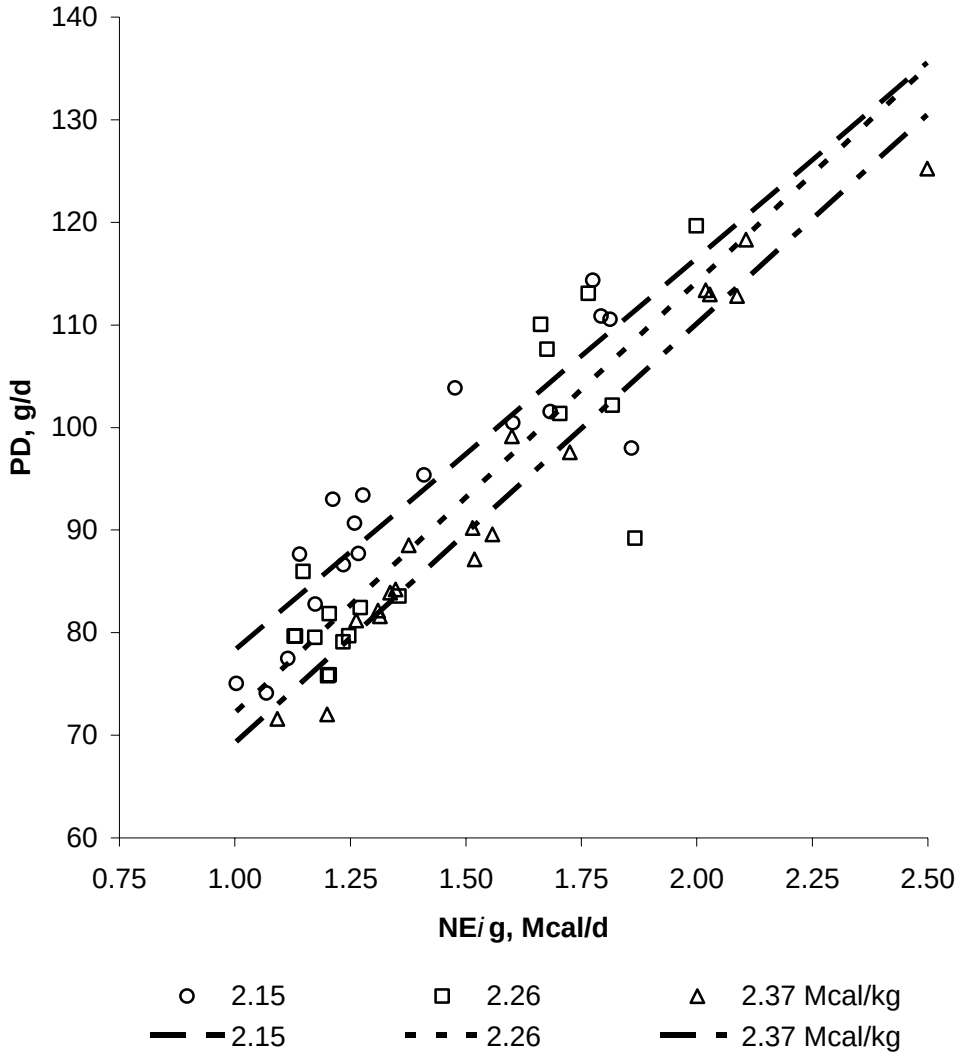

Figure 6.3. Effect of NE for growth on PD rate in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations: [2.15, Mcal/kg]: PD = 40 + 38NE*i*g, R^2 0.81; [2.26, Mcal/kg]: PD = 306 + 42NE*i*g, R^2 0.77; [2.37, Mcal/kg]: PD = 28 + 41NE*i*g, R^2 0.97. Slopes differed significantly ($P < 0.002$).

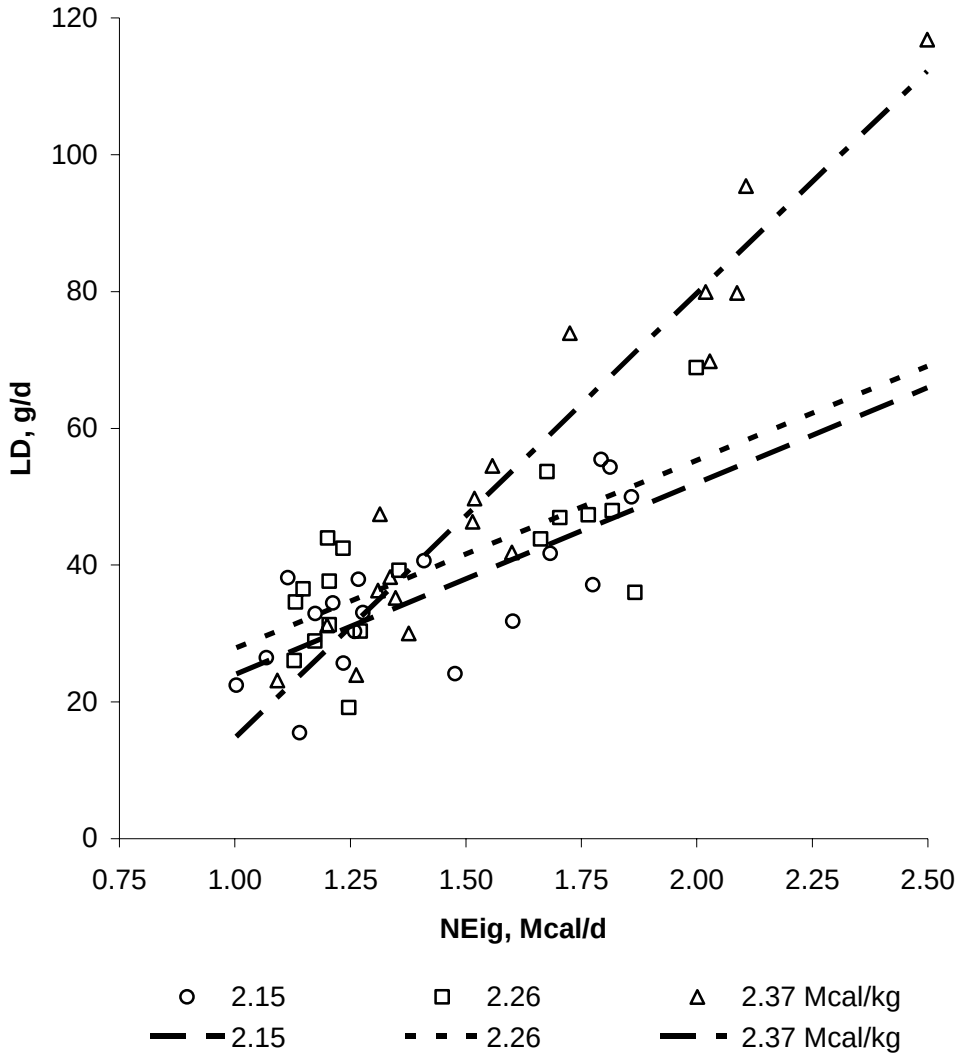

Figure 6.4. Effect of NE for growth on LD rate in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations: [2.15, Mcal/kg]: LD = -4.00 + 30.0NE*i*g, R^2 0.55; [2.26, Mcal/kg]: LD = 0.28 + 27.5NE*i*g, R^2 0.53; [2.37, Mcal/kg]: LD = -50.33 + 65.0NE*i*g, R^2 0.92. Slopes differed significantly ($P < 0.001$).

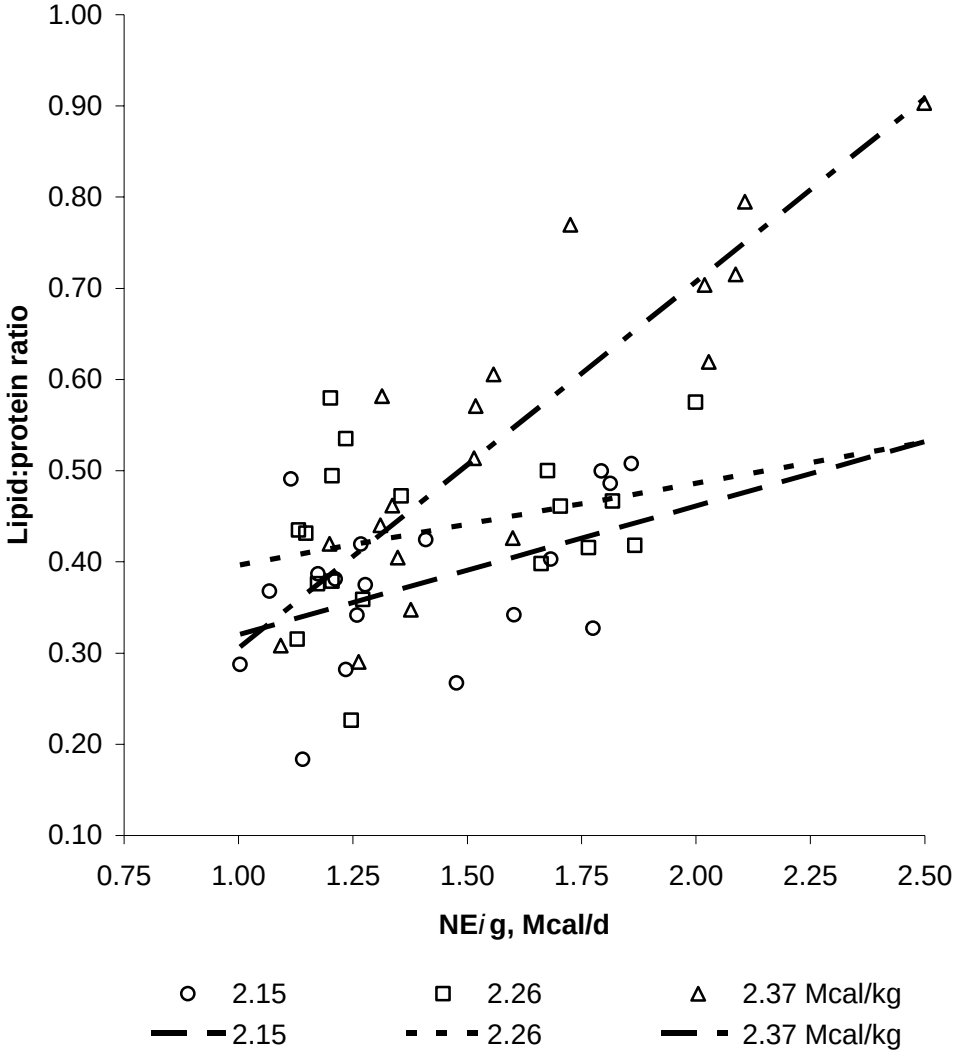

Figure 6.5. Effect of NE for growth on LD:PD ratio in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations: [2.15, Mcal/kg]: LD:PD ratio = 0.20 + 0.18NE*i*g, R^2 0.21; [2.26, Mcal/kg]: LD:PD ratio = 0.32 + 0.11NE*i*g, R^2 0.10; [2.37, Mcal/kg]: LD:PD ratio = -0.04 + 0.49NE*i*g, R^2 0.78. Slopes differed significantly ($P < 0.003$).

Table 6.6. Protein, lipid and lipid:protein ratio as a function of energy intake in barrows fed diets with increasing NE concentration at three different feeding levels[a,b,c,d]

No.	Equation	R^2	RSD
1	PD = -47.79 + 58.70DE*i* – 4.65DEi^2	0.87	5.26
2	LD = 143.52 – 89.30DE*i* + 17.58DEi^2	0.71	10.61
3	LD:PD ratio = 1.39 - 0.73DE*i* + 0.13DEi^2	0.42	0.11
4	PD = -31.65 + 77.42NE*i* – 8.78NEi^2	0.83	5.95
5	LD = 114.92 - 108.25NE*i* + 34.04NEi^2	0.78	9.09
6	LD:PD ratio = 1.14 – 0.88NE*i* + 0.25NEi^2	0.51	0.10

[a]Regression analyses were conducted using Proc REG of SAS.
[b]PD and LD were expressed in g/d; and DE*i* and NE*i* were expressed in Mcal/d.
[c]Energy intake (DE*i* and NE*i*, Mcal/d) were calculated from dietary actual DE concentration (or determined NE concentration) as fed × ADFI (see Table 6.5).
[d]n = 54; $P < 0.0001$ for all equations.

Total Retained energy (RE), ERP and ERL were related to DE intake using DE*i* (kcal/kg $BW^{0.75}$ per d) as the independent variable and RE, ERP and ERL (kcal/kg $BW^{0.75}$ per d) as dependent variables (Figure 6.6). Digestible energy for maintenance (DE*m*) was estimated at 118 kcal/kg $BW^{0.75}$ per d (i.e. 65.89/0.56) from the following regression equation:

$$RE = -65.89 + 0.56DEi \quad (6.6)$$

Similarly, using RE, ERP and ERL (kcal/kg $BW^{0.75}$ per d) as dependent variables, regression analyses were conducted with ME intake (ME*i*; kcal/kg $BW^{0.75}$ per d) as the independent variable (Figure 6.7).

$$RE = -71.00 + 0.61MEi \quad (6.7)$$

Equation 6.7 when extrapolated to zero ME*i* provides an estimate of the NE required for maintenance (NE*m*, the ME*i* at zero RE) at 71 kcal/kg $BW^{0.75}$ per d. The ME for maintenance (ME*m*) was calculated as 116 kcal/kg $BW^{0.75}$ per d (i.e. 71.00/0.61).

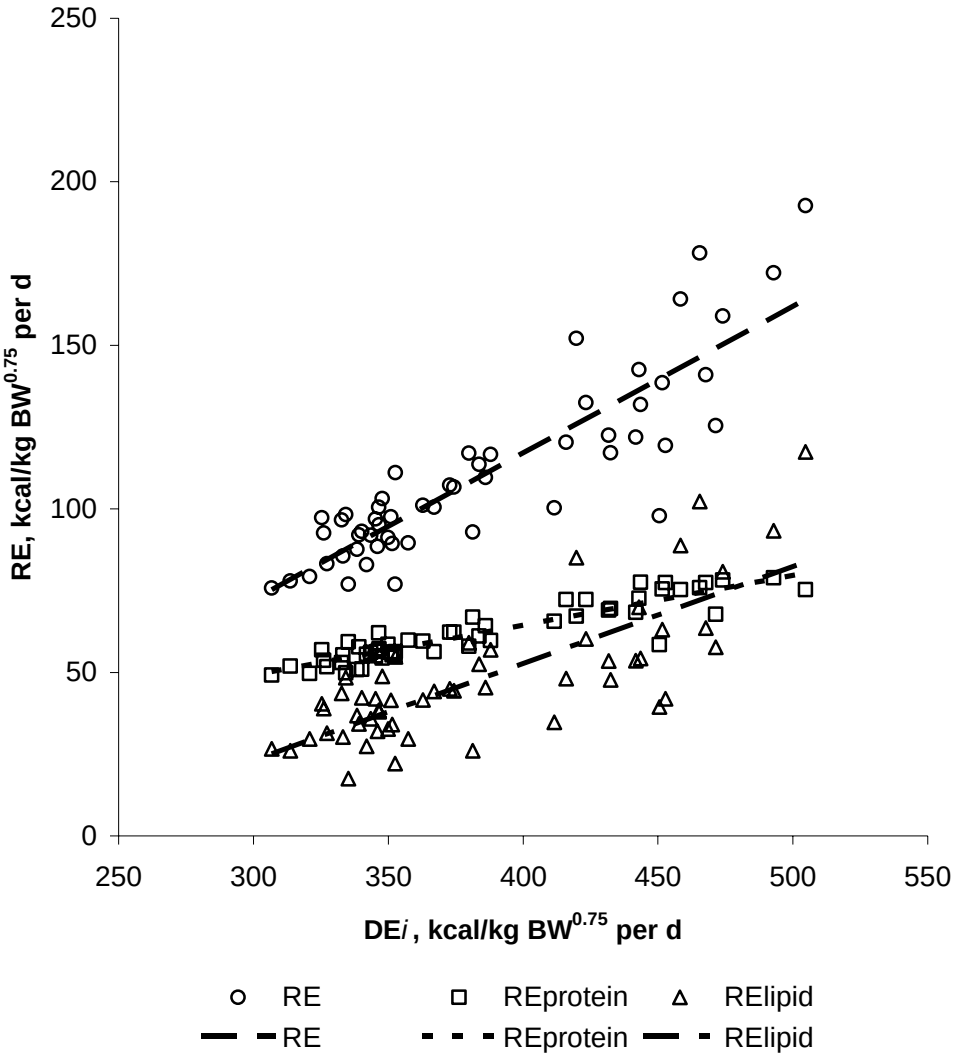

Figure 6.6. Effect of DE intake on energy retention in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations ($P < 0.001$; n = 54): RE = -65.89 + 0.56DE*i*, $R^2 = 0.82$, RSD = 11.72; ERP = 4.02 + 0.18DE*i*; $R^2 = 0.84$, RSD = 3.62; ERL = -65.66 + 0.36DE*i*, $R^2 = 0.61$, RSD = 12.95.

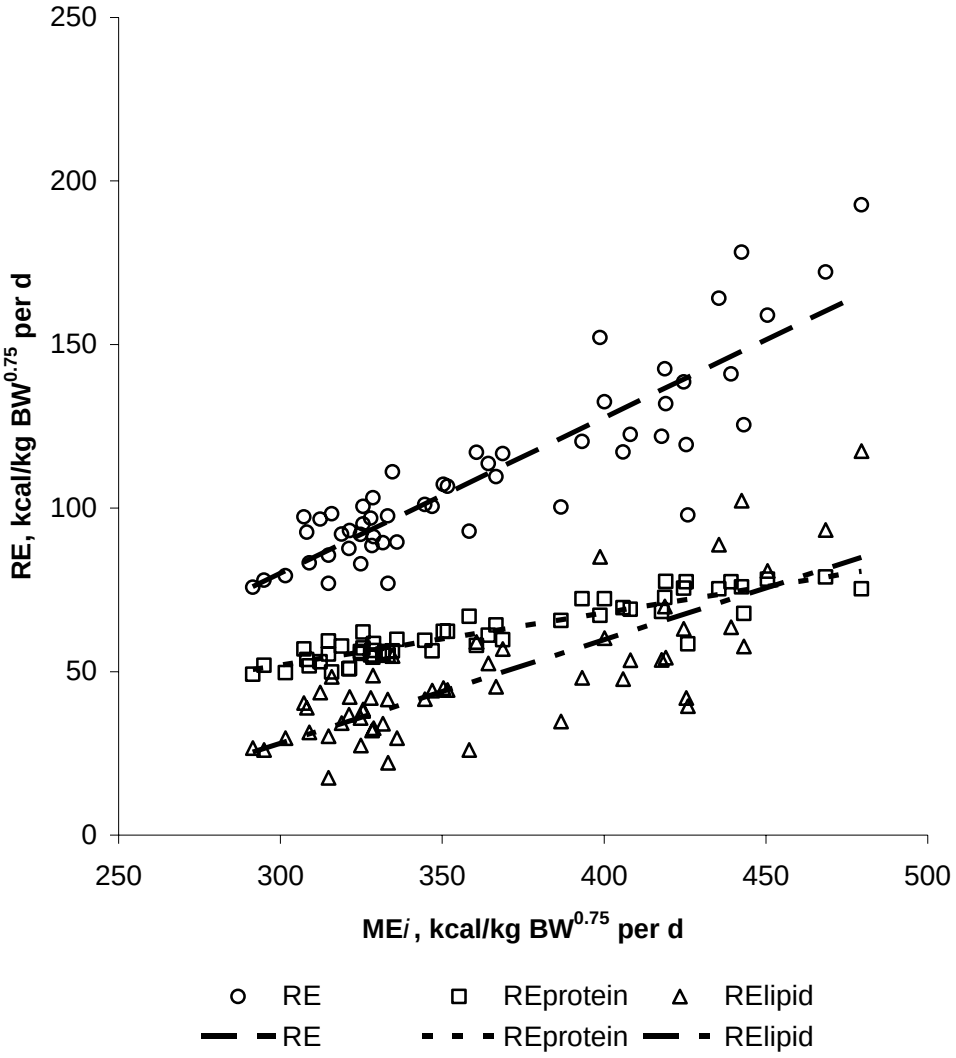

Figure 6.7. Effect of ME intake on energy retention in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations ($P < 0.001$; n = 54): RE = -71.00 + 0.61ME*i*, $R^2 = 0.86$, RSD = 10.51; ERP = 2.38 + 0.20ME*i*, $R^2 = 0.88$, RSD = 3.11; ERL = -71.28 + 0.40ME*i*; $R^2 = 0.66$, RSD = 12.05.

Apparent Digestibility

Apparent digestibility of GE, dry matter, crude fat and ash were increased (Table 6.7; $P < 0.001$) and crude protein increased ($P < 0.05$) with increased dietary NE concentration. Apparent GE and DM digestibility increased up to 2%, while CP, ash and crude fat digestibility were increased up to 1, 7 and 34%, respectively, with increased dietary NE concentration. Conversely, apparent crude fiber digestibility declined ($P < 0.001$) by as much as 23% with increased dietary NE concentration.

The effect of feeding level on apparent digestibility was similar for GE, DM, CP, crude fat, crude fiber and ash, declining with increasing feeding level ($P < 0.001$). No interaction between dietary NE concentration and feeding level was detected for all digestibility coefficients ($P > 0.05$). As expected, actual DE and NE concentration increased from the low to the high NE diet, but declined with increasing feeding level ($P < 0.001$). The ratios of NE:DE and NE:GE increased with increased dietary NE concentration ($P < 0.001$). Also, NE:DE ratio increased with increasing feeding level while NE:GE ratio declined ($P < 0.001$).

Table 6.7. Effect of dietary NE concentration and feeding level on apparent digestibility of energy, organic matter and ash, and determined energy content of diets in barrows fed diets with increasing NE concentration at three different feeding levels[a,b]

	NE, Mcal/kg[c]			Feeding level, %[d]				*P* values		
Item, %	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	27	27	27	27	27	27				
Gross energy	83.2	84.8	84.9	86.0	84.8	82.1	0.3	0.0001	0.0001	0.4412
Dry matter	83.9	85.4	85.6	86.5	85.4	83.0	0.2	0.0001	0.0001	0.5194
Crude protein	83.8	85.0	84.8	86.6	85.1	82.0	0.3	0.0361	0.0001	0.2589
Crude fat	51.2	57.3	68.5	62.9	58.8	55.3	1.4	0.0001	0.0001	0.2969
Crude fiber	45.2	40.8	35.0	44.5	42.6	33.9	2.4	0.0001	0.0001	0.8793
Ash	60.3	63.5	64.5	65.0	63.0	60.4	0.4	0.0001	0.0001	0.2900
DE, Mcal/kg[e]	3.35	3.45	3.49	3.50	3.45	3.34	0.01	0.0001	0.0001	0.4231
NE, Mcal/kg[f]	2.15	2.26	2.37	2.30	2.27	2.21	0.01	0.0001	0.0001	0.2479
NE/DE	64.2	65.4	67.9	65.6	65.7	66.3	0.1	0.0001	0.0001	0.2124
NE/GE	53.5	55.5	57.7	56.5	55.7	54.4	0.1	0.0001	0.0001	0.3452

[a]Data are presented as least square means. The experiment included a total of 81 barrows, from on average 31 to 62 days of age. Thus, there were 9 barrows per NE × feeding level combination.

[b]Apparent digestibility coefficients were based on analyses conducted on individual pig's faecal grab samples collected over three consecutive days (d 15 to 17). Acid insoluble ash in feed (0.77, 0.73 and 0.67% as fed in diet 1, 2 and 3, respectively) and faeces was used as index marker.

[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).

[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

[e]Determined digestible energy concentration.

[f]Estimated according to CVB (1994) equation.

The correlation between dietary nutrient content and apparent digestibility coefficients and energy concentration are presented in Table 6.8. Apparent digestibility of GE and crude fat were negatively correlated with dietary crude protein, ash and crude fiber content, but positively correlated with fat and starch content ($P < 0.01$). Apparent digestibility of crude protein was not correlated with dietary nutrient content ($P > 0.05$).

Apparent digestibility of crude fiber was positively correlated with dietary crude protein, ash and crude fiber content, but negatively correlated with crude fat and starch content ($P < 0.01$). In contrast, apparent digestibility of ash was negatively correlated with dietary crude protein, crude fiber and ash content, but positively correlated with crude fat and starch content ($P < 0.01$). As expected, actual DE and determined NE concentration were both negatively correlated with dietary crude protein, ash and crude fiber content, but positively correlated with crude fat and starch content ($P < 0.01$).

Table 6.8. Correlation coefficients (*r*) between dietary nutrient content, apparent digestibility coefficients and energy concentration[a,b]

	Dietary nutrient content, g/kg DM				
Item	Crude protein	Crude fat	Starch	Ash	Crude fiber
Digestibility coefficient, %					
Gross energy	-0.3031*	0.2328*	0.3028*	-0.2891*	-0.3215*
Crude protein	-0.1525	0.0943	0.1523	-0.1397	-0.1725
Crude fat	-0.7752*	0.7827*	0.7755*	-0.7875*	-0.7353*
Crude fiber	0.4322*	-0.4212*	-0.4323*	0.4352*	0.4170*
Ash	-0.5138*	0.4337*	0.5136*	-0.5001*	-0.5269*
DE, Mcal/kg DM	-0.5347*	0.4618*	0.5345*	-0.5231*	-0.5434*
NE, Mcal/kg DM	-0.9016*	0.8926*	0.9019*	-0.9114*	-0.8634*

[a]Apparent digestibility coefficients used in the correlation analysis were based on analyses conducted on individual pig's faecal grab samples collected over three consecutive days (d 15 to 17); n = 81.

[b]All chemical analyses were conducted according to AOAC (1990) procedures; GE was conducted with bomb calorimeter; starch was determined enzymatically (AOAC, 2002).

*$P < 0.01$.

Body Chemical Composition

The results of carcass, organ and empty body chemical composition of the ISG and experimental animals are shown in Table 6.9. Protein content in carcass and empty body declined up to 3% with increased dietary NE concentration ($P < 0.05$). There was a tendency ($P < 0.10$) for protein content in carcass and empty body to decline with increasing feeding level.

Ash content in carcass and empty body tended to decline with increased dietary NE concentration ($P < 0.10$) and declined with increasing feeding level ($P < 0.01$). Except for a tendency for water and lipid content in organ to decline and increase, respectively, with increasing feeding level ($P < 0.10$), there were no effects of dietary NE concentration and feeding level on the chemical composition of organ ($P > 0.05$).

A NE × feeding level interaction was detected in water, lipid and GE content in carcass and empty body ($P < 0.01$; Table 6.9). As shown in Table 6.10 and Figure 6.8, the interaction was illustrated by a reduced water and increased lipid and GE content in the carcass and empty body of pigs given ad libitum access to the high NE concentration diet.

Table 6.9. Effect of dietary NE concentration and feeding level on carcass, organ and empty body chemical composition of barrows at 25 kg BW when fed diets with increasing NE concentration at three different feeding levels[a,b]

		NE, Mcal/kg[c]			Feeding level, %[d]				*P* values		
Item, g/kg	ISG[e]	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	6	18	18	18	18	18	18				
Carcass											
Water	713	703	699	691	702	700	691	3	0.0104	0.0097	0.0031
Protein	160	176	173	170	174	174	170	2	0.0028	0.0804	0.9670
Lipid	91	83	90	104	86	87	104	3	0.0001	0.0001	0.0020
Ash	34.0	33.5	33.9	32.3	34.3	33.6	31.8	0.6	0.0903	0.0036	0.5182
GE, Mcal/kg	1.72	1.74	1.78	1.90	1.75	1.77	1.91	0.02	0.0001	0.0001	0.0067
Organ											
Water	821	800	798	796	800	798	795	1	0.3051	0.0960	0.2061
Protein	142	159	159	161	159	160	159	1	0.5258	0.6210	0.6189
Lipid	20	23	24	25	23	23	26	1	0.1855	0.0729	0.4677
Ash	11.1	12.4	12.5	12.4	12.3	12.4	12.7	0.3	0.9114	0.6085	0.2851
GE, Mcal/kg	1.01	1.13	1.15	1.17	1.14	1.15	1.17	0.01	0.1058	0.1028	0.1612
Empty body											
Water	733	721	718	711	720	718	711	3	0.0248	0.0398	0.0036
Protein	156	173	170	168	171	172	168	2	0.0120	0.0735	0.9180
Lipid	77	72	78	89	74	76	89	2	0.0001	0.0002	0.0026
Ash	29.6	29.5	30.0	28.6	30.3	29.7	28.0	0.6	0.0638	0.0013	0.4824
GE, Mcal/kg[f]	1.59	1.63	1.66	1.76	1.64	1.65	1.76	0.02	0.0003	0.0003	0.0055
GE, Mcal/kg[g]	1.62	1.66	1.70	1.79	1.67	1.69	1.79	0.02	0.0015	0.0030	0.0059

[a]Data are presented as least square means of 54 individually housed barrows from on average 31 to 62 days of age. Thus, there were 6 barrows per NE × feeding level combination.
[b]Carcass is the eviscerated pig including the head and feet; organ is the pooled individual organs including emptied GIT and blood; empty body is the sum of the carcass and organ.
[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).
[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.
[e]Data of the initial slaughter group (ISG, n = 6) were used to estimate the initial body composition of the experimental pigs and were not included in the statistical analysis. BW at slaughter was 9.4 ± 1.0 kg (mean ± SD).
[f]Bomb calorimeter analysis.
[g]Calculated from analyzed protein and lipid content using 5.66 and 9.46 kcal/g for protein and lipid, respectively (Ewan, 2001).

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Table 6.10. Carcass and empty body water, lipid and GE content of barrows at 25 kg BW when fed diets with increasing NE concentration at three different feeding levels[a,b]

		Carcass			Empty body		
NE, Mcal/kg[c]	Feeding level, %[d]	Water, g/kg	Lipid, g/kg	GE, Mcal/kg	Water, g/kg	Lipid, g/kg	GE, Mcal/kg
2.15	70	704	80	1.70	721	70	1.60
	80	702	82	1.73	720	71	1.62
	100	703	89	1.78	722	75	1.65
2.26	70	697	90	1.78	715	79	1.67
	80	704	85	1.73	721	74	1.63
	100	698	94	1.82	717	81	1.70
2.37	70	707	87	1.75	724	75	1.64
	80	695	95	1.83	714	82	1.71
	100	671	129	2.11	694	110	1.94
SEM		5	5	0.04	4	4	0.04
P values							
NE		0.0104	0.0001	0.0001	0.0248	0.0001	0.0003
Feeding level		0.0097	0.0001	0.0001	0.0398	0.0002	0.0003
NE × Feeding Level		0.0031	0.0020	0.0067	0.0036	0.0033	0.0055

[a]Data are presented as least square means of 54 individually housed barrows from on average 31 to 62 days of age. Thus, there were 6 barrows per NE × feeding level combination.

[b]Carcass is the eviscerated pig including the head and feet; empty body is the sum of the carcass and organ (taken as the sum of pooled individual organs including emptied GIT and blood).

[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).

[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

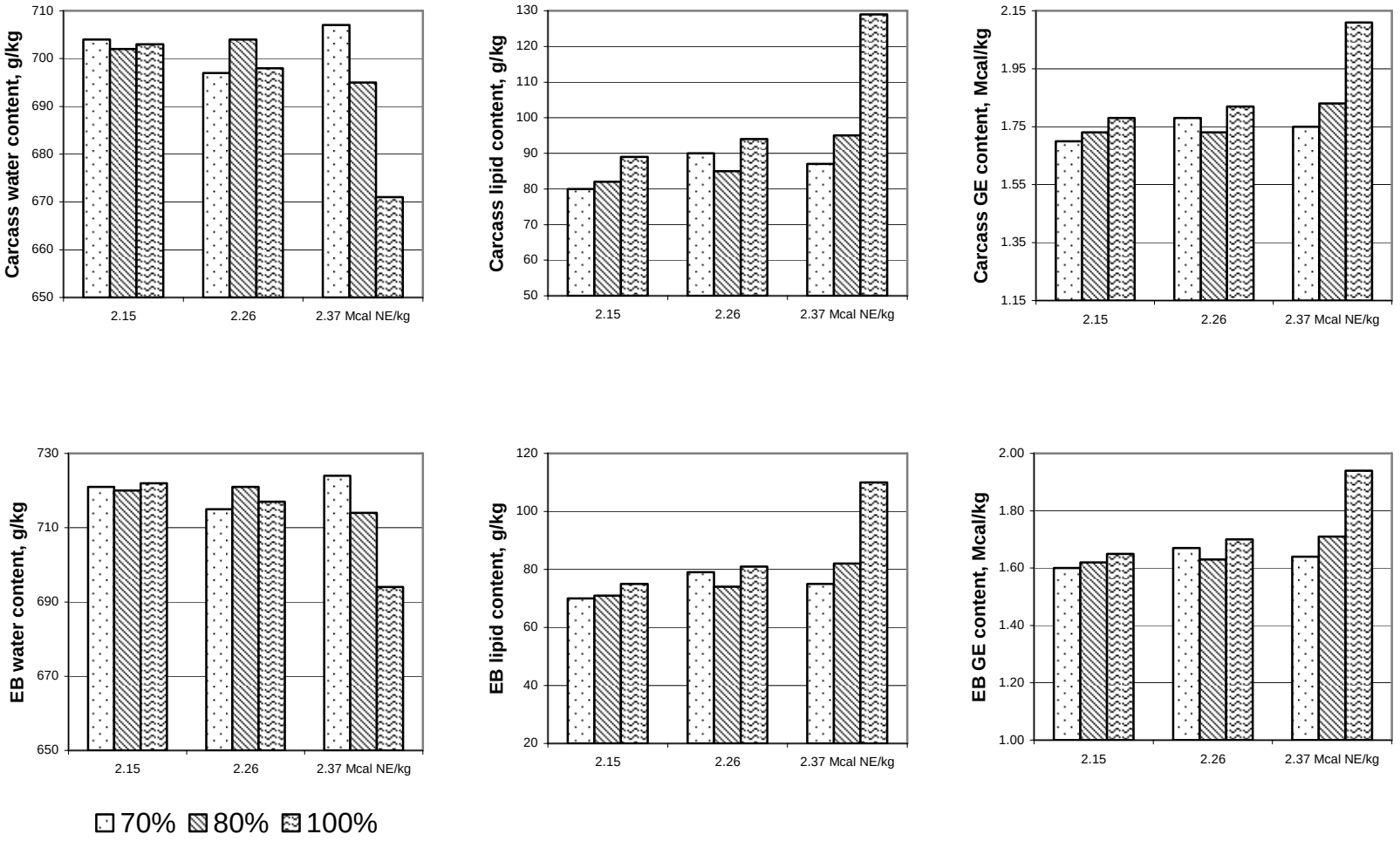

Figure 6.8. Carcass and empty body water, lipid and GE content of barrows at 25 kg BW when fed diets with increasing NE concentration at three different feeding levels. SEM = 5, 5, 0.04, 4, 4 and 0.04 for carcass water, lipid, GE, and empty body water, lipid and GE content, respectively (see Tables 6.9 and 6.10 for *P* values).

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Nutrient Deposition Rates and Ratios

The results of carcass and organ deposition rates of water, protein, lipid, ash, lipid:protein (LD:PD ratio), protein:water and ash:protein ratios, and retained energy (RE) are shown in Table 6.11. The rates of water, protein, lipid and ash deposition and RE in organ were not affected by dietary NE concentration ($P > 0.05$) but were increased with increasing feeding level ($P < 0.001$). Ash:protein and protein:water ratios were not affected by NE concentration and feeding level in organ ($P > 0.05$).

The rates of water, protein, and ash deposition in carcass were not affected by dietary NE concentration ($P > 0.05$). In addition, ash:protein ratio decreased in carcass ($P < 0.001$) with increasing feeding level but Protein:water ratio was not affected by neither dietary NE concentration nor feeding level ($P > 0.05$). However, a NE × feeding level interaction was detected in carcass LD, LD:PD ratio and RE ($P < 0.001$).

The results of empty body deposition rates of water, protein, lipid, ash, LD:PD ratio, protein:water ratio, ash:protein ratio and RE are shown in Table 6.12. Reflective of the effect on carcass and organ, the rates of water, protein and ash deposition, protein:water and ash:protein ratios in empty body were not affected by dietary NE concentration ($P > 0.05$). In contrast, water, protein and ash deposition rates were increased with increasing feeding level ($P < 0.01$). Ash:protein ratio decreased with increasing feeding level ($P < 0.05$) whereas protein:water ratio was unaffected by feeding level ($P > 0.05$). A NE × feeding level interaction was detected in RE:energy intake ratios (RE:GE, RE:DE, RE:ME, RE:NE; $P < 0.01$; Table 6.12).

Table 6.11. Effect of dietary NE concentration and feeding level on deposition rates of water, protein, lipid, ash and energy retention in the carcass and organs of barrows between 9 and 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a,b]

	NE, Mcal/kg[c]			Feeding level, %[d]				*P* values		
Item, g/d	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	18	18	18	18	18	18				
Carcass										
Water	288	285	295	257	272	339	4	0.2296	0.0001	0.1713
Protein	77	75	77	67	72	89	2	0.1744	0.0001	0.1127
Lipid	33	37	51	30	34	57	3	0.0001	0.0001	0.0001
Ash	13.7	13.9	13.7	12.8	13.2	15.3	0.5	0.9047	0.0001	0.0329
Lipid:protein ratio	0.42	0.49	0.64	0.45	0.47	0.63	0.02	0.0001	0.0001	0.0019
Protein:water ratio	0.27	0.26	0.26	0.26	0.26	0.26	0.01	0.2249	0.8628	0.4047
Ash:protein ratio	0.18	0.19	0.18	0.19	0.18	0.17	0.01	0.1691	0.0091	0.4364
RE, Mcal/d	0.73	0.75	0.90	0.65	0.71	1.02	0.02	0.0001	0.0001	0.0004
Organ										
Water	76	74	78	64	68	97	3	0.6923	0.0001	0.7673
Protein	16	16	17	14	15	21	1	0.3119	0.0001	0.8192
Lipid	2.4	2.6	2.9	2.0	2.2	3.6	0.2	0.1888	0.0001	0.4264
Ash	1.3	1.3	1.3	1.0	1.2	1.7	0.1	0.9176	0.0001	0.3246
Lipid:protein ratio	0.14	0.16	0.17	0.15	0.14	0.17	0.01	0.2600	0.0735	0.6194
Protein:water ratio	0.217	0.217	0.221	0.217	0.221	0.217	0.004	0.6743	0.7791	0.6526
Ash:protein ratio	0.079	0.079	0.078	0.078	0.076	0.082	0.003	0.9270	0.4451	0.1487
RE, Mcal/d	0.12	0.12	0.13	0.10	0.11	0.16	0.01	0.2455	0.0001	0.5913

[a]Data are presented as least square means of 54 individually housed barrows from on average 31 to 62 days of age. Thus, there were 6 barrows per NE × feeding level combination.

[b]Carcass is the eviscerated pig including the head and feet; organ is the pooled individual organ including emptied GIT and blood.

[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).

[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

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Table 6.12. Effect of dietary NE concentration and feeding level on deposition rates of water, protein, lipid, ash and energy retention in the empty body of barrows between 9 and 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a,b]

	NE, Mcal/kg[c]			Feeding level, %[d]				*P* values		
Item, g/d	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	18	18	18	18	18	18				
Water	364	359	374	321	341	436	6	0.2879	0.0001	0.3248
Protein	93	90	94	81	87	110	2	0.2111	0.0001	0.1507
Lipid	35	40	54	33	36	60	3	0.0001	0.0001	0.0001
Ash	15.0	15.2	15.0	13.9	14.4	17.0	0.5	0.9344	0.0001	0.0759
Lipid:protein ratio	0.37	0.44	0.55	0.40	0.41	0.55	0.02	0.0001	0.0001	0.0020
Protein:water ratio	0.26	0.25	0.25	0.25	0.26	0.25	0.01	0.4612	0.7975	0.2428
Ash:protein ratio	0.16	0.17	0.16	0.17	0.16	0.15	0.01	0.1836	0.0037	0.4730
RE, Mcal/d[e]	0.85	0.87	1.03	0.75	0.82	1.18	0.03	0.0001	0.0001	0.0007
RE, Mcal/d[f]	0.86	0.88	1.05	0.77	0.84	1.19	0.03	0.0001	0.0001	0.0003
RE as protein, Mcal/d[f]	0.53	0.51	0.53	0.46	0.49	0.62	0.01	0.2112	0.0001	0.1517
RE as lipid, Mcal/d[f]	0.33	0.37	0.51	0.31	0.34	0.57	0.02	0.0001	0.0001	0.0002
RE as protein, % of RE[g]	62.1	58.3	53.3	60.4	59.8	53.5	1.3	0.0001	0.0006	0.0522
RE as lipid, % of RE[g]	37.9	41.7	46.7	39.6	40.2	46.5	1.3	0.0001	0.0006	0.0522
RE:GE intake	0.22	0.23	0.26	0.23	0.22	0.25	0.01	0.0001	0.0001	0.0020
RE:DE intake	0.26	0.27	0.30	0.26	0.26	0.31	0.01	0.0001	0.0001	0.0004
RE:ME intake	0.28	0.29	0.32	0.28	0.28	0.32	0.01	0.0001	0.0001	0.0005
RE:NE intake	0.41	0.41	0.44	0.40	0.40	0.46	0.01	0.0044	0.0001	0.0005

[a]Data are presented as least square means of 54 individually housed barrows from on average 31 to 62 days of age. Thus, there were 6 barrows per NE × feeding level combination.
[b]Empty body is the sum of the carcass and organ.
[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).
[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.
[e]Bomb calorimeter analysis.
[f]Calculated from protein and lipid deposition rates as 5.66 and 9.46 kcal/g for protein and lipid, respectively (Ewan, 2001).
[g]Percent RE as protein and lipid of the calculated RE values.

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A NE × feeding level interaction in LD, LD:PD ratio, RE and RE as lipid were detected ($P < 0.001$; Table 6.12). The interaction of NE and feeding level on LD, LD:PD ratio and RE in carcass and empty body are shown in Table 6.13. Figure 6.9 illustrates the increased LD, LD:PD ratio and RE in the carcass and empty body of pigs given ad libitum access to the high NE concentration diet.

Physical Body Composition at Slaughter

The body composition of the ISG and experimental animals at slaughter are reported in Table 6.14. Carcass, organ and empty body weight (EBW) and as a percentage of liveweight were not affected by NE concentration ($P > 0.05$). In addition, carcass, EBW and EBW as a percentage of liveweight were not affected by feeding level ($P > 0.05$). Organ weight and organ weight as a percentage of liveweight increased up to 10 and 7%, respectively, with increasing feeding level ($P < 0.05$). On the other hand, carcass weight as a percentage of liveweight declined up to 2% with increasing feeding level ($P < 0.05$).

Generally, no effect of NE concentration was detected for individual organ weights, and as a percentage of empty body (Table 6.14; $P > 0.05$). There was a 7, 14 and 16% increase in empty digestive tract, kidneys and liver weight, respectively, with increasing feeding level ($P < 0.05$). These organ weights as a percentage of empty body weight increased in a manner similar to the level of intakes ($P < 0.06$). Blood, heart, lung and spleen weight (and as percentage of empty body) were not affected by dietary NE concentration and feeding level ($P > 0.05$).

Table 6.13. Deposition rates of lipid, ash, Lipid:protein ratio and retained energy in the carcass and empty body of barrows between 9 and 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a,b]

		Carcass				Empty body		
NE, Mcal/kg[c]	Feeding level, %[d]	Lipid, g/d	Ash, g/d	Lipid:protein ratio	RE, Mcal/d	Lipid, g/d	Lipid:protein ratio	RE, Mcal/d
2.15	70	27	13.2	0.39	0.62	28	0.35	0.71
	80	31	13.8	0.40	0.71	33	0.36	0.82
	100	41	14.0	0.47	0.86	44	0.41	1.01
2.26	70	33	13.1	0.49	0.66	35	0.44	0.76
	80	31	13.0	0.45	0.67	33	0.40	0.76
	100	48	15.5	0.54	0.94	51	0.47	1.10
2.37	70	32	12.1	0.48	0.68	35	0.42	0.78
	80	40	12.8	0.55	0.76	42	0.48	0.87
	100	82	16.2	0.89	1.26	86	0.76	1.43
SEM		4	0.7	0.04	0.04	4	0.04	0.05
P values								
NE		0.0001	0.9047	0.0001	0.0001	0.0001	0.0001	0.0001
Feeding level		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
NE × Feeding level		0.0001	0.0329	0.0019	0.0004	0.0001	0.0020	0.0007

[a]Data are presented as least square means of 54 individually housed barrows from on average 31 to 62 days of age. Thus, there were 6 barrows per NE × feeding level combination.

[b]Carcass is the eviscerated pig including the head and feet; empty body is the sum of the carcass and organ (taken as the sum of pooled individual organ including emptied GIT and blood).

[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).

[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

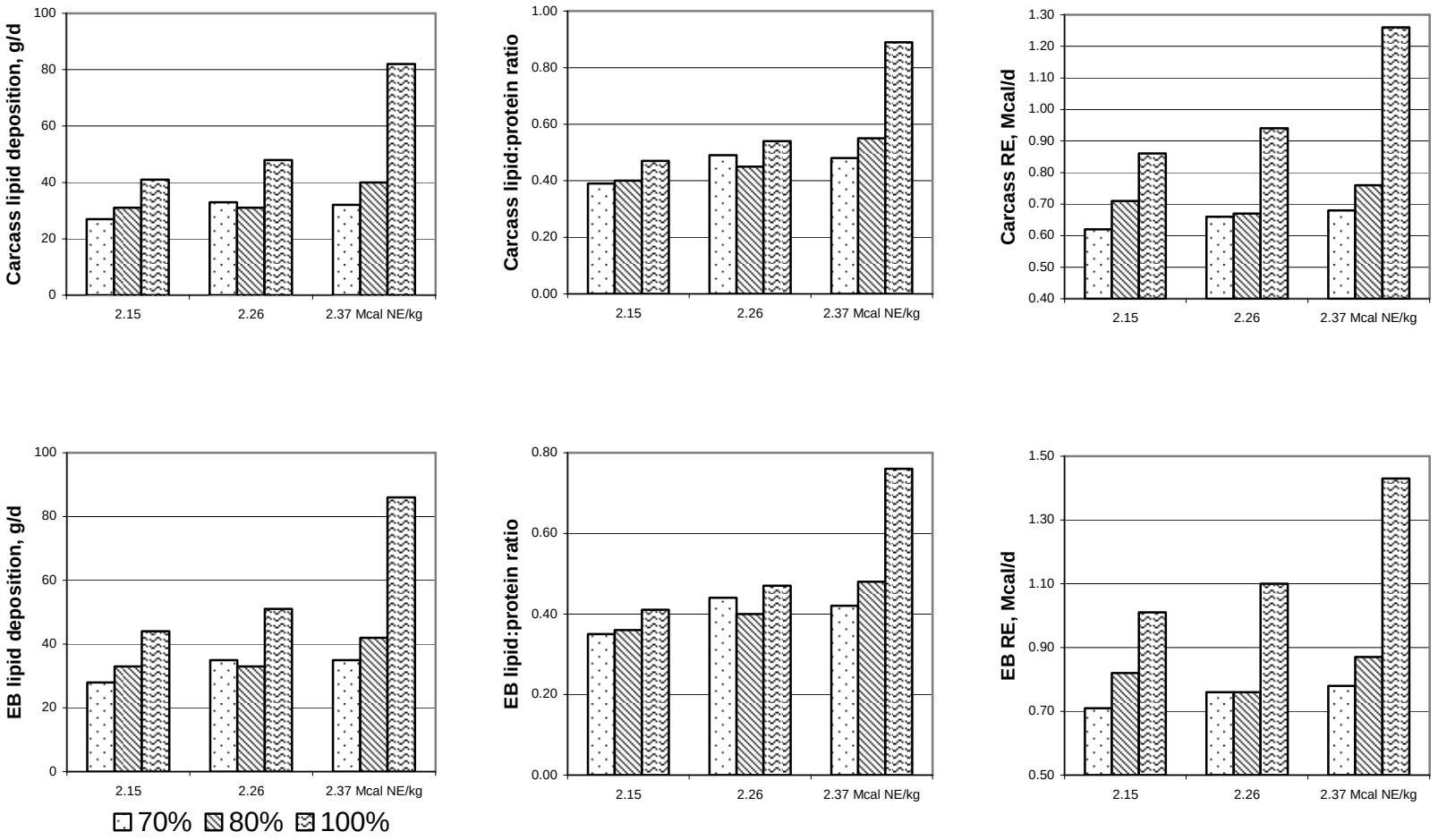

Figure 6.9. Deposition rates of lipid, lipid:protein ratio and retained energy in the carcass and empty body of barrows between 9 and 25 kilograms fed diets with increasing NE concentration at three different feeding levels. SEM = 5, 0.04, 0.04, 4, 0.04 and 0.05 for carcass lipid, lipid:protein ratio, RE, and empty body lipid, lipid:protein ratio and RE, respectively (see Tables 6.11, 6.12 and 6.13 for *P* values).

Table 6.14. Effect of dietary NE content and feeding level on physical body composition at slaughter of barrows of 25 kilograms fed diets with increasing NE content at three different feeding levels[a,b]

		NE, Mcal/kg[c]			Feeding level, %[d]				*P* values		
Item	ISG[e]	2.15	2.26	2.37	70	80	100	SEM	NE	Feeding level	NE × Feeding level
Number of pigs	6	18	18	18	18	18	18				
Weight, kg											
Carcass	7.1	18.4	18.8	18.8	18.6	18.8	18.5	0.3	0.2796	0.7069	0.1651
Organ	1.6	4.2	4.2	4.3	4.1	4.2	4.5	0.1	0.6228	0.0123	0.6282
Empty body	8.7	22.6	23.0	23.1	22.7	23.0	23.0	0.3	0.1876	0.6907	0.2064
Weight, g/kg liveweight											
Carcass	746	743	749	750	754	751	736	5	0.5302	0.0234	0.1374
Organ	173	170	169	172	166	168	177	4	0.7394	0.0369	0.6226
Empty body	919	913	918	923	921	920	914	3	0.1945	0.3267	0.1457
Organ weight, g											
Empty digestive tract	716	1761	1779	1800	1735	1730	1854	50	0.9278	0.0495	0.5242
Blood	391	893	922	998	881	960	971	39	0.1618	0.2259	0.7824
Liver	258	807	790	789	745	775	867	25	0.8420	0.0027	0.4562
Heart	62	149	152	146	147	154	147	5	0.6124	0.3995	0.7071
Lung	122	351	352	357	365	344	351	16	0.9696	0.6407	0.4088
Kidneys	59	178	166	174	165	165	188	5	0.2813	0.0035	0.1366
Spleen	21	69	73	71	70	68	74	6	0.8759	0.7125	0.2359
g/kg EBW[f]											
Empty digestive tract	83	78	77	77	76	75	81	3	0.8949	0.0581	0.3361
Blood	45	39	40	43	39	42	42	2	0.2349	0.2463	0.7136
Liver	30	36	34	34	33	34	38	1	0.5200	0.0051	0.4263
Heart	6.9	6.6	6.6	6.3	6.5	6.7	6.4	0.2	0.5188	0.4587	0.6524
Lung	14.3	15.6	15.3	15.4	16.1	15.0	15.3	0.7	0.9709	0.5334	0.4695
Kidneys	7.1	7.9	7.2	7.5	7.3	7.2	8.2	0.2	0.1804	0.0080	0.0668
Spleen	2.2	3.1	3.2	3.0	3.1	3.0	3.2	0.2	0.9203	0.7261	0.2143

[a]Data are presented as least square means of 54 individually housed barrows from on average 31 to 62 days of age. Thus, there were 6 barrows per NE × feeding level combination.

[b]Carcass is the eviscerated pig including the head and feet; organ is the pooled individual organ including emptied GIT and blood; empty body is the sum of the carcass and organ.

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[c]NE concentration of each diet across feeding levels as estimated from digestible nutrients (CVB, 1994).
[d]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.
[e]Data of the initial slaughter group (ISG, n = 6) were not included in the statistical analysis. BW at slaughter was 9.4 ± 1.0 kg (mean ± SD).
[f]EBW, empty body weight.

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Plasma Insulin-Like Growth Factor I Concentrations

There was no effect of dietary NE concentration on plasma IGF-I concentrations (Table 6.15; $P > 0.05$). However, IGF-I concentrations increased with increasing feeding level and were higher on d 21 than d 7 ($P < 0.001$).

Table 6.15. Effect of dietary NE concentration, feeding level and collection time on plasma insulin-like growth factor I concentrations (ng/ml) in barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a]

NE, Mcal/kg	Feeding level, %[b]	Day 7	Day 21
2.15	70	61	99
	80	59	141
	100	101	233
2.26	70	60	110
	80	60	79
	100	111	242
2.37	70	60	104
	80	70	134
	100	112	277
SEM		16	16
P values			
NE	0.2227		
Feeding level	0.0001		
Day	0.0001		
NE × Day	0.3831		
NE × Feeding level	0.2421		
Feeding level × Day	0.0001		
NE × Feeding level × Day	0.3922		

[a]Data are presented as least square means. The experiment included a total of 81 individually housed barrows, from on average 31 to 62 days of age. Thus, there were 27 pigs per NE level, 27 pigs per feeding level and 9 barrows per NE × feeding level combination. Blood samples were collected from pigs on d 7 and 21 of test.
[b]100% pigs were allowed unrestricted access to experimental diets; 80 and 70% are the respective feed allowances based on the ad libitum feed consumption on a BW basis of pigs within each dietary NE concentration.

Correlation among Performance Variables, Empty Body Parameters and Actual DE or Determined NE Concentration

The results of correlation analyses are shown in Table 6.16. Average daily gain and ADFI were strongly positively correlated with DE and NE intake ($P < 0.001$) but not gain:feed ratio ($P > 0.05$). Furthermore, empty body lipid content, LD, PD and LD:PD ratio were all strongly positively correlated with DE and NE intake ($P < 0.001$). Empty body CP content was weakly negatively correlated with NE intake ($P < 0.05$).

Table 6.16. Correlations among actual DE intake, determined NE intake and performance, empty body nutrient content and deposition rates in barrows between 9 and 25 kilograms fed diets with increasing NE concentration at three different feeding levels[a]

Variables	Correlation coefficient	*P* values
DE intake, and		
ADG	0.9157	0.0001
ADFI	0.9862	0.0001
Gain:feed ratio	-0.1350	0.2295
Actual DE concentration	-0.4776	0.0001
Empty body CP content	-0.2347	0.0876
Empty body lipid content	0.6005	0.0001
Empty body PD	0.9261	0.0001
Empty body LD	0.8003	0.0001
Empty body LD:PD ratio	0.6004	0.0001
NE intake, and		
ADG	0.8982	0.0001
ADFI	0.9636	0.0001
Gain:feed ratio	-0.1219	0.2784
Determined NE concentration	-0.0803	0.4759
Empty body CP content	-0.2858	0.0362
Empty body lipid content	0.6592	0.0001
Empty body PD	0.9068	0.0001
Empty body LD	0.8476	0.0001
Empty body LD:PD ratio	0.6663	0.0001

[a]Correlation coefficients were computed using individual barrow's actual DE and determined NE concentration (see Table 6.7); n = 81, performance variables; n = 54, empty body parameters.

6.4 Discussion

Design

The present study looked at the interaction of NE concentration and daily feed intake, an approach never before considered in the weanling pig. Bikker et al. (1995), Quiniou et al. (1995) and Weis et al. (2004) studied the influence of varying energy supply, achieved by controlling daily feed intake, on growth performance and body composition in growing pigs, but no one has conducted such a study in the weanling pig. On the other hand, there have been numerous studies on the effect of energy concentration on the growth performance of weanling pigs. For example, Tokach et al. (1995), Reis de Souza et al. (2000) and Levesque (2002) evaluated increasing metabolizable, gross or digestible energy, respectively, on performance. However, no one has looked at the interaction of dietary energy concentration and daily feed intake.

Without doubt, studies on controlling daily feed intake explain how the pig uses energy for growth and nutrient accretion; however, in commercial practice, dietary energy concentration and not daily feed allowance is under the control of nutritionists. Therefore, combining these two approaches into a single study gives a far greater understanding of energy metabolism in weaned pigs.

Since young pigs are said to be in ‘protein- and energy-dependent’ phases of growth (Campbell and Dunkin, 1983a; Kyriazakis and Emmans, 1992a,b; Bikker, 1994), a preliminary trial (Chapter 5) was conducted to evaluate the response of weaned pigs to decreasing daily energy intake, with amino acid intake either declining at a constant proportion with energy or declining at a reduced rate. Based

on these results, reduced energy intake achieved through restriction of feed intake must be conducted at no greater than 30% restriction if a single diet is to be used. By applying these results in the current study, we ensured that amino acid intake did not limit performance and thus, the response to energy intake was not confounded by amino acid supply.

Furthermore, the optimum total lysine:DE ratio used in the present study was based on the ratio determined in a previous experiment (Chapter 3). Employing a 5% higher ratio in this experiment than the determined requirement further ensured that dietary lysine content was not limiting performance. Other amino acids were formulated on an ideal amino acid ratio basis according to NRC (1998). To further avoid secondary nutrient effects on experimental results, ingredients were pre-assayed for amino acid content. Finally, according to a factorial estimation of lysine requirement based on different models, we confirmed that, indeed, amino acid intake was not limiting performance.

Diets

According to the results of a previous study (Chapter 4) and those reported by Levesque (2002) and Rijnen et al. (2004), actual DE and NE values may differ from formulated values. For a more accurate interpretation of results and to confirm that dietary energy concentration was indeed varied, NE was determined using the actual digestibility of individual components of the diet and applying the CVB (1994) prediction equation. Although the determined NE values of diets were lower than formulated, the range in NE was virtually identical to the intended (220 and 210 kcal,

respectively). The range in actual DE differed from formulated (140 vs. 90 kcal). While it was important to measure actual DE, the primary focus of this study was NE.

The increase in NE was confirmed and was achieved with a gradual decline in dietary CP and crude fiber content with a concomitant increase in fat. The analyzed CP content was similar to formulated value.

Performance

It has long been recognized that energy concentration is an important determinant of voluntary feed intake of pigs allowed ad libitum access to feed (NRC, 1987; Lewis, 2001), with feed intake declining as energy concentration is increased. However, in the present study, increasing dietary NE concentration did not affect feed intake. Reis de Souza et al. (2000) reported no effect on feed intake with DE concentration increasing from 3.24 to 3.50 Mcal/kg in weaned pigs between 7 to 25 kg BW. Conversely, Levesque (2002) found a 6.3% decline in feed intake of weaned pigs between 7 to 20 kg BW when actual DE concentration increased from 3.18 to 3.59 Mcal DE/kg. In our previous study (Chapter 4), increasing determined NE concentration reduced the feed intake of pigs. It is generally accepted that dietary energy concentration is not the only driver of feed intake in the weaned pig (Patience et al., 1995).

Certain dietary factors, for example, bulkiness (Whittemore et al., 2001) and fat content (e.g. Xing et al., 2004) exert direct or indirect physiological effects that may reduce feed intake. Since dietary fat is suggested to reduce digesta passage rate (Azain, 2001), elevated dietary fat content may pose a constraint on feed intake, and

may explain part of the reduction in feed intake observed in other studies when dietary energy concentration was increased (Van Lunen and Cole, 1998; Smith et al., 1999a; Levesque, 2002). Dietary fat content was increased up to a maximum of 13.1, 6.8 and 8.2%, respectively, in these other studies compared with 5.4% in the present study. The results of the present study suggest that the physiological effect of dietary components may be an important factor in determining feed intake above simple NE concentration.

As with feed intake, feed efficiency was not affected by dietary NE concentration. This is contrary to our previous studies in which feed efficiency was improved with increasing DE concentration (Levesque, 2002; Oresanya et al., 2002). Feed efficiency would be expected to increase either when a reduction in feed intake occurs without changes in growth rate (Pettigrew and Moser, 1991; Xing et al., 2004) or an increase in growth rate occurs without any change in feed intake. Since dietary NE concentration exerted no influence on either feed intake or growth rate in the present study, feed efficiency would be expected to remain similar across diets.

We hypothesized that increasing NE concentration will increase growth performance. However, our results on growth and feed efficiency are clearly contrary to what one might expect assuming energy concentration is limiting the energy supply to the pig. To remove an important roadblock in our understanding of energy metabolism in weaned pigs, we aimed to answer the question of how does NE concentration affect energy intake, body composition and nutrient deposition rates.

Since the pigs did not reduce their feed intake as dietary NE concentration increased, NE intake also increased. This observation is consistent with the suggestion that weaned pigs have limited ability to regulate energy intake based on energy density (NRC, 1987). However, it must be noted that DE intake calculated from actual DE concentration in the diet was not affected by dietary treatment. This would suggest that the response of weaned pigs to energy concentration should be expressed in terms of the total available energy equivalent (i.e. determined NE intake). This is supported by a stronger correlation of empty body composition and nutrient deposition rates with NE intake as compared to DE intake.

The fact that NE intake increased with increased dietary NE concentration, without increasing growth rate, strongly suggests that pigs on the low NE diet were able to consume sufficient energy to maximize growth rate. The adequacy of the low NE diet is further confirmed by the decreased slope observed when comparing ADG against NE intake among the three diets (Figure 6.2); the increase in ADG per unit of NE intake was lower on the high NE diet. A different picture develops when we looked at the response to NE in terms of the composition of body weight gain, as opposed to the overall whole body results; this will be discussed below.

It should be noted that contrary to the response of ADG to changes in NE concentration, increasing daily feed intake did increase ADG. However, body protein content tended to decline with increased feed intake, whereas NE concentration interacted with feed intake on both body water and lipid content in the empty body. As discussed below, the results of empty body composition and nutrient deposition rates further support the adequacy of the low NE diet. The undesirable effect of

increasing dietary energy concentration on the lean growth of weaned pigs therefore becomes readily apparent.

Chemical and Physical Body Composition

Little is known on the interactive effects of dietary energy concentration and feed (energy) intake on the chemical composition of the body of the weaned pig. A previous study by Campbell and Dunkin (1983a) reported an interaction of energy and protein intake on the empty body chemical composition of weaned pigs. They reported a decline in empty body protein content with increasing energy intake when pigs growing between 7 and 19 kg BW were given a high CP (22%) but not low CP (15%) diet. Conversely, empty body lipid content increased with energy intake but at a greater rate in pigs fed the low CP diet compared with the high CP diet (Campbell and Dunkin, 1983a).

In the present study, empty body protein content declined with increasing NE concentration but not feeding level. In contrast, an interaction of NE concentration and feeding level in empty body water and lipid content resulted in a lower water and a higher lipid content in the empty body of pigs with unrestricted access to the high NE diet compared with pigs on the other treatments.

Increasing dietary NE concentration did not affect carcass, organ or empty body weight (absolute weight and gram per kilogram liveweight) at slaughter. These findings indicate that the failure of growth rate to improve with increased NE concentration is not due to modifications in physical body composition. Only small changes were observed with increasing feeding level in carcass and organ weight

(gram per kilogram liveweight). The increase in organ weight in the present study was predominantly due to an increase in the weight of GIT, liver and kidneys. Bikker (1994) indicated that the metabolically active organs (intestines, liver, kidneys and pancreas) are very sensitive to the amount and type of ingested nutrients. The decline in carcass weight with increasing feeding level may be due to an increase in gut fill at higher feeding levels (Bikker, 1994). The effect of feeding level on organ weight in the present study is consistent with those reported in growing pigs by other workers (Rao and McCracken, 1992; Bikker et al., 1995, 1996; Gomez et al., 2002).

Together, these results strongly suggest that the adverse effects of increasing NE concentration, in terms of body chemical composition but not in terms of physical composition, may explain the lack of improved BW gain in the weaned pig when dietary energy concentration is increased.

Nutrient Deposition Rates

In the present study, protein, water and ash deposition rates in the empty body were not affected by dietary NE concentration, but were increased with increasing feeding level. Other research in growing pigs has reported a concomitant increase in protein, water and ash with increasing feeding level (Quiniou et al., 1995, 1996b; Bikker et al., 1995; Gomez et al., 2002).

As observed in other studies that evaluated the response of weaned pigs to energy intake (Gädecken et al., 1985; Kyriazakis and Emmans, 1992a; Collin et al., 2001), the present results indicate that weaned pigs deposited more protein than lipid. Empty body PD increased with increasing feeding level but was not affected by

dietary NE concentration. Similarly, empty body LD increased with increasing feeding level, but unlike PD, NE concentration interacted with feeding level on LD. Indeed, a 95% greater LD was observed in pigs given ad libitum access to the high compared to low NE diet. The increase in empty body PD and LD with increasing feeding level observed in the present study is consistent with studies in growing pigs (Campbell et al., 1983; Bikker et al., 1995).

It is well recognized that PD increases linearly with increasing energy intake when the diet is limiting only in energy (de Lange et al., 2001b). Assuming that increasing the dietary energy concentration is a way to increase lean growth and/or to remove the limitation from physical gut capacity, one might expect PD to increase with increased NE concentration. A piece of striking evidence from this study was that only LD but not PD increased with increasing dietary NE concentration. Contrary to the preceding assumption, this study demonstrates that increasing energy concentration only increases LD in weaned pigs.

The lipid:protein ratio is an indicator of the associated variations of BW gain (Whittemore and Fawcett, 1976) and of lean growth. It assumes that below maximum PD, LD:PD ratio is constant and independent of BW (Whittemore and Fawcett, 1976) and energy intake (Whittemore, 1983). In the present study, LD:PD ratio was increased concomitant to an increase in energy intake with increasing NE concentration (Figure 6.5). This demonstrates that LD:PD ratio in the weaned pig is increased by both energy intake and energy concentration. Indeed, LD:PD ratio in the empty body increased 38% and 49% with increasing feeding level and energy

concentration, respectively. Clearly, then, increasing the supply of utilizable energy through any means appears to increase LD:PD ratio.

An increasing LD:PD ratio with increased dietary energy concentration indicates a greater increase in LD than in PD. Ultimately, the poorer lean growth with increasing NE concentration would explain the lack of increase in growth rate with increased NE concentration reported herein and with increasing dietary energy concentration in other studies (Reis de Souza et al., 2000; Levesque, 2002). The present observation of an increase in LD:PD ratio with energy intake is in congruence with observations in growing pigs (Bikker et al., 1995; Quiniou et al., 1996a).

The increase in LD and the concomitant increase in LD:PD ratio with dietary NE concentration were the result of increased NE intake. Lipid deposition, PD and LD:PD ratio are all highly correlated with DE and NE intake (Tables 6.6 and 6.16). The quadratic increase in LD and LD:PD ratio to NE intake was primarily a consequence of the increase in pigs that were fed the high NE diet (Figures 6.4 and 6.5). As dietary NE concentration increased, pigs were unable to reduce intake to match the need for lean growth. The excess energy ingested above that needed to maximize PD by pigs on the medium and high NE diets was used for LD. This corroborates our previous report (Oresanya et al., 2004) that estimated a lower NE intake is required to maximize growth rate and PD compared to LD in ad libitum fed weanling pigs.

There was no relationship between NE intake and LD:PD ratio on the low and medium NE diets ($P > 0.05$). However, due to the increase in LD:PD ratio in pigs allowed unrestricted access to the high NE diet, the LD:PD ratio increased linearly

with NE intake available for growth, that is the quantity of NE consumed above maintenance (R^2, 0.78; $P < 0.05$; Figure 6.5). This further demonstrates a negative effect of increasing NE from 2.15 to 2.37 Mcal/kg on the lean growth of pigs.

In general, the effect of dietary NE concentration and feeding level on water and ash deposition rates in carcass, organ and empty body closely resembled the effect described for PD. In fact, these three chemical components in the body are known to be closely associated (Kotarbinska, 1971; de Greef, 1992). Thus, empty body protein:water ratio was constant across dietary NE concentration and feeding level (mean = 0.25). Likewise ash:protein ratio was not influenced by dietary NE concentration (mean = 0.16). However, due to the fact that empty body PD increased at a faster rate compared to ash, ash:protein ratio declined with increasing feeding level. In contrast, Kyriazakis and Emmans (1992a) found that energy intake of pigs between 12 to 28 kg BW did not change the empty body ash:protein ratio (0.19).

When the results of growth, body composition and nutrient deposition rates are taken together, they suggest that restricting feed (energy) intake would be necessary to minimize body lipid content and lipid deposition rate and achieve a desirable lean growth in the weaned pig when dietary NE concentration is increased. However, because this is not a practical approach, an arbitrary increase in dietary energy concentration when energy intake has not been demonstrated to limit growth is not recommended.

Energy Utilization

Increasing NE concentration increased the amount of lipid deposited per Mcal of energy. This may be related to the increase in dietary fat content and intake. Chudy and Schiemann (1969) indicated that dietary fat is utilized with a greater efficiency for body lipid deposition than carbohydrates. This is due to lower heat losses associated with the incorporation of dietary fatty acids into body lipid. Daily LD was related to digestible fat intake ($r = 0.71$, $P < 0.001$). However, LD was equally related to starch intake ($r = 0.88$, $P < 0.001$). The poorer efficiency of energy utilization for growth with increasing NE concentration (Table 6.5; Figure 6.2) and feeding level is clearly due to the changing body composition, demonstrated by the decline in empty body protein and increase in lipid content. Since 1 kg of lean muscle contains 77 to 80% water compared to only 5% for adipose tissue, the energy cost of lean growth is considerably less than adipose tissue deposition (NRC, 1998). Furthermore, due mostly to an increase in LD, there was an increase in RE:DE, RE:DE and RE:NE ratios with increasing NE concentration and energy intake (Table 6.12; interaction, $P < 0.001$).

Our estimate of 118 kcal/kg $BW^{0.75}$ per day for DE*m* is similar to the 122 kcal/kg $BW^{0.75}$ per day for weaned pigs estimated by Campbell and Dunkin (1983a) and the estimate of 110 kcal/kg $BW^{0.75}$ per day reported by the NRC (1998). Our estimated NE for maintenance (71 kcal/kg $BW^{0.75}$) per day agrees with that reported by Robles and Ewan (1982) and is similar to the 78 kcal/kg $BW^{0.75}$ per day reported by Just (1982).

The simultaneous estimation of ME*m*, and the efficiency of energy utilization for protein and lipid deposition (kp and kl) using the factorial approach (Kielanowski, 1966), resulted in a low kp (<0.35) and a biologically unreal kl (>1). This is probably due to the colinearity and interdependence of the regression coefficients of PD and LD (Le Bellego et al., 2002; Nieto et al., 2002). Other reasons discussed by Wenk et al. (1998) may be responsible. First, the variation of ME intake may be insufficient, and consequently led to inadequate variation in RE; second, ME*m* is independent of ME for growth. For instance, PD is only a small fraction of total protein turnover, and energy retained as protein (ERP) and energy retained as lipid (ERL) are subjected to physiological limitation that is not easily altered.

The ERP and ERL of pigs were used in conjunction with estimated kp and kl (0.64 and 0.83, respectively; Noblet et al., 1999) and our estimated NE for maintenance (71 kcal/kg $BW^{0.75}$) to calculate total NE used. The total NE used per day calculated with this factorial approach was close to the calculated NE intake (Figure 6.10), supporting the accuracy of existing factorial estimates of the efficiency of energy utilization for protein and lipid deposition.

Plasma IGF-I Concentrations

Insulin-like growth factors (IGF), and particularly IGF-I mediate the growth-stimulating action of growth hormone (GH; Simmen et al., 1998) and GH dependent increases in PD (Boyd and Bauman, 1989). Circulating IGF-I reflects endogenous GH secretion and overall growth in well-nourished humans and animals (Blum et al., 1993; Simmen et al., 1998). The effect of increasing dietary energy concentration and

feeding level on circulating concentrations of IGF-I in the weaned pig has not previously been established.

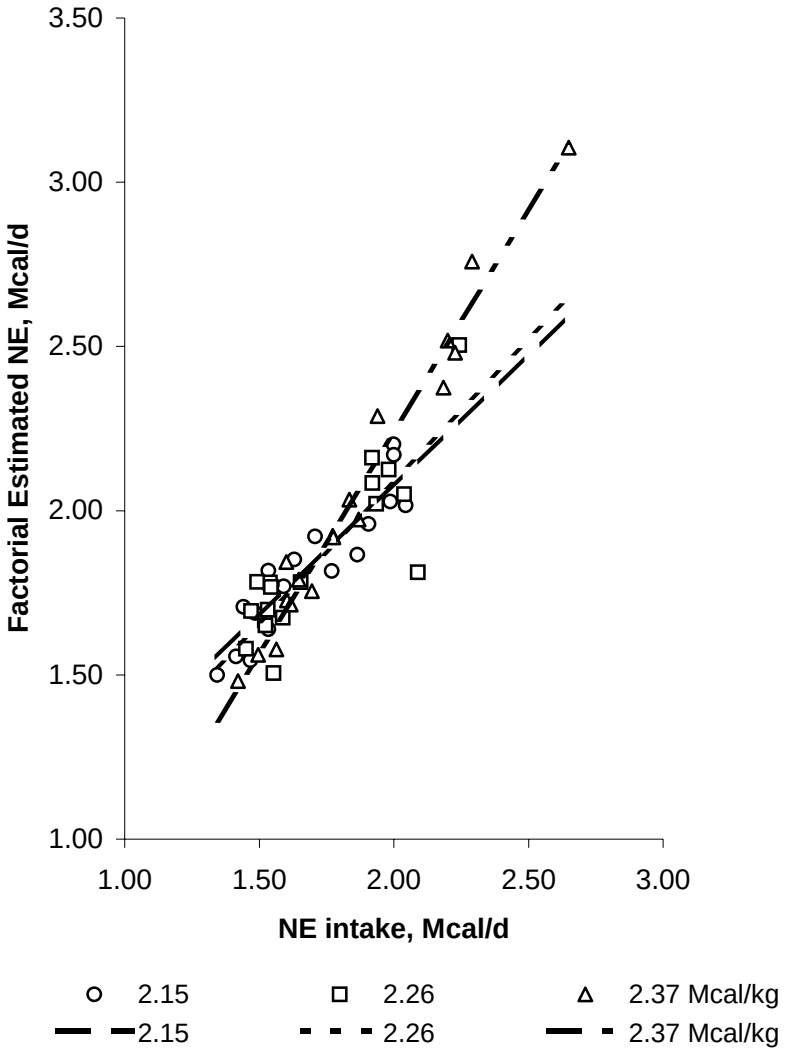

Figure 6.10. Factorial estimate of NE used relative to NE intake of barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels. Linear regression equations: [2.15, Mcal/kg]: Factorial Estimated NE = 0.48 + 0.80NE intake, R^2 0.84; [2.26, Mcal/kg]: Factorial Estimated NE = 0.39 + 0.85NE intake, R^2 0.74; [2.37, Mcal/kg]: Factorial Estimated NE = -0.43 + 1.34NE intake, R^2 0.97. $P < 0.0001$. Factorial estimated NE used differed from NE intake by 0.14, 0.13 and 0.19 in pigs fed the 2.15, 2.26 and 2.37 Mcal NE/kg diet, respectively.

An important observation of this study was that feeding level but not NE concentration had a considerable effect on plasma IGF-I. The lack of effect of dietary NE concentration on plasma IGF-I concentrations is consistent with that of Lee et al. (2002) who found that increasing dietary DE concentration from 2.95 to 3.50 Mcal/kg in growing pigs from 59 to 105 kg BW did not affect serum IGF-I concentrations.

Although the liver is thought to be the primary source of circulating IGF-I (Brameld et al., 1996), non-hepatic tissues, mainly muscle and adipose tissues, constitute a significant portion of the IGF-I pool in the pig (Lee et al., 1993; Coleman et al., 1994). Therefore, considering the fact that both liver weight and body lipid content were increased with increasing feeding level in the present study, an increase in plasma IGF-I concentration would be expected.

Buonomo et al. (1987) indicated that circulating concentrations of IGF-I are positively correlated with growth rate in pigs. Plasma IGF-I concentrations in the present study increased 105% from d 7 to 21, and is consistent with the increase in growth rate within that period.

On the basis of these results, we therefore conclude that increasing dietary NE concentration and feeding level increased NE intake, whereas PD and overall growth rate were not increased with increased NE concentration. The effects of NE concentration and feeding level on growth, PD and plasma IGF-I concentration are additive. However, an interactive effect of increased NE concentration and feeding level on empty body lipid content, LD and LD:PD ratio indicates that increasing energy concentration is not desirable for optimal lean growth in weaned pigs. Finally,

determined NE intake offers an advantage over actual DE intake in predicting body composition and rate of gain in weanling pigs.

6.5 Implications

A very clear understanding of dietary energy utilization on growth, body composition and nutrient deposition rates is essential. The results of the present study indicate that increasing dietary NE concentration increased energy intake, body lipid content and deposition rate but not protein deposition rate. These adverse effects on body composition explain the lack of improved BW gain with increasing energy concentration. Since weaned pigs fed the diet with low NE concentration in this study could achieve energy intake adequate for optimal growth performance, there is no benefit of increasing energy intake with increased dietary energy concentration on lean growth, at least not for pigs with this genetic potential for growth and consuming this amount of feed. Therefore, the practice of increasing dietary energy concentration for weaned pigs in order to increase growth rate should be reconsidered.

7. GENERAL DISCUSSION

Introduction

Energy is well recognised as the largest single cost factor in commercial pork production (SCA, 1987; de Lange and Birkett, 2004). Based on the available literature, our current knowledge on energy metabolism in the young pig is limited, and driven in part by poorly supported assumptions. It was widely speculated that physical gut capacity limits energy intake and restricts the young pig from achieving its genetic potential for growth (Campbell, 1987; Whittemore, 1993). Increasing dietary energy concentration is assumed to be a possible solution to overcome the limitation to energy intake (Van Lunen and Cole, 1998). Recent studies have failed to support this assumption or demonstrate a clear relationship between energy concentration and animal growth (Smith et al., 1999a; Reis de Souza et al., 2000; Levesque, 2002).

In addition, the literature suggests that feed intake in ad libitum fed pigs depends on energy concentration (NRC, 1987; Kerr et al., 2003; Noblet and van Milgen, 2004). However, weaned pigs have been noted to lack the ability to increase energy intake when dietary energy concentration is too low (e.g. Whittemore et al., 2001) and to decrease intake when energy concentration is elevated (NRC, 1987; Levesque, 2002).

Taken together, an accurate understanding of energy metabolism would require a simultaneous and detailed evaluation of dietary energy concentration and daily energy intake, especially in weaned pigs.

The general aim of this project was to develop a clearer understanding of the effect of energy concentration and intake on body composition, nutrient deposition, overall growth and energy utilization in weaned pigs. In the first experiment (Chapter 3) the objective was to determine the optimum total lysine:DE ratio for the weaned pig from 7.5 to 23 kg, in terms of growth performance and plasma urea nitrogen concentration in order to ensure that amino acid nutriture would not confound our studies on energy. In the second experiment (Chapter 4) the objective was to determine if a more predictable growth, nutrient accretion and energy utilization in the weaned pig is achieved with NE or DE and develop a better understanding of the relative merits of the two systems in diet formulations. In the fourth experiment (Chapter 6), for the first time, the interaction between daily energy intake and dietary energy concentration on body weight gain and on tissue (protein, lipid, ash, water) deposition rates and ratios (lipid:protein, protein:water, ash:protein) was investigated. Secondary objectives were to evaluate the accuracy of existing factorial estimates of the efficiency of energy utilization for protein and lipid deposition and to determined whether actual (measured) DE intake or estimated NE intake (CVB-based) is more effective in predicting animal growth performance. Prior to experiment 4, a preliminary study (Chapter 5) was conducted to clarify the response of weaned pigs to energy and amino acid intake simultaneously. This determined the greatest degree

of energy intake restriction at which amino acid intake is not a factor confounding the response to energy. This information was previously unavailable.

Protein and Energy Dependent Phases of Growth

Energy in the form of adenosine triphosphate (ATP) is required for protein synthesis and deposition; amino acids, in addition to non-protein sources, are potential source of ATP (Moughan, 1995). The fact remains that amino acids are most efficiently used for PD rather than deamination to yield energy (Kyriazakis and Emmans, 1992b; Edwards and Campbell, 1993). An accurate definition of the optimal amino acid:energy ratio ensures that amino acids are supplied to the pig in a manner that maximizes efficiency for PD. Body lipid content is known to increase whereas the efficiency of nitrogen utilization declines when amino acid:energy ratio is below requirement (Bikker, 1994).

Lysine is often the limiting amino acid in complete pigs' diets (Nam and Aherne, 1994; Chang et al., 2000; Lewis, 2001); therefore, the starting point of the studies conducted in this thesis was to determine the optimum level of total lysine:DE for the weaned pig. This ensures that responses in subsequent studies are indeed attributable to energy.

As expected, at lower lysine:DE ratios, amino acid supply limits growth and consequently, growth improved as lysine:DE ratio increased. However, in the present study, contrary to those by Smith et al. (1999a) and Van Lunen and Cole (1998), no DE × lysine:DE ratio interaction on growth rate and other performance parameters

was detected. This indicated that pigs in the present study were in a lysine-dependent, as opposed to energy-dependent circumstance.

Furthermore, the lack of response to increasing lysine:DE ratio in the last two wks of this study (13 to 22.5 kg BW) would suggest that the requirement was met even at the lowest level investigated. This result supports a phase-feeding program for weaned pigs in the 7.5 to 22.5 kg BW. Therefore, a higher requirement (4.46 g/Mcal) for the 7.5 to 13 kg BW can be replaced with a lower lysine:DE ratio thereafter. In the absence of a phase-feeding program in this BW range, the optimum level (4.27 g/Mcal) determined for the entire study (7.5 to 22.5 kg BW) would be applicable. By applying the optimum total lysine:DE ratio in experiments 2, 3 and 4, we ensured that dietary amino acid supply and intake did not limit the performance of pigs.

The results of experiment 3 (Chapter 5) support the concept of protein and energy dependent phases in protein deposition (PD) and growth previously described in the young pig (Campbell and Dunkin, 1983a; Kyriazakis and Emmans, 1992a; Edwards and Campbell, 1993; Bikker, 1994). It appeared that amino acids were limiting the growth of pigs on the regime with amino acid intake at constant proportion to energy (ConP) but not those on the amino acid intake at increasing proportion to energy (RedP) regime. Contrary, energy, but not amino acid intake was limiting the growth of pigs on the RedP regime.

A previous study with weaned pigs by Kyriazakis and Emmans (1992b) found that PD is dependent only on the rate of protein supply at low levels of protein intake, while at high rates of protein intake, PD is dependent only on energy supply. In other words, when amino acid intake was limiting, irrespective of a high level of energy

intake, PD did not improve, while once amino acid intake becomes adequate, the excess amino acid supply did not improve PD.

Amino acid supply and intake imposed a bigger restriction on growth in the early nursery phase in experiment 1 and is supported by Close (1994) (Appendix E). However, amino acid intake was maintained at or above requirement in experiments 2, 3 (pigs on RedP fed regime) and 4. As demonstrated with the factorial calculations of amino acid requirement, we are certain that amino acid intake was not limiting the response of pigs to energy in experiment 4 (Table 7.1).

Table 7.1. True ileal digestible lysine intake:requirement ratio of barrows from 9 to 25 kilograms fed diets with increasing NE concentration at three different feeding levels

	NE, Mcal/kg			Feeding level, %			
	2.15	2.26	2.37	70	80	100	SEM
TID intake, g/d[a]	11.5	11.5	12.2	9.9	11.2	14.1	0.3
TID lysine required, g/d[b]	7.8	8.4	8.1	9.0	8.7	6.7	0.2
maintenance, g/d[b]	0.36	0.37	0.37	0.36	0.37	0.37	0.01
protein deposition, g/d[b]	7.8	8.0	7.8	8.6	8.3	6.3	0.2
Intake/requirement	1.57	1.48	1.59	1.14	1.35	2.14	0.07
Protein deposition, g/d[b]	92	91	96	81	86	112	2
Protein deposition, g/d[c]	93	90	94	81	87	110	2

[a]True ileal digestible lysine intake. Calculated from ADFI and estimated dietary TID lysine content (g/kg) based on lysine digestibility coefficient of individual ingredient (NRC, 1998).
[b]Calculated according to Close (1994). See Table in Appendix E (Table E1) for the various assumptions.
[c]Measured empty body protein deposition rates.

Energy Intake and Lean Growth

In Chapter 3, DE intake increased in the high energy diets without increasing growth rate. Levesque (2002) reported similar findings. Interestingly, similar result of increasing energy intake with no improvement in growth was observed when the interactive effect of energy concentration and intake was investigated in Chapter 6. In experiment 2 (Chapter 4), the curvilinear relationship between energy intake and growth suggest that although growth increased with energy intake there is a limit at which further increase in energy does not produce growth response. This is well supported by the greater breakpoint in energy intake to maximize LD compared to PD and overall growth.

Taken together, these results suggest that pigs on the control diets in experiments 2 and 4 were able to consume sufficient energy to maximize growth rate. In contrast to growth rate, there was an interaction of NE concentration and intake on empty body lipid content and deposition rate. Furthermore, the results of these studies revealed that increased NE concentration produced little (experiment 2) to no changes (experiment 4) in physical body composition.

With the LD:PD ratio as an indicator of the associated variations of BW gain (Whittemore and Fawcett, 1976) and of lean growth, there is clearly a negative effect of increasing dietary energy concentration on lean growth. This would definitely explain the failure to improve growth rate in this thesis with energy concentration (Experiments 1, 3 and 4) and in previous studies that investigated the response of weaned pigs to increasing energy concentration (e.g. Tokach et al., 1995; Smith et al., 1999a; Reis de Souza et al., 2000; Levesque, 2002). These results nullify such notions

that energy intake is limiting lean growth in the weaned pig without specifying that at certain level of dietary energy concentration, pigs are able to achieve intake for a desirable lean growth rate.

Modelling Nutrient Deposition Rates in the Pig

Body compositional analysis is not a routine experimental approach in study of energy metabolism in the pig. However, from the results of experiments 2 and 4, it became apparent that measuring BW gain versus measuring the composition of that gain produces different outcome. In both studies, weight gain remained unchanged or poorer compared to control diets, whereas, larger changes in body composition and nutrient deposition rates were detected. Therefore, modelling growth in the weaned pig for the purpose of developing an optimal feeding strategy requires an accurate quantification of the response to energy intake in both BW gain and body composition.

There was a negative quadratic coefficient of PD with increasing energy intake (see Table 6.6), indicating that PD would not improve beyond an optimal intake level required to maximize the operational PD potential of pigs. In contrast, the positive quadratic coefficients of LD and LD:PD ratio to energy intake indicate the undesirable consequence of energy intake on lean growth once that optimal level is exceeded.

The slope of the linear relationship between PD and energy intake quantifies the additional amount of protein deposited from each additional unit increase in energy intake, and represents the marginal partitioning of energy intake between PD and LD. In Chapter 6, PD increased linearly to increasing DE intake:

$$PD = 5.8 + 26.8 \times DE_i \quad (7.1)$$

where PD is in g/d and DE intake is in Mcal/d; n = 54, R^2, 0.86.

The slope (27 g PD per Mcal/DE intake) is intermediate to 33 g PD per Mcal/DE intake reported by Weis et al. (2004) for pigs at 22 kg BW and 24 g PD per Mcal/DE intake for pigs between 20 to 45 kg BW reported by Bikker et al. (1995).

Also, PD increased linearly to increasing NE intake:

$$PD = 12.9 + 37.3 \times NE_i \quad (7.2)$$

where PD is in g/d and NE intake is in Mcal/d; n = 54, R^2, 0.82

When the actual PD and LD rates are known, prediction of empty body nutrient deposition ratios is necessary to determine ash and water content in the empty body. Compared to LD:PD ratio, protein:water deposition ratio was not affected by NE concentration (experiment 2) and NE concentration and feeding level (experiment 4). Therefore, a simple model (without intercept) was developed from the results of both studies to predict water deposition (g/d) from PD (g/d) (Figure 7.1):

$$\text{Water deposition} = 3.91 \times PD \quad (7.3)$$

where water deposition and PD are in g/d.

Although, ash:protein ratio was not affected by NE concentration (experiments 2 and 4; $P > 0.05$), it was affected by feeding level in experiment 4. Nonetheless, using the results from both studies, the following equation (no intercept) provided a reasonable prediction of ash deposition from PD (Figure 7.2):

$$\text{Ash deposition} = 0.16 \times \text{PD} \quad (7.4)$$

where ash deposition and PD are in g/d.

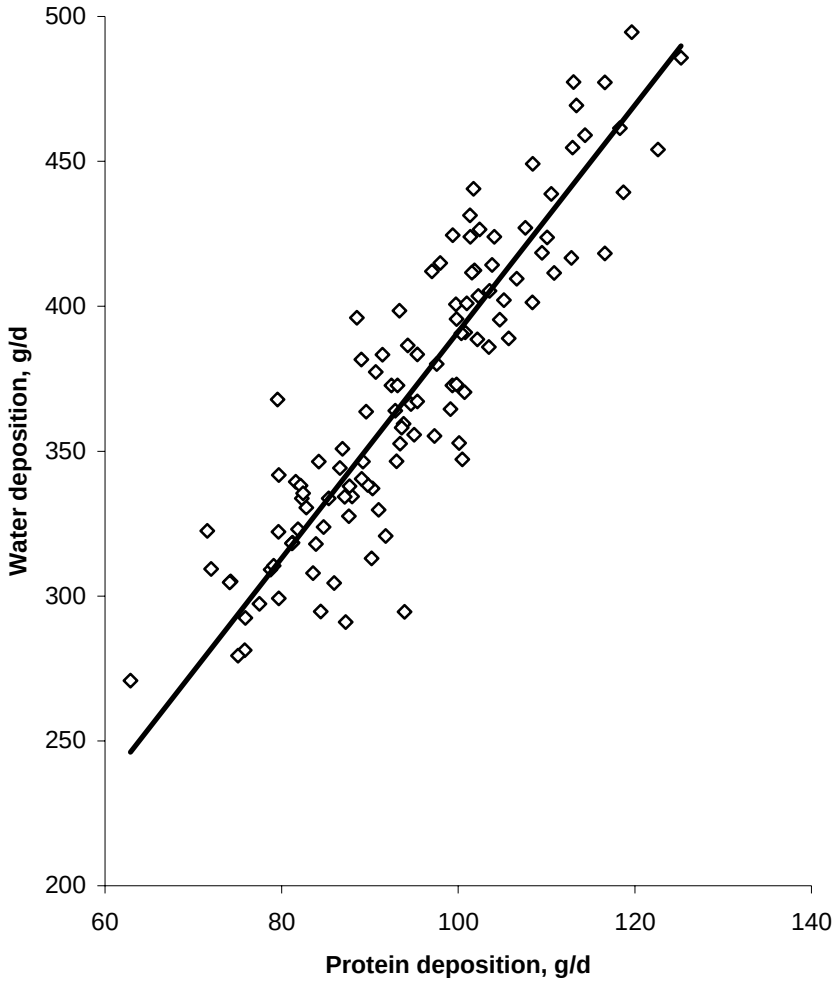

Figure 7.1. The relationship between protein and water deposition rates in the empty body of pigs between 9 to 25 kg BW. $P < 0.0001$; n = 114; $R^2 = 0.99$.

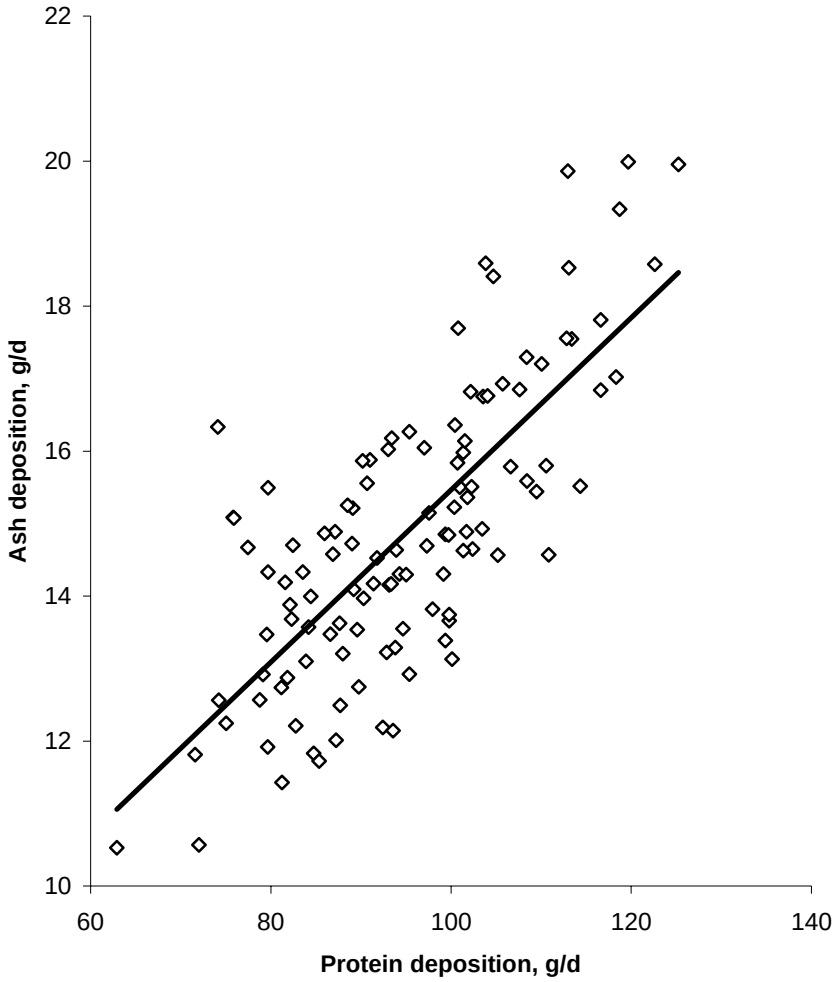

Figure 7.2. The relationship between protein and ash deposition rates in the empty body of pigs between 9 to 25 kg BW. $P < 0.0001$; n = 114; $R^2 = 0.99$.

Energy System in Diet Formulations

Given that the primary goal of diet formulation is to accurately match the energy supply to the pigs' energy requirement for maintenance and productive functions, the selected energy system should within reason fulfill such a goal (Van Es, 1980b; Cole, 1995; Noblet, 2000).

In experiment 2 (Chapter 4) three important points could be made relating to energy systems. First, it is possible to achieve similar formulated and/or determined DE concentrations with a diverse array of dietary chemical composition. Second, irrespective of similar DE concentration, the formulated NE and indeed, determined NE concentration, estimated from digestible nutrient increased up to 11% from diet 1 to diet 3. Third, such variation in chemical composition and the increase in NE concentration elicited a negative influence on growth, body composition and nutrient accretion of pigs. From the standpoint of achieving predictable performance in weaned pigs, these points cannot be ignored in selecting an energy system for weaned pigs.

Noblet (1997) indicated that NE is superior to DE and ME for predicting performance of pigs. The author found that energy efficiency, calculated as Mcal NE/kg BW over the 30 to 100 kg BW was similar irrespective of the declining dietary CP content whereas the Mcal DE/kg BW gain was greater in the high CP diet. Recently, Hageman (2004) reported that a 17% reduction in the CP content of diets formulated at ideal protein and taking into account the NE value of ingredients did not affect performance and carcass quality of pigs from 30 to 110 kg BW. In other words, when dietary CP content is reduced, NE concentration should be considered.

To the best of our knowledge, this is the first study to determine the relative merit of the DE and NE system for diet formulation for weaned pigs.

The correlation analyses in Chapter 4 revealed that both NE intake and determined NE concentration were more correlated with empty body nutrient content and deposition rates than actual DE concentration and DE intake. In addition, in Chapter 6, a stronger correlation of empty body composition and nutrient deposition rates with NE intake as compared to DE intake all suggest that NE gives a marginal advantage over DE on predictable body composition rather than overall growth performance.

Predicting Dietary Energy Concentration for Weaned Pigs

Since digestible nutrients vary among physiological states (Noblet and van Milgen, 2004; de Lange and Birkett, 2004), irrespective of the energy system, the energy value ascribed to a particular feed ingredient should be reconciled with the digestive physiology of the particular age of the animal.

As suggested by Rijnen et al. (2004), due to the variation in chemical composition of ingredients, especially with fiber, values determined for one age of animal may not be suitable for another. In addition, the results of experiment 4 (Chapter 6) indicate that the dietary energy content decreased with increasing feeding level. Therefore, if existing values are determined with grower pigs at restricted feeding levels, it is clearly apparent that the DE and NE values would be further removed from a realistic value applicable for weaned pigs.

NE is usually measured as fasting heat production (FHP) plus retained energy (RE; Noblet et al., 1994). The CVB (1994, 2003) estimates NE from digestible nutrients using fixed partial efficiencies. The results of experiments 2 and 4 were combined to develop equations applicable to predict NE concentration of the weaned pig diet.

Since heat production measurements were not conducted in these experiments, FHP was taken as 193 kcal/kg $BW^{0.60}$ (Collin et al., 2001), and using the RE data, NE was calculated for each diet (n = 8). As well, NE of each diet was estimated from digestible nutrients according to the CVB (1994) equation. The value estimated from digestible nutrients was well correlated with that calculated as FHP plus RE, and the average of the two calculations was used for the purpose of predicting NE from dietary chemical composition and digestible nutrients (Table 7.2).

Table 7.2. Prediction of the NE concentration of weaned pigs' diets from digestible energy concentration and chemical characteristic, digestible nutrients and chemical characteristics[a,b,c]

No.	Equation	R^2	RSD
1	NE = 0.72 × DE + 0.80 × ST - 5.06 × Ash	0.99	25
2	NE = 0.54 × DE + 2.46 × EE + 1.33 × ST	1.00	15
3	NE = 3.60 × DCP + 7.86 × DEE + 3.49 × ST + 2.02 × DRES	0.99	31
4	NE = 1820 + 4.56 × EE + 1.64 × ST	0.97	19
5	NE = 1667 + 5.02 × EE + 1.75 × ST + 0.31 × CP	0.98	20

[a]NE and DE are in kcal/kg DM; ST, starch; EE, ether extract; CF, crude fiber; DCP, digestible CP; DEE, digestible ether extract; DRES, digestible residuals = digestible organic matter – (DCP + DEE + ST + DCF) all in g/kg DM.
[b]n = 8 diets; see Tables 4.1, 4.2, 6.1 and 6.2 for ingredients and chemical composition of diets.
[b]Determined NE value was from 12 observations per diet (n = 5) in experiment 2. There were 27 observations per diet (n = 3) for NE estimated from digestible nutrients, but 18 observations per diet for NE calculated from FHP plus RE in experiment 4. NE of each of the 8 diets used in the prediction was the average of the two calculations.

As a result of the large deviation observed in the actual vs. formulated DE content of the experimental diets fed to the weaned pig, the suitability of the values used in diet formulation for weaned pigs is questionable (Levesque, 2002; Rijnen et al., 2004). This represents a major flaw in most studies that evaluated the response of the weaned pigs to dietary energy concentration. As discussed previously (Chapters 2, 4 and 6), it is important that values used are appropriate for the physiological state of the pig. Furthermore, sound and accurate interpretation of the respones of the weaned pig to dietary energy concentration should be based on actual DE values.

In the absence of a bomb calorimeter, the GE content of diets can be predicted with good accuracy from established chemical equations (e.g. Schiemann, 1988; Ewan; 1989; Noblet and Perez, 1993). By using all the 20 diets used in the work of this thesis (Table 7.3), the GE content was predicted from dietary chemical characteristics. Equations were based on chemical determinations that are rapid and widely availability. Thus, only CP, ether extract, ash and crude fiber were considered. Furthermore, since only 2 or 3 of these assays may be available, the max r statement of SAS was used to generate the four listed equations (Table 7.4).

As well, without calorimetric measurement, it is necessary to predict the DE values of diets. The effects of dietary treatments on apparent GE digestibility in experiments 1, 2 and 4 closely resembled that obtained with apparent DM digestibility (see Chapters 3, 4 and 6). Therefore, simple equations (with or without intercept) to predict apparent digestibility of energy (DEc) were developed from apparent DM digestibility (Figure 7.3):

$$DEc = -2.55 + 1.02 \times DMc \qquad (7.5)$$

$$DEc = 0.99 \times DMc \quad (7.6)$$

where DEc and DMc are the apparent digestibility coefficient of GE and DM, respectively (R^2 = 0.96 and 1.00, equation 7.5 and 7.6, respectively; $P < 0.0001$).

By combining the GE predicted from chemical characteristic (Table 7.4) with the predicted apparent digestibility coefficient of GE, dietary DE concentration can be estimated accurately for weaned pigs.

Table 7.3. Ingredient and nutrient composition of diets used in experiments 1, 2, 3 and 4

Item	Number of diets	Minimum	Maximum	Mean
Ingredients[a]				
Wheat	19	8.00	63.24	43.48
Barley	12	1.68	30.05	15.16
Corn	7	2.50	38.65	15.48
Soybean meal	20	5.70	27.75	13.36
Full-fat soybean	2	14.00	28.00	21.00
Menhaden fish meal	20	5.50	11.00	8.07
Soy protein concentrate	13	2.25	4.30	3.60
Spray dried whey	15	5.00	7.50	5.83
Lactose	15	5.00	10.00	8.33
Spray dried plasma	10	2.20	3.20	2.70
Spray dried whole blood	5	2.50	2.50	2.50
Dried skimmed milk	5	2.50	5.90	3.51
Canola oil	18	0.50	4.54	2.34
Dicalcium phosphate	17	0.32	0.85	0.61
Limestone	20	0.32	0.77	0.49
Salt	20	0.30	0.43	0.31
Celite	8	0.50	0.50	0.50
Mineral premix	20	0.50	0.72	0.51
Vitamin premix	20	0.50	0.72	0.51
Choline chloride	20	0.05	0.07	0.05
l-lysine HCl	18	0.03	0.66	0.28
l-threonine	19	0.01	0.31	0.10
dl-methionine	17	0.001	0.27	0.09
l-tryptophan	14	0.004	0.11	0.04
LS-20	20	0.10	0.10	0.10
Analyzed nutrients[b]				
GE, Mcal/kg		3.92	4.40	4.10
DM, %		89.8	93.1	91.0
Crude protein, %		19.9	30.4	24.6
Crude fat, %		2.5	9.1	4.9
Crude fiber, %		1.9	3.3	2.4
Ash, %		5.2	8.7	6.2

[a]Others include valine, isoleucine, leucine, phenyalanine, and $NaHCO_3$.
[b]Analyzed nutrient content conducted on all 20 diets (as fed).

Table 7.4. Prediction of GE content of diets fed to weaned pig from chemical characteristic[a,b]

No.	Equation	R^2	RSD
1	GE = 4201 + 5.6 × EE	0.92	35
2	GE = 4115 + 5.4 × EE + 3.5 × CF	0.94	32
3	GE = 4135 + 5.3 × EE + 5.1 × CF – 0.8 × Ash	0.94	32
4	GE = 4055 + 5.4 × EE + 4.1 × CF – 2.0 × Ash + 0.7 × CP	0.95	31

[a]n = 20 diets. See Table 7.3 for average chemical and ingredient composition of diets.
[b]GE is in kcal/kg DM; EE, ether extract; CF, crude fiber; CP, crude protein are in g/kg DM.

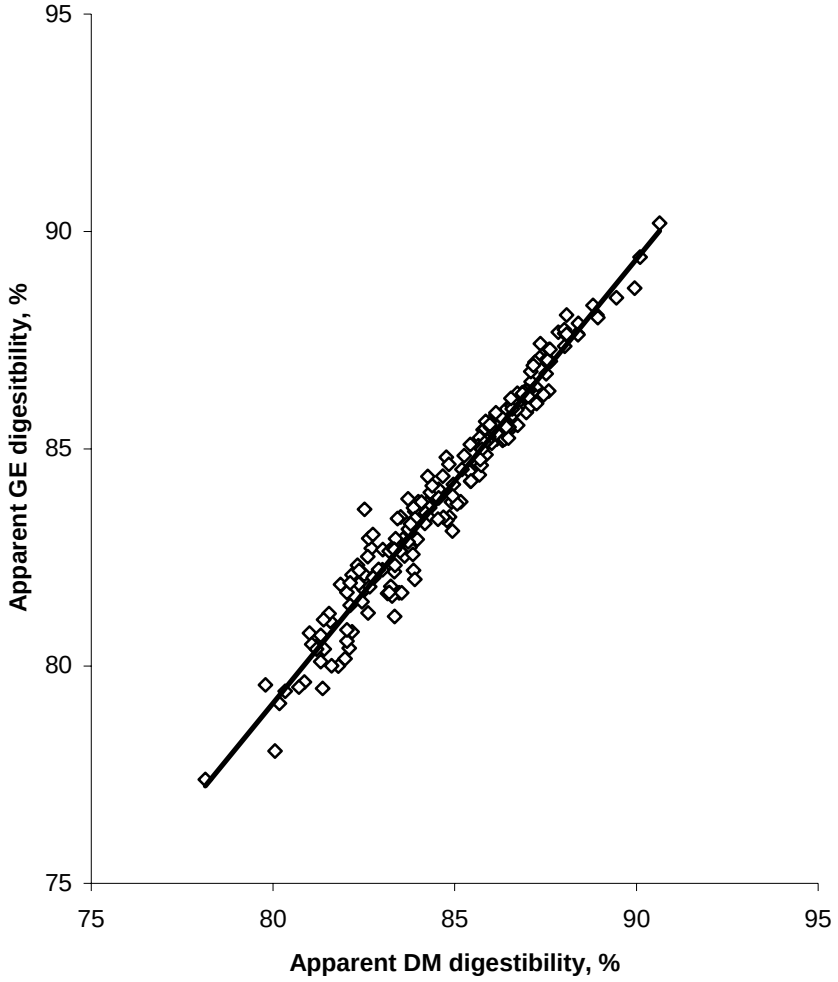

Figure 7.3. The relationship between apparent DM and GE digestibility in weaned pig. $R^2 = 0.96$, RSD = 0.49; $P < 0.0001$; n = 221.

Limitation of Study and Future Direction

A major limitation of this study was that energy values of ingredients used in diet formulation were based on a NE system that was developed with grower pigs. According to the literature, the digestive utilization of nutrients is clearly affected by physiological state (Le Goff and Noblet, 2001; de Lange and Birkett, 2004) and therefore, the accuracy and suitability of such values and NE equation that we used for weanling pigs is uncertain (Levesque, 2002; de Lange and Birkett, 2004; Rijnen et al., 2004). Also, since we did not measure heat production, the estimate of FHP (Collin et al., 2001) used in calculating NE concentration may not be accurate. We mitigated this limitation by conducting digestibility measurements on GE, and other nutrients in order to estimate dietary NE concentration. In this manner, even if the absolute values were wrong, we are confident that the NE concentration of experimental increased according to the study design.

Another limitation of this study was the dependence on the comparative slaughter technique (CST) to determine RE and nutrient deposition. This approach is based on the assumption that the body composition of the experimental group of pigs at the beginning of an experiment can be estimated accurately and precisely from the empty body composition of comparable pigs from the same population that are slaughtered at the beginning of the experimental period. Since no two pigs are exactly identical, the CST necessarily involves the slaughter of fairly large numbers of pigs to reduce errors attached to the estimates. The CST is limited in greater part by the difficulty in getting a representative sample at grinding, errors associated with gravimetric determination of dry matter, sampling during various chemical assays,

and probably to a lesser extent, error caused by assuming a 6.25 factor for nitrogen to calculate CP. It must be noted, however, that precautions were taken to minimize these errors in the conduct of the study. The variation in body composition of pigs at ~ 9 kg BW is relatively small compared to those at heavier BW; nevertheless, we selected an appropriate number of pigs for the ISG. Furthermore, all chemical analyses on samples were conducted according to established analytical procedures, known standards were employed and assays were appropriately repeated as required.

This study was further limited by the lack of information on the intermediary metabolism of nutrients (amino acids, starch, sugars, fatty acids) used for meeting the requirements for ATP, protein and lipid synthesis. These nutrients are subjected to different biochemical pathways and the efficiency of ATP synthesis, lipid, protein synthesis and deposition and hence growth depends on the biochemical transformation of the nutrient, and biophysical and physiological processes (van Milgen et al., 2001). However, our objectives were focused on overall body growth and composition of gain, and hence, intermediary metabolism was beyond the scope of this thesis.

A final limitation of the study is the inability to determine if the poorer body composition with increasing dietary energy concentration observed in weanling pigs at 25 kg BW would elicit any effect on body composition and carcass quality of growing-finishing pigs. The latter was beyond the scope the thesis. Consequently, future studies are required to determine appropriate energy values of ingredients to use in diet formulation and establish a NE system adapted to weanling pigs. Also, a follow-up study to determine the impact of changes in body composition

at 25 kg BW on body composition and carcass quality of pigs at market weight is warranted.

8. GENERAL CONCLUSIONS

- Total lysine:DE ratio to maximize growth performance is 4.46 g/Mcal for weaned pigs between 7.5 to 13 kg BW. A lower ratio, 4.27 g/Mcal would be required for the 7.5 to 22.5 kg BW range. The optimum lysine:DE ratio is independent of dietary DE concentration within the range of 3.4 to 3.6 Mcal DE/kg.
- DE did not accurately predict performance and inconsistencies were obtained in growth performance with determined dietary NE concentration. NE is marginally better than DE in describing the composition of gain and nutrient deposition rather than overall animal performance.
- Increased dietary energy concentration exerted little influence on feed intake, but produced an increased energy intake.
- The feed intake of pig between 7 to 25 kg BW feed exposed to diets with actual dietary DE concentration between 3.31 and 3.58 Mcal DE/kg is adequate to achieve optimal daily DE intake for growth. Similarly, weaned pigs will maintain optimal NE intake for growth in diets with determined NE concentration between 2.15 and 2.55 Mcal NE/kg.
- As opposed to existing assumption, ad libitum fed weaned pigs would ingest sufficient energy (DE and NE) to achieve protein deposition potential. Growth and protein deposition were maximized at lower energy intake compared with

lipid deposition. Therefore, energy intake exerts a rather greater restriction on lipid deposition.

- The interaction of NE concentration with energy intake on empty body lipid content, LD and LD:PD ratio indicates that increasing energy concentration is not desirable for optimal lean growth in weaned pigs. Increasing NE concentration above 2.15 Mcal/kg estimated in the control diet neither increase growth nor PD rates of weaned pigs.

9. REFERENCES

Albin, D. M, M. R. Smiricky, J. E. Wubben, and V. M. Gabert. 2001. The effect of dietary level of soybean oil and palm oil on apparent ileal amino acid digestibility and postprandial flow patterns of chromic oxide and amino acids in pigs. Can. J. Anim. Sci. 81:495-503.

AOAC. 1990. Official methods of analysis. 15th ed. Assoc. Offic. Anal. Chem., Arlington, VA.

AOAC. 2002. Official Methods of Analysis. 17th ed., Vol 2. Assoc. of Offic. Anal. Chem., Arlington, VA.

ARC. 1981. The nutrient requirement of pigs: Technical Review. Rev. ed. Commonwealth Agricultural Bureau, Slough, England.

Armsby, H. P. 1917. The nutrition of farm animals. MacMillan, New York.

Armsby, H. P., and J. A. Fries. 1915. Net energy values of feeding-stuffs for cattle. J. Agric. Res. 3:435-491.

Atwater, W. O., and A. P. Bryant. 1900. The availability and fuel value of food materials. Ann. Rep. (1899), Storrs, Conn. Agric. Exp. Stn. 12th ed.

Azain, M. J. 2001. Fat in swine nutrition. Pages 95-106 in Swine nutrition. A. J. Lewis and L. L. Southern, ed. CRC Press LLC, Boca Raton, Fl.

Bach Knudsen, K. E., and J. A. Hansen. 1991. Gastrointestinal implications in pigs of wheat and oat fractions I. Digestibility and bulking properties of polysaccharides and other major constituents. Br. J. Nutr. 65:217-232.

Baidoo, S. K., E. J. Clowes, and F. X. Aherne. 1996. The digestible energy value of canola oil for growing pigs as measured by level of inclusion. Anim. Feed Sci. Technol. 62:111-119.

Baldwin, R. L., and A. C. Bywater. 1984. Nutritional energetic of animals. Annu. Rev. Nutr. 4:101-114.

Baldwin, R. L., and R. D. Sainz. 1995. Energy partitioning and modeling in animal nutrition. Annu. Rev. Nutr. 15:191-211.

Bikker, P. 1994. Protein and lipid accretion in body components of growing pigs. Effects of body weight and nutrient intake. Ph.D. Thesis, Wageningen Agric. Univ., Wageningen, The Netherlands.

Bikker, P., M. W. A. Verstegen, and R. G. Campbell. 1993. Deposition, utilization and requirements of protein in growing pigs: A factorial approach. Page102-110 in Nitrogen Flow in Pig Production and Environmental Consequences. M. W. A. Verategen, L. A. Den Hartog, G. J. M. Van Kempen, and J. H. M. Metz, ed. Proc. of the 1st Int. Symp. on Nitrogen Flow in Pig Production and Environmental Consequences, June 1993. EAAP Publication No. 69. Pudoc Scientific Publishers, Wageningen, The Netherlands.

Bikker, P., V. Karabinas, M. W. Verstegen, and R. G. Campbell. 1995. Protein and lipid accretion in body components of growing gilts (20 to 45 kilograms) as affected by energy intake. J. Anim. Sci. 73:2355-2363.

Bikker, P., M. W. A. Verstegen, B. Kemp, and M. W. Bosch. 1996. Performance and body composition of finishing gilts (45 to 85 kilograms) as affected by energy intake and nutrition in earlier life: I. Growth of the body and body components. J. Anim. Sci. 74:806-816.

Birkett, S., and K. de Lange. 2001. A computational frame for a nutrient flow representation of energy utilization by growing monogastric animals. Br. J. Nutr. 86:661-674.

Black, J. L. 1971. A theoretical consideration of the effect of preventing rumen fermentation on the efficiency of utilization of dietary energy and protein in lambs. Br. J. Nutr. 25:31-55.

Black, J. L. 1974. Manipulation of body composition through nutrition. Proceedings of the Australian Society of Animal Production 10:211-218.

Black, J. L. 1995. The evolution of animal growth models. Pages 3-10 in Modelling growth in the pig. P. J. Moughan, M. W. A. Verstegen, and M. I. Visser-Reyneveld ed. Wageningen Pers, Wageningen, The Netherlands.

Black, J. L. 2000. Bioavailability: the energy component of a ration for monogastric animals. Pages 133-152 in Feed evaluation: principles and practice. P. J. Moughan, M. W. A. Verstegen, and M. I. Visser-Reyneveld ed. Wageningen Pers, Wageningen, The Netherlands.

Blaxter, K. L. 1989. Energy metabolism in animals and man. Cambridge University Press, Cambridge, U.K.

Blaxter, K. L., and A. W. Boyne. 1978. The estimation of the nutritive value of feeds as energy sources for ruminants and the derivation of feeding systems. J. Agric. Sci. 90:47-68.

Blum, W. F., K. Albertsson-Wikland, S. Rosberg, and M. B. Ranke. 1993. Serum levels of insulin-like growth factor I (IGF-I) and IGF binding protein 3 reflect spontaneous growth hormone secretion. J. Clin. Endocrinol. Metab. 76:1610-1616.

Boisen, S., and M. W. A. Verstegen. 1998. Evaluation of feedstuffs and pig diets. Energy or nutrient-based evaluation systems? Limitations of present energy evaluation systems. Acta Agriculturae Scandinavica. Sect. A. Animal Science 48:86-94.

Boisen, S., and M. W. A. Verstegen. 2000. Developments in the measurement of the energy content of feeds and energy utilization in animals. Pages 57-75 in Feed evaluation: principles and practice. P. J. Moughan, M. W. A. Verstegen, and M. I. Visser-Reyneveld ed. Wageningen Pers, Wageningen, The Netherlands.

Bounomo, F. C., T. J. Lauterio, C. A. Baile, and D. R. Campion. 1987. Determination of insulin-like growth factor I (IGF1) and IGF binding protein levels in swine. Domest. Anim. Endocrinol. 4:23-31.

Boyd, R. D., and D. E. Bauman. 1989. Mechanisms of action for somatotropin in growth. Pages 257-293 in Animal growth regulation. D. R. Campion, G. J. Hausman, and R. J. Martin ed. Plenum Publishing, New York.

Brafield, A. E. and M. J. Llewellyn. 1982. Animal energetics. Blackie, Glasgow, U.K.

Brameld, J. M., J. L. Atkinson, J. C. Saunders, J. M. Pell, P. J. Buttery, and R. S. Gilmour. 1996. Effects of growth hormone administration and dietary protein intake on insulin-like growth factor I and growth hormone receptor mRNA expression in porcine liver, skeletal muscle and adipose tissue. J. Anim. Sci. 74:1832-1841.

Brody, S. 1945. Bioenergetics and growth. Reinhold, New York.

Brouwer, E. 1965. Report of sub-committee on constant and factors. Pages 441-443 in Proceedings of the 3rd symposium. London – New York.

Burrin, D. G. 2001. Nutrient requirements and metabolism. Pages 309-389 in Biology of the domestic pig. W. G. Pond, and H. J. Mersmann, ed. Cornell University Press, Ithaca, New York.

Buttin, P. 1998. Dynamic amino acid balance in growing-finishing diets: More methionine for lower protein, higher energy hog feeds. Feed Management, May, 1998.

Cameron, N. D., E. McCullough, K. Troup, and J. C. Penman. 2003. Serum urea concentration as a predictor of dietary lysine requirement in selected lines of pigs. J. Anim. Sci. 81:91-100.

Campbell, R. G. 1987. Energy and protein metabolism in the pig. Pages 85-95 in Manipulating pig production. J. L. Barnett, ed. Australian Pig Science Association, Werribee, Australia.

Campbell, R. G. 1988. Nutritional constraints to lean tissue accretion in farm animals. Nutr. Res. Rev. 1:233-253.

Campbell, R. G., and A. C. Dunkin. 1983a. The influence of dietary protein and energy intake on the performance, body composition and energy utilization of pigs growing from 7 to 19 kg. Anim. Prod. 36:185-192.

Campbell, R. G., and A. C. Dunkin. 1983b. The effect of energy intake and dietary protein in nitrogen retention, growth performance, body composition and some aspects of energy metabolism of baby pigs. Br. J. Nutr. 49:221-230.

Campbell, R. G., and M. R. Taverner. 1986a. A note on the response of pigs weaned at 28 days to dietary protein. Anim. Prod. 46:427-429.

Campbell, R. G., and M. R. Taverner. 1986b. The effect of dietary fibre, source of fat and dietary energy concentration on the voluntary food intake and performance of growing pigs. Anim. Prod. 43:327-333.

Campbell, R. G., and M. R. Taverner. 1988. Genotype and sex effects on the relationship between energy intake and protein deposition in growing pigs. J. Anim. Sci. 66:667-686.

Campbell, R. G., M. R. Taverner, and D. M. Curic. 1983. The influence of feeding level from 20-45 kg live weight on the performance and body composition of female and entire male pigs. Anim. Prod. 36:193-199.

Campbell, R. G., M. R. Taverner, and D. M. Curic. 1985a. The influence of feeding level on the protein requirement of pigs between 20 and 45 kg live weight. Anim. Prod. 40:489-496.

Campbell, R. G., M. R. Taverner, and D. M. Curic. 1985b. Effects of sex and energy intake between 48 and 90 kg live weight on protein deposition in growing pigs. Anim. Prod. 40:497-504.

Campbell, R. G., M. R. Taverner, and P. D. Mullaney. 1975. The effect of dietary concentration of digestible energy on the performance and carcass characteristics of early-weaned pigs. Anim. Prod. 21:285-294.

Canadian Council on Animal Care. 1993. Guide to the care and use of experimental animals. Volume 1. 2nd ed. E. D. Olfert, B. M. Cross, and A. A. McWilliam, ed. CCAC, Ottawa, ON.

Cera, K. R., D. C. Mahan, and G. A. Reinhart. 1988. Effects of dried whey and corn oil on weanling pig performance, fat digestibility and nitrogen utilization**.** J. Anim. Sci. 66:1438-1445.

Chadd. S. A., and D. J. A. Cole. 1999. The performance response of growing and finishing pigs fed differing proportions of oatfeed as a dietary fibre source. EAAP Annual Meeting, Zurich.

Chang, W. H., J. D. Kim, Z. N. Xuan, W. T. Cho, I. K. Han, B. J. Chae, and I. K. Paik. 2000. Optimal lysine:DE ratio for growing pigs of different sexes. Asian Aus. J. Anim. Sci. 13:31-38.

Chiba, L. I. 2000. Feeding systems for pigs. Pages 181-209 in Feeding systems and feed evaluation models. M. K. Theodorou, and J. France, ed. CABI Publishing, Wallinford, U.K.

Chudy, A., and R. Schiemann. 1969. Utilization of dietary fat for maintenance and fat deposition in model studies with rats. Page 161 in Energy metabolism of farm animals. K. L. Blaxter, J. Kielanowski, and G. Thorbek, ed. EAAP publ. 26. Butterworths, London.

Close, W. H. 1994. Feeding new genotypes: Establishing amino acid/energy requirement. Pages 123-140 in Principles of pig science. D. J. A. Cole, J. Wiseman, and M. A. Varley, ed. Nottingham Univ. Press, England.

Close, W. H. 1996. Modelling the growing pig: Predicting nutrient needs and responses. Pages 289-297 in Biotechnology in the Feed Industry. The living gut: Bridging the gap between nutrition and performance. Proc. of Alltech's 12th Annual Symposium. T. P. Lyons and K. A. Jacques ed. Nottingham University Press, Nottingham, U.K.

Close, W. H., F. Berschauer, and R. P. Heavens. 1983. The influence of protein:energy value of the ration and level of feed intake on the energy and nitrogen metabolism of the growing pig. Br. J. Nutr. 49:255-269.

Close, W. H., M. W. Stanier, and M. R. Sanz Sampelayo. 1979. The energy requirements for growth in the early-weaned pig. Proc. Nutr. Soc. 38:47A.

Cole, M. 1995. Energy systems in pig feed formulation. Feed-Compounder 15:18-19.

Coleman, M. E., L. Russell, and T. D. Etherton. 1994. Porcine somatotropin (pST) increases IGF-I mRNA abundance in liver and subcutaneaous adipose tissue but not in skeletal muscle of growing pigs. J. Anim. Sci. 72:918-924.

Collin, A., J. van Milgen, S. Dubois, and J. Noblet. 2001. Effect of high temperature and feeding level on energy utilization in piglets. J. Anim. Sci. 79:1849-1857.

Coma, J., D. Carrion, and D. R. Zimmerman. 1995. Use of plasma urea nitrogen as a rapid response criterion to determine the lysine requirement of pigs. J. Anim. Sci. 73:472-481.

Coudenys, K. 1998. Effect of energy intake and body weight on chemical and physical body composition in a defined population of pigs. M.Sc. Thesis. University of Guelph.

Crozier, S. J., D. R. Bolster, A. K. Reiter, S. R. Kimball, and L. S. Jefferson. 2002. β-oxidation of free fatty acids is required to maintain translational control of protein synthesis in heart. Am. J. Physiol. Endocrinol. Metab. 283:E1144-E1150.

CVB. 1994. Table of feedstuffs. Information about composition, digestibility and feeding values. Centraal Veevoederbureau, Lelystad, The Netherlands.

CVB. 1998. Table of feedstuffs. Information about composition, digestibility and feeding values. Centraal Veevoederbureau, Lelystad, The Netherlands.

CVB. 2003. Table of feedstuffs. Information about composition, digestibility and feeding values. Centraal Veevoederbureau, Lelystad, The Netherlands.

Davidson, M. B. 1987. Effect of growth hormone on carbohydrate and lipid metabolism. Endocr. Rev. 8:115-131.

de Greef, K. H. 1992. Prediction of production: Nutritional induced tissue partitioning in growing pigs. Ph.D. Thesis. Wageningen Agric. Univ., Wageningen, The Netherlands.

de Greef, K. H., and M. W. A. Verstegen. 1993. Partitioning of protein and lipid deposition in the body of growing pigs. Livest. Prod. Sci. 35:317-328.

de Greef, K. H., and M. W. A. Verstegen. 1995. Evaluation of a concept on energy partitioning in growing pigs. Pages 137-149 in Modelling growth in the pig. P.

J. Moughan, M. W. A. Verstegen, and M. I. Visser-Reyneveld ed. Wageningen Pers, Wageningen, The Netherlands.

de Greef, K. H., M. W. A. Verstegen, B. Kemp, and P. L. van der Togt. 1994. The effect of body weight and energy intake on the composition of deposited tissue in pigs. Anim. Prod. 58:263-270.

De la Llata, M., S. S. Dritz, M. D. Tokach, R. D. Goodband, J. L. Nelssen, and T. M. Loughin. 2001. Effects of dietary fat on growth performance and carcass characteristics of growing-finishing pigs reared in a commercial environment. J. Anim. Sci. 79:2643-2650.

de Lange, C. F. M, B. J. Marty, S. Birkett, P. Morel, and B. Szkotnicki. 2001a. Application of pig growth models in commercial pork production. Can. J. Anim. Sci. 81:1-8.

de Lange, C. F. M., S. H. Birkett, and P. C. H. Morel. 2001b. Protein, fat, and bone tissue growth in swine. Pages 65-84 in Swine nutrition. A. J. Lewis, and L. L. Southern, ed. CRC Press LLC, Boca Raton, Fl.

de Lange, C. F. M., and S. H. Birkett. 2004. Characterization of useful energy content in swine and poultry feed ingredients. Proceedings of CSAS Annual Meeting, Edmonton, AB, July 2004.

Dunshea, F. R., R. H. King, P. J. Eason, and R. G. Campbell. 1998. Interrelationships between dietary ractopamine, energy intake, sex in pigs. Aust. J. Agric. Res. 49: 565-574.

Edwards, A. C., and R. G. Campbell. 1993. Energy-protein interaction in pigs. Pages 30-46 in Recent Developments in Pig Nutrition 2. D. J. A. Cole, W. Haresign, and P. C. Garnsworthy, ed. Nottingham Univ. Press, England.

Eggum, B. O. 1970. Blood urea measurement as a technique for assessing protein quality. Br. J. Nutr. 24:983-988.

Emmans, G. C. 1994. Effective energy: a concept of energy utilization applied across species. Br. J. Nutr. 71:801-821.

Emmans, G. C. 1999. Energy flows. Pages 363-377 in A quantitative biology of the pig. I. Kyriazakis ed. CABI International, New York.

Endres, B., F. X. Aherne, L. Ozimek, and H. Spicer. 1988. The effects of fat supplementation on ileal versus fecal fat digestibilities, performance and body composition of weaned pigs. Can. J. Anim. Sci. 68:225-231.

Englyst, H. N. 1989. Classification and measurement of plant polysaccharides. Anim. Feed Sci. Technol. 3:27-42.

Englyst, H. N., and G. J. Hudson. 1987. Colorimetric method for routine measurement of dietary fiber as non-starch polysaccharides. A comparison with gas-liquid chromatography. Food Chem. 24:63-76.

Enser, M. 1991. Animal carcass fats and fish oil. Pages 329-394 in Analysis of oilseeds, fats and fatty acid foods. J. B. Rossel and J. L. R. Pritchard, ed. Elsevier, London, U.K.

Ewan, R. C. 1989. Predicting the energy utilization of diets and feed ingredients by pigs. Pages 215-218 in Energy metabolism of farm animals. Y. van der

Honing, and W. H. Close, ed. Proceedings of the 11th Symposium, Lunteren, The Netherlands.

Ewan, R. C. 2001. Energy utilization in swine nutrition. Pages 85-94 in Swine nutrition. A. J. Lewis, and L. L. Southern, ed. CRC Press LLC, Boca Raton, Fl.

Farrell, D. J. 1979. Energy systems for pig and poultry: A review. J. Aust. Inst. Agric. Sci. 34:21-34.

Fawcett, J. K. and J. E. Scott. 1960. A rapid precise method for the determination of urea. J. Clin. Pathol. 13:156-159.

Fuller, M. F., R. McWilliam, T. C. Wang, and L. R. Giles. 1989. The optimum dietary amino acid pattern for growing pigs. 2. Requirement for maintenance and for tissue protein accretion. Br. J. Nutr. 62:255-267.

Fuller, M. F., and T. C. Wang. 1987. Amino acid requirement for the growing pig. Page 97 in Manipulating Pig Production. Proc. of the Inaugural Conf. of the Australasian Pig Science Association (A.P.S.A), November 23 to 25, 1987, Albury. A.P.S.A., Werribee, Victoria, Australia.

Gädecken, D., H. J. Oslage, and H. Bohme. 1985. Energy requirement for maintenance and energy costs of protein and fat deposition in piglets. Arch. Tierernaehr. 35:481-494.

Galloway, S. T. and R. C. Ewan. 1989. Energy evaluation of tallow and oat groats for young swine. J. Anim Sci. 67:1744-1750.

Garthoff, L. H., G. R. Henderson, A. O. Sager, T. J. Sobotka, D. W. Gaines, M. W. O'Donnell, Jr., R. Chi, S. J. Chirtel, C. N. Barton, L. H. Brown, F. A.

Hines, T. Solomon, J. Turkleson, D. Berry, H. Dick, F. Wilson, and M. A. Khan. 2002. Pathological evaluation, clinical chemistry and plasma cholecystokinin in neonatal and young miniature swine fed soy trypsin inhibitor from 1 to 39 weeks of age. Food and Chem. Toxicol. 40:501-516.

Gatel, F., G. Buron, and J. Fekete. 1992. Total amino acid requirements of weaned piglets 8 to 25 kg live weight given diets based on wheat and soya-bean meal fortified with free amino acids. Anim. Prod. 54:281-287.

Gomez, R. S., A. J. Lewis, P. S. Miller, H. Y. Chen, and R. M. Diedrichsen. 2002. Body compositon and tissue accretion rates of barrows fed corn-soybean meal diets or low-protein, amino acid-supplemented diets at different feeding levels. J. Anim. Sci. 80:654-662.

Graham, H., K. Hesselman, and P. Aman. 1986. The influence of wheat bran and sugar-beet pulp on the digestibility of dietary components in a cereal-based pig diet. J. Nutr. 116:242-251.

Gregory, N. G., B. W. Moss, and R. H. Leeson. 1987. An assessment of carbon dioxide stunning in pigs. Vet. Rec. 121:517-518.

Gregory, P. C., M. McFadyen, and D. V. Rayner. 1989. Relation between gastric emptying and short-term regulation of food intake in the pig. Physiol. Behav. 45:677-683.

Hagemann. L. 2004. State Office for Consumer Protection and Agriculture of Branden burg, Germany. Trial Report: 13.62.02001. Cited in Deggusa Facts and Figures, Swine No. 46.

Halas, V. 2004. Dietary influences on nutrient partitioning and anatomical body composition of growing pigs: modeling and experimental approaches. Ph.D. Thesis. University of Kaposvár, Kaposvár, Hungary.

Harris, D. M., F. R. Dunshea, D. E. Bauman, R. D. Boyd, S. Y. Wang, P. A. Johnson, and S. D. Clarke. 1993. Effect of in vivo somatotropin treatment of growing pigs on adipose tissue lipogenesis. J. Anim. Sci. 71:3293-3300.

Hartel, H. 1977. Beziehungen zwischen der N-korrigierten umsetzbaren energie und den nahrstoffgehalten des futters beim huhn. Archiv. Geflügelkunde 41:152-181.

Hedges, J. 2003. Net energy diets pay dividends. [Online] Available: http://www.hubbardfeeds.com/swine/ss-mayo3netenergy.shtml [May 2003].

Henry, Y. 1985. Dietary factors involves in feed intake regulation in growing pigs: A review. Livest. Prod. Sci. 12:339-354.

Henry, Y. 1987. Self-selection by growing pigs of diets differing in lysine content. J. Anim. Sci. 65:1257-1265.

Hill, F. W., and D. L. Anderson. 1958. Comparison of metabolizable energy and productive energy determinations with growing chicks. J. Nutr. 64:587-604.

Hoenderken, R. 1983. Electrical and carbondioxide stunning of pigs for slaughter. Pages 59-63 in Stunning of animals for slaughter. G. Eikelenboom, ed. Martinus Nijhoff Publishers, Boston, MA.

Hoffman, L., M. Beyer, and W. Jentsch. 1993. Abhängigkeit von Bruttoverdaulicher und umsetzbarer Energie des Futters sowie des Energieansatzes vom Gehalt an verdaulichen Nährstoffen unter

Berucksichtigung von Stärke und Zuker. Ein Beitrag zur Weiterentwiicklung der energetischen Futterbewertung. Arch. Anim. Nutr. 44:123-137.

Hoffman, L., W. Jentsch, and M. Beyer. 1992. The energy metabolism of growing swine in a live weight range of 10-50 kg. 3. Energy maintenance requirement of growing swine. Arch Tierernahr 42:235-248.

INRA (Institut National de la Recherche Agronomique). 2002. L'alimentation des monogastriques. INRA, Paris, France.

Just, A. 1982. The net energy value of balanced diets for growing pigs. Livest. Prod. Sci. 8:541-555.

Just, A., H. Jørgensen, and J. A. Fernandez. 1983. Maintenance requirement and the net energy value of different diets for growth in pigs. Livest. Prod. Sci. 10:487-506.

Kerr, B. J., L. L. Southern, T. D. Bidner, K. G. Friesen, and R. A. Easter. 2003. Influence of dietary protein level, amino acid supplementation, and dietary energy levels on growing-finishing pig performance and carcass composition. J. Anim. Sci. 81:3075-3087.

Kerr, D. E., B. Laarveld, and J. G. Manns. 1990. Effects of passive immunization of growing guinea-pigs with an insulin-like growth factor-I monoclonal antibody. J. Endocrinol. 124:403-415.

Kielanowski, J. 1966. Conversion of energy and the chemical composition of gain in bacon pigs. Anim. Prod. 8:121-128.

Kielanowski, J. 1976. The chemical composition of the live-weight gain and the performance of growing pigs. Livest. Prod. Sci. 3:257-269.

Kim, I. H., J. D. Hancock, D. B. Jones, and P. G. Reddy. 1999. Extrusion processing of low-inhibitor soybeans improves growth performance of early-weaned pigs. Asian-Aus. J. Anim. Sci. 12:1251-1257.

Kimball, S. R. 2002. Regulation of global and specific mRNA translation by amino acids. J. Nutr. 132:883-886.

Kimball, S. R., and L. S. Jefferson. 2002. Control of protein synthesis by amino acid availability. Curr. Opin. Clin. Nutr. Metab. Care 5:63-67.

King, R. H., R. G. Campbell, R. J. Smits, W. C. Morley, K. Ronnfeldt, K. L. Butler and F. R. Dunshea. 2004. The influence of dietary energy intake on growth performance and tissue deposition in pigs between 80 and 120 kg liveweight. Aust. J. Agric. Res. 55:1271-1281.

Kleiber, M. 1932. Body size and metabolism. Hilgardia 6:315-353.

Kleiber, M. 1975. The fire of life. 2nd ed. R. E. Krieger, New York.

Knap, P. W. 2000. Variation in maintenance requirements of growing pigs in relation to body composition: A simulation study. Ph.D. Thesis, Wageningen Agric. Univ., Wageningen, The Netherlands.

Kolstad, K., and O. Vangen. 1996. Breed differences in maintenance requirement of growing pigs when accounting for changes in body composition. Livest. Prod. Sci. 47:23-32.

Kolstad, K., U. T. Brenøe, and O. Vangen. 2002. Genetic differences in energy partitioning in growing pigs. Acta Agric. Scand., Sect. A, Animal Sci. 52:213-220.

Konturek, S. J., J. W. Konturek, T. Pawlik, and T. Brzozowski. 2004. Brain-gut axis and its role in the control of food intake. J. Physiol. Pharmacol. 55:137-154.

Kotarbinska, M. 1971. The chemical composition of the body in growing pigs. Roczniki Nauk Rol B-93:129-135.

Kyriazakis, I., and G. C. Emmans. 1992a. The effects of varying protein and energy intakes on the growth and body composition of pigs. 1. The effects of energy intake at constant, high protein intake. Br. J. Nutr. 68:603-613.

Kyriazakis, I., and G. C. Emmans. 1992b. The effects of varying protein and energy intakes on the growth and body composition of pigs. 2. The effects of varying both energy and protein intake. Br. J. Nutr. 68:615-625.

Kyriazakis, I., and G. C. Emmans. 1995. The voluntary feed intake of pigs given feeds based on wheat bran, dried citrus pulp and grass meal in relation to measurement of feed bulk. Br. J. Nutr. 73:191-207.

Kyriazakis, I., and G. C. Emmans. 1999. Voluntary feed intake and diet selection. Pages 229-248 in A quantitative biology of the pig. I. Kyriazakis ed. CABI International, Wallingford. U.K.

Langer, S., and M. F. Fuller. 1996. The effect of excessive amounts of protein on lysine utilization in growing pigs. Br. J. Nutr. 76:743-754.

Lawrence, B. V., O. Adeola, and T. R. Cline. 1994. Nitrogen utilisation and lean growth performance of 20 to 50 kilogram pigs fed diets balanced for lysine:energy ratio. J. Anim. Sci. 72:2887-2895.

Le Bellego, L., J. van Milgen, and J. Noblet. 2002. Effects of high ambient temperature on protein and lipid deposition and energy utilization in growing pigs. Anim. Sci. 75:85-96.

Le Bellego, L., J. van Milgen, S. Dubois, and J. Noblet. 2001. Energy utilization of low-protein diets in growing pigs. J. Anim. Sci. 79:1259-1271.

Lee C. Y., S. C. Chung, and F. A. Simmen. 1993. Ontogeny of the porcine insulin-like growth factor system. Mol. Cell. Endocrinol. 93:71-80.

Lee C. Y., H. P. Lee, J. H. Jeong, K. H. Baik, S. K. Jin, J. H. Lee, and S. H. Sohn. 2002. Effects of restricted feeding, low-energy diet, and implantation of trenbolone acetate plus estradiol on growth, carcass traits, and circulating concentrations of insulin-like growth factor (IGF)-I and IGF-binding protein-3 in finishing barrows. J. Anim. Sci. 80:84-93.

Le Goff, G., and J. Noblet. 2001. Comparative total tract digestibility of dietary energy and nutrients in growing pigs and adult sows. J. Anim. Sci. 79:2418-2427.

Leibbrandt, V. D., R. C. Ewan, V. C. Speer, and D. R. Zimmerman. 1975. Effect of age and calorie:protein ratio on performance and body composition of baby pigs. J. Anim. Sci. 40:1070-1076

Levesque, C. L. 2002. The effects of dietary digestible energy content and site of weaning on weanling pig performance. M.Sc. Thesis. University of Saskatchewan.

Lewis, A. J. 2001. Amino acids in swine nutrition. Pages 131-150 in Swine nutrition. A. J. Lewis and L. L. Southern, ed. CRC Press LLC, Boca Raton, Fl.

Li, S., and W. C. Sauer. 1994. The effect of dietary fat content on amino acid digestibility in young pigs. J. Anim. Sci. 72:1737-1743.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76:1216-1231.

Livesey, G. 1984. The energy equivalent of ATP and the energy values of food proteins and fats. Br. J. Nutr. 51:15-28.

Llames, C. R., and J. Fontaine. 1994. Determination of amino acids in feeds: collaborative study. J. AOAC Int. 77:1362-1402.

Louveau, I., and F. Gondret. 2004. Regulation of development and metabolism of adipose tissue by growth hormone and the insulin-like growth factor system. Domest. Anim. Endocrinol. 27:241-255.

Louveau, I., and M. Bonneau. 2001. Biology and actions of somatotropin in the pig. Pages 113-131 in Biotechnology in Animal Husbandry. R. Renaville, and A. Burny, ed. Kluwer Academic Publishers, The Netherlands.

Lowrey, R. S., W. G. Pond, J. K. Loosli, and J. H. Maner. 1962. Effect of dietary fat level on apparent nutrient digestibility by growing swine. J. Anim. Sci. 21:746-750.

Lusk, G. 1926. A history of metabolism. Pages 3-78 in Endocrinology and metabolism, Vol. 3. L. F. Barker, ed.

Magri, K. A., M. Adamo, D. LeRoith, and T. D. Etherton. 1990. The inhibition of insulin action and glucose metabolism by porcine growth hormone in porcine adipocytes is not the result of any decrease in insulin binding or insulin receptor kinase activity. Biochem. J. 266:107-113.

Matzinger, D., L. Degen, J. Drewe, J. Meuli, R. Duebendorfer, N. Ruckstuhl, M. D'Amato, L. Rovati, and C. Beglinger. 2000. The role of long chain fatty acids in regulating food intake and cholecystokinin release in humans. Gut 46:688-693.

McCarthy, J. F., F. X. Aherne, and D. B. Okai. 1974. Use of HCl insoluble ash as an index material for determining apparent digestibility with pigs. Can. J. Anim. Sci. 54:107-109.

Milligan L. P., and M. Summers. 1986. The biological basis of maintenance and its relevance to assessing responses to nutrients. Proc. Nutr. Soc. 45:185-193.

Möhn, S., and C. F. M. de Lange. 1998. The effect of body weight on the upper limit to protein deposition in a defined population of growing gilts. J. Anim. Sci. 76:124-133.

Möhn, S., A. M. Gillis, P. J. Moughan, and C. F. M. de Lange. 2000. Influence of dietary lysine and energy intakes on body protein deposition and lysine utilization in the growing pig. J. Anim. Sci. 78:1510-1519.

Morgan, D. J., D. J. A. Cole, and D. Lewis. 1975. Energy values in pig nutrition. I. The relationship between digestible energy, metabolizable energy and total digestible nutrient values of a range of feedstuffs. J. Agric. Sci. 84:7-17.

Moughan, P. J. 1995. Modelling protein metabolism in the pig: critical evaluation of a simple reference model. Pages 103-112 in Modelling growth in the pig. P. J. Moughan, M. W. A. Verstegen, and M. I. Visser-Reyneveld ed. Wageningen Pers, Wageningen, The Netherlands.

Moughan, P. J., and W. C. Smith. 1984. Prediction of dietary protein quality based on a model of the digestion and metabolism of nitrogen in the growing pig. N. Z. J. Agric. Res. 27:501-507.

Moughan, P. J., W. C. Smith, and G. Pearson. 1987. Description and validation of a model simulating growth in the pig (20-90 kg live weight). N. Z. J. Agric. Res. 30:481-490.

Nam, D. S., and F. X. Aherne, 1994. The effects of lysine:energy ratio on the performance of weanling pigs. J. Anim. Sci. 72:1247-1256.

Nehring, K., and G. F. W. Haenlein. 1973. Feed evaluation and ration calculation based on net energy. J. Anim. Sci. 36:949-964.

Nieto, R., A. Miranda, M. A. Garcia, and J. F. Aguilera. 2002. The effect of dietary protein content and feeding level on the rate of protein deposition and energy utilization in growing Iberian pigs from 15 to 50 kg body weight. Br. J. Nutr. 88:39-49.

Noblet, J. 2000. Digestive and metabolic utilization of feed energy in swine: application to energy evaluation systems. J. Appl. Anim. Res. 17:113-132.

Noblet, J. 1997. Energy evaluation systems for pig diets [Online] Available:.http://www.sbz.org.br/anais1997/Simp/palest6.pdf.

Noblet, J., H. Fortune, X. S. Shi, and S. Dubois. 1994. Prediction of net energy value of feeds for growing pigs. J. Anim. Sci. 72:344-354.

Noblet, J., and J. M. Perez. 1993. Prediction of digestibility of nutrients and energy values of pig diets from chemical analysis. J. Anim. Sci. 71:3389-3398.

Noblet, J., C. Karege, and S. Dubois. 1991. Influence of growth potential on energy requirements for maintenance in growing pigs. Page 107 in Energy metabolism of farm animals. Proc. of the 12th symposium. C. Wenk, and M. Boessinger, ed. European Association for Animal Production Publication No. 58, Juris Druck+Verlag, Zürich.

Noblet, J., C. Karege, S. Dubois, and J. van Milgen. 1999. Metabolic utilization of energy and maintenance requirements in growing pigs: Effects of sex and genotype. J. Anim. Sci. 77:1208-1216.

Noblet, J., H. Fortune, and S. Dubois. 1993. Digestible, metabolizable and net energy values of 13 feedstuffs for growing pigs: effect of energy system. Anim. Feed Sci. Technol. 42:131-149.

Noblet, J., and J. van Milgen. 2004. Energy value of pig feeds: Effect of pig body weight and energy evaluation system. J. Anim. Sci. 82(E. Suppl.):E229-E238.

Noblet, J., and Y. Henry. 1993. Energy evaluation systems for pig diets: A review. Livest. Prod. Sci. 36:121-141.

NRC. 1987. Predicting feed intake of food-producing animals. Natl. Acad. Press, Washington, DC.

NRC. 1988. Nutrient requirements of swine. 9th ed. Natl. Acad. Press, Washington, DC.

NRC. 1994. Metabolic modifiers: Effects on the nutrient requirements of food-producing animals. Natl. Acad. Press, Washington, DC.

NRC. 1998. Nutrient requirements of swine. 10th ed. Natl. Acad. Press, Washington, DC.

Nyachoti, C. M., J. F. Patience, R. T. Zijlstra, D. Gillis, R. D. Boyd, and J. Usry. 2000. Response of grower-finisher pigs to declining energy intake at constant or proportional daily amino acid intake levels. J. Anim. Sci. 78 (Suppl.2):66 (Abstr.).

Nyachoti, C. M., R. T. Zijlstra, C. F. M. de Lange, and J. F. Patience. 2004. Voluntary feed intake in growing-finishing pigs: A review of the main determining factors and potential approaches for accurate predictions. Can. J. Anim. Sci. 84:549-566.

Omogbenigun, F. O., C. M. Nyachoti, and B. A. Slominski. 2004. Dietary supplementation with multienzymes preparations improves nutrient utilization and growth performance in weaned pigs. J. Anim. Sci. 82:1053-1061.

Oresanya, T. F., J. F. Patience, and A. D. Beaulieu. 2002. Response of weaned pigs to increasing lysine:digestible energy ratio. J. Anim. Sci. 80 (Suppl.2):61 (Abstr.).

Oresanya, T. F., A. D. Beaulieu, and J. F. Patience. 2004. Growth, body composition and nutrient deposition rates in weaned pigs fed diets with similar digestible but different estimated net energy concentration. J. Anim. Sci. 82 (Suppl.2):78 (Abstr.).

Parr, T. M., B. J. Kerr, and D. H. Baker. 2003. Isoleucine requirement of growing (25 to 45 kg) pigs. J. Anim. Sci. 81:745-752.

Patience, J. F., A. D. Beaulieu, R. T. Zijlstra, M. Nyachoti, D. A. Gillis, R. D. Boyd, and J. Usry. 2002. Performance and body compositional responses to

changes in dietary energy intake by offspring of line 65 sires. Monograph No. 02-09. Prairie Swine Centre Inc., Saskatoon.

Patience, J. F., P. Thacker, and C. F. M. de Lange. 1995. Swine Nutrition Guide. 2nd edition. Prairie Swine Centre, Inc., Univ. of Saskatchewan, Saskatoon.

Patience, J. F., R. E. Austic, and R. D. Boyd. 1987. Effect of dietary electrolyte balance on growth and acid-base status in swine. J. Anim. Sci. 64:1079-1085.

Pettigrew, J. E., and R. L. Moser. 1991. Fat in swine nutrition. Pages 133-145 in Swine nutrition. E. R. Miller, D. E. Ullrey, and A. J. Lewis, ed. Butterworth-Heinemann, Stoneham, MA.

Piao, X. S., J. H. Kim, J. Jin, J. D. Kim, J. H. Lee, I. S. Shin, and I. K. Han. 2000. Effects of L-carnitine on the nutritive value of extruded full-fat soybean in weaned pigs. Asian-Aus. J. Anim. Sci. 13:1263-1271.

Pomar, C., D. L. Harris, and F. Minvielle. 1991. Computer simulation model of swine production systems: I. Modeling the growth of young pigs. J. Anim. Sci. 69:1468-1488.

Pond, W. G., D. C. Church, and K. R. Pond. 1995. Energy metabolism. Pages 149-166 in Basic animal nutrition and feeding. Wiley, New York.

Quiniou, N., J. Noblet, J. van Milgen, and J. Y. Dourmad. 1995. Effect of energy intake on performance, nutrient and tissue gain and protein and energy utilization in growing boars. Anim. Sci. 61:133-143.

Quiniou, N., S. Dubois, and J. Noblet. 2000. Voluntary feed intake and feeding behaviour of group-housed growing pigs are affected by ambient temperature and body weight. Livest. Prod. Sci. 63:245-253.

Quiniou, N., J. Y. Dourmad, and J. Noblet. 1996a. Effect of energy intake on the performance of different types of pig from 45 to 100 kg body weight. 1. Protein and lipid deposition. Anim. Sci. 63:277-288.

Quiniou, N., J. Noblet, and J. Y. Dourmad. 1996b. Effect of energy intake on the performance of different types of pig from 45 to 100 kg body weight. 2. Tissue gain. Anim. Sci. 63:289-296.

Quiniou, N., J. Noblet, J. Y. Dourmad, and J. van Milgen. 1999. Influence of energy supply on growth characteristics in pigs and consequences for growth modelling. Livest. Prod. Sci. 60:317-328.

Rao, D. S., and K. J. McCracken. 1991. Effect of energy intake on protein and energy metabolism of boars of high genetic potential for lean growth. Anim. Prod. 52:499-507.

Rao, D. S., and K. J. McCracken. 1992. Energy:protein interaction in growing boars of high genetic potential for lean growth. 2. Effects on chemical composition of gain and whole-body protein turn-over. Anim. Prod. 54:83-93.

Reis de Souza, T. C., A. Aumaitre, J. Mourot, and J. Peiniau, 2000. Effect of graded level of tallow in the diet on performance, digestibility of fat, lipogenesis and body lipid deposition of the weaned piglet. Asian Austr. J. Anim. Sci. 13:497-505.

Renaudeau, D., N. Quiniou, and J. Noblet. 2001. Effects of exposure to high ambient temperature and dietary protein level on performance of multiparous lactating sows. J. Anim. Sci. 79:1240-1249.

Rijnen, M. M. J. A. 2003. Energetic utilization of dietary fiber in pigs. Ph.D Thesis. Wageningen University, Wageningen Institute of Animal Science. Wageningen, The Netherlands.

Rijnen, M. M. J. A., J. Doorenbos, J. Mallo, and L. A. den Hartog. 2004. The application of the net energy system for swine. Proceedings of the 25th Western Nutrition Conference. Saskatoon, SK.

Robles, A., and R. C. Ewan. 1982. Utilization of energy of rice and rice bran by young pigs. J. Anim. Sci. 55:572-577.

Roth, F. X., K. Eder, M. Rademacher, and M. Kirchgessner. 2000. Effect of apparent ileal digestible lysine to energy ratio on performance of growing pigs at different dietary metabolizable energy levels. J. Anim. Physiol. Anim. Nutr. 83:181-192.

Rudolph, B. C., L. S. Boggs, D. A. Knabe, T. D. Tanksley, Jr., and S. A. Anderson. 1983. Digestibility of nitrogen and amino acids in soybean products for pigs. J. Anim. Sci. 57:373-386.

SAS Institute Inc. 1996. SAS/STAT user's guide. Release 6.12. SAS Institute, Inc., Cary, NC.

Sauvant, D., J. M. Perez, and G. Tran. 2004. Tables of composition and nutritional value in feed materials. INRA Editions, Wageningen Academic Publishers, Wageningen, The Netherlands.

SCA. 1987. Feeding standards for Australian livestock. Pigs. Commonwealth Scientific and Industrial Research Organization, East Melbourne, Australia.

Schiemann, R. 1988. Stoff- und energieansatz beim ausgewachsenen, vorwiegend fettbildenen tier. Pages 131-160 in Tierproduktion tierernährung, G. Gebhardt, ed. VEB Deutscher Landwirtschaftsverlag, Berlin, Germany.

Schiemann, R., K. Nehring, L. Hoffmann, W. Jentsch, and A Chudy. 1972. Energetische Futterbevertung und Energienormen. VEB Deutscher Landwirtschaftsverlag, Berlin, Germany.

Schiemann, R., W. Jentsch, and L. Hoffmann. 1989. The energy maintenance requirement of growing pigs of different sexes given normal and high protein diets. 1. Experiments in castrates. Arch. Tierernahr 39:5-24.

Schinckel, A. P., and C. F. M. de Lange. 1996. Characterization of growth parameters needed as inputs for pig growth models. J. Anim. Sci. 74:2021-2036.

Schoenherr, W. D., T. S. Stahly, and G. L. Cromwell. 1986. Effects of environmental temperature and dietary fat additions on maintenance and partial efficiency of energy retention in growing swine. J. Anim. Sci. 63 (Suppl. 1):122 (Abstr.).

Schrama, J. W., M. W. Bosch, M. W. A. Verstegen, A. H. P. M. Vorselaars, J. Haaksma, and M. J. W. Heetkamp. 1998. The energetic value of nonstarch polysaccharides in relation to physical activity in group-housed, growing pigs. J. Anim. Sci. 76:3016-3023.

Shah, O. J., S. R. Kimball, and L. S. Jefferson. 2000. Acute attenuation of translation initiation and protein synthesis by glucocorticoids in skeletal muscle. Am. J. Physiol. Endocrinol. Metab. 278:E76-E82.

Shi, X. S., and J. Noblet. 1993. Digestible and metabolizable energy values of ten feed ingredients in growing pigs fed ad libitum and sows fed at maintenance level; comparative contribution of the hindgut. Anim. Feed Sci. Technol. 42:223-236.

Simmen, F. A., L. Badinga, M. L. Green, I. Kwak, S. Song, and R. C. Simmen. 1998. The porcine insulin-like growth factor system: at the interface of nutrition, growth and reproduction. J. Nutr. 128:315S-320S.

Simon, O. 1989. Metabolism of protein and amino acids. Pages 273-366 in Protein metabolism in farm animals. Evaluation, digestion, absorption, and metabolism. H. D. Bock, O. B. Eggum, A. G. Low, O. Simon and T. Zebrowska, ed. Oxford University Press, U.K.

Skiba, G., H. Fandrejewski, St. Raj, and D. Weremko. 2002. The influence of previous protein or energy restriction of young pigs on their daily gain composition. J. Anim. Feed. Sci. 11:299-308.

Smith, II, J. W., M. D. Tokach, J. L. Nelssen, and R. D. Goodband. 1999a. Effects of lysine:calorie ratio on growth performance of 10- to 25-kilogram pigs. J. Anim. Sci. 77:3000-3006.

Smith, II, J. W., M. D. Tokach, P. R. O'Quinn, J. L. Nelssen, and R. D. Goodband. 1999b. Effects of dietary energy density and lysine:calorie ratio on growth performance and carcass characteristics of growing-finishing pigs. J. Anim. Sci. 77:3007-3015.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics. 2nd ed. McGraw-Hill, New York.

Tess, M. W., G. E. Dickerson, J. A. Nienaber, and Ferrell, C. L. 1984. The effect of body composition on fasting heat production in pigs. J. Anim. Sci. 58:99-110.

The National Committee for Pig Production. 2002. Annual report 2002. [Online] Available: http://www.danskeslagterier.dk/smmedia/LU_AnnualReport_2002_pdf?mb_GUID=B6AF6 [October 2002].

Tokach, M. D., J. E. Pettigrew, L. J. Johnson, M. Øverland, J. W. Rust, and S. G. Cornelius. 1995. Effect of adding fat and (or) milk products to the weanling pig diets on performance in the nursery and subsequent grow-finish stages. J. Anim. Sci. 73:3358-3368.

Urynek, W., and L. Buraczewska. 2003. Effect of dietary energy concentration and apparent ileal digestible lysine:metabolizable energy ratio on nitrogen balance and growth performance of young pigs. J. Anim. Sci. 81:1227-1236.

Van Es, A. J. H. 1980a. Energy cost of protein deposition. Pages 215-224 in protein deposition in animals. P. J. Buttery, and D. B. Lindsay, ed. Butterworths, London.

Van Es, A. J. H. 1980b. Feed evaluation, a survey. Pages 85-94 in L. E. Mount (ed.), Proceedings of the eight symposium on energy metabolism held at Churchill College, Cambridge. Butterworths, London.

Van Es, A. J. H., and H. A. Boekholt. 1987. Energy metabolism of farm animals. Pages 3-19 in Energy metabolism in farm animals. M.W.A. Verstegen, and A.M. Henken, ed. Martinus Nijhoff Publishers, Dordrecht, Netherlands.

van Heugten, E., M. T. Coffey, and J. W. Spears. 1996. Effects of immune challenge, dietary energy density, and source of energy on performance and immunity in weanling pigs. J. Anim. Sci. 74:2431-2440.

Van Lunen, T. A., and D. J. A. Cole. 2001. Energy-amino acid interaction in modern pig genotypes. Pages 439-466 in Recent developments in pig nutrition 3. P. C. Garnsworthy, and J. Wiseman ed. Nottingham University Press, Nottingham, U.K.

Van Lunen, T. A., and D. J. A. Cole. 1998. The effect of dietary energy concentration and lysine/digestible energy ratio on growth performance and nitrogen deposition of young hybrid pigs. Anim. Sci. 67:117-129.

van Milgen, J., and J. Noblet. 1999. Energy partitioning in growing pigs: The use of a multivariate model as an alternative for the factorial analysis. J. Anim. Sci. 77:2154-2162.

van Milgen, J., and J. Noblet. 2003. Partitioning of energy intake to heat, protein, and fat in growing pigs. J. Anim. Sci. (E. Suppl. 2):E86-E93.

van Milgen, J., J. F. Bernier, Y. Lecozler, S. Dubois, and J. Noblet. 1998. Major determinants of fasting heat production and energetic cost of activity in growing pigs of different body weight and breed/castration combination. Br. J. Nutr. 79:509-517.

van Milgen, J., N. Quiniou, and J. Noblet. 2000. Modelling the relation between energy intake and protein and lipid deposition in growing pigs. Anim. Sci. 71:119-130.

Verstegen, M. W. A. 1971. Influence of environmental temperature on energy metabolism of growing pigs housed individually and in groups. Meded. Landbhhogerch, Wageningen, The Netherlands.

Verstegen, M. W. A. 2001. Developments towards net energy systems in feeds and animals. Proceedings of the 22nd Western Nutrition Conference. Saskatoon, SK.

Walstra, P. 1980. Growth and carcass composition from birth to maturity in relation to feeding level and sex in Dutch Landrace pigs. Ph.D. Thesis, Wageningen Agric. Univ., Wageningen, The Netherlands.

Wang, Z., and L. A. Goonewardene. 2004. The use of mixed models in the analysis of animal experiments with repeated measures data. Can. J. Anim. Sci. 84:1-11.

Webster, M. J., R. D. Goodband, M. D. Tokach, J. L. Nelssen, S. S. Dritz, J. C. Woodworth, M. De La Llata, and N. W. Said. 2003. Evaluating processing temperature and feeding value of extruded-expelled soybean meal on nursery and finishing pig growth performance. J. Anim. Sci. 81:2032-2040.

Weis, R. N., S. H. Birkett, P. C. H. Morel, and C. F. M. de Lange. 2004. Effect of energy intake and body weight on physical and chemical body composition in growing entire male pigs. J. Anim. Sci. 82:109-121.

Wenk, C., G. E. Carstens, and H. Jørgensen. 1998. Summary of the discussion. Pages 265-267 in Energy metabolism of farm animals. Proceedings of the 14th Symposium on Energy Metabolism, Newcastle, Co. Down, Northern

Ireland, 14-20 September 1997. K. J. McCracken, E. F. Unsworth, and A. R. G. Wylie, ed.

Wenk, C., P. C. Colombani, J. van Milgen, and A. Lemme. 2000. Glossary: Terminology in animal and human energy metabolism. Pages 409-421 in Energy metabolism in animals. Proceeding of the 15th symposium on energy metabolism in animals. A. Chwalibog, and K. Jakobsen ed. EAAP publication No. 103 Snekkersten, Denmark. Wageningen Pers, Wageningen.

White, C. R., and R. S. Seymour. 2003. Mammalian basal metabolic rate is proportional to body mass$^{2/3}$. Proc. Natl. Acad. Sci. USA 100:4046-4049.

Whittemore, C. T. 1983. Development of recommended energy and protein allowances for growing pigs. Agric. Syst. 11:159.

Whittemore, C. T. 1986. An approach to pig growth modeling. J. Anim. Sci. 63:615-621.

Whittemore, C. T. 1993. The science and practice of pig production. Longman Scientific and Technical, Harlow.

Whittemore, C. T. 1997. An analysis of methods for the utilization of net energy concepts to improve the accuracy of feed evaluation in diets for pigs. Anim. Feed Sci. Technol. 68:89-99.

Whittemore, C. T., G. C. Emmans, B. J. Tolkamp, and I. Kyriazakis. 2001. Tests of two theories of food intake using growing pigs 2. The effect of a period of reduced growth rate on the subsequent intake of foods of differing bulk content. Anim. Sci. 72: 361-373.

Whittemore, C. T. and R. H. Fawcett. 1976. Theoretical aspects of a flexible model to simulate protein and lipid growth in pigs. Anim. Prod. 22:87-96.

Wiesemuller, W., S. Poppe, and W. Hackl. 1988. The energy metabolism of swine at a feed level of live weight equilibrium. Arch. Tierernahr 38:603-617.

Williams, N. H., T. S. Stahly, and D. R. Zimmerman. 1997. Effect of level of chronic immune system activation on the rate, efficiency and composition of growth and lysine needs of pigs fed from 6 to 27 kg. J. Anim. Sci. 75:2463-2471.

Woodworth, J. C., M. D. Tokach, R. D. Goodband, J. L. Nelssen, P. R. O'Quinn, D. A. Knabe, and N. W. Said. 2001. Apparent ileal digestibility of amino acids and the digestible and metabolizable energy content of dry extruded-expelled soybean meal and its effects on growth performance of pigs. J. Anim. Sci. 79:1280-1287.

Wu, J. F., and R. C. Ewan. 1979. Utilization of energy of wheat and barley by young swine. J. Anim. Sci. 49:1470-1477.

Xing, J. J., E. van Heugten, D. F. Li, K. J. Touchette, J. A. Coalson, and J. Odle. 2004. Effects of emulsification, fat encapsulation, and pelleting on weanling pig performance and nutrient digestibility. J. Anim. Sci. 82:2601-2609.

Zar, J. H. 1984. Biostastistical analysis. Chp. 18. Comparing simple linear regression equations. Prentice-Hall, Englewood Cliffs, N.J.

APPENDIX A

Manufacturer's label for Co-op Ultrawean 21 (Phase I)

CO-OP® ULTRAWEAN 21 (Diet for Starting Piglets)
CLAIM
Medicated with 0.0022 % (22 mg/kg) lincomycin from lincomycin hydrochloride monohydrate and 0.0022 % (22 mg/kg) spectinomycin from spectinomycin sulfate tetrahydrate as an aid in prevention of Swine Dysentery (Vibrionic Dysentery, Bloody Scours) in growing swine only.

This feed contains added selenium at 0.300 mg/kg.
GUARANTEED ANALYSIS

Crude Protein	Min.	19.00 %
Crude Fat	Min.	6.00 %
Crude Fibre	Max.	1.40 %
Calcium	Act.	1.00 %
Phosphorous	Act.	0.88 %
*Sodium	Act.	0.60 %
Zinc	Act.	300 mg/kg
Copper	Act.	120 mg/kg
Vitamin A	Min.	12,000 IU/kg
Vitamin D_3	Min.	1,500 IU/kg
Vitamin E	Min.	50 IU/kg

*Equivalent to approximately 1.5 % salt.

INGREDIENTS
A list of ingredients used in this feed may be obtained from the manufacturer or the registrant.
FEEDING DIRECTIONS

1. Feed this medicated feed as sole ration to growing swine up to 57 lb bodyweight.
2. Feed CO-OP Ultrawean 21 as the first feed to piglets weaned at 21 days of age.
3. Do not offer more feed to the piglets than they will consume in each 24 hour period during the first three days past weaning. thereafter, feeders can be filled with UltraWean 21.
4. Provide piglets with an adequate, continuous source of good quality water after which switch feed to CO-OP GI Max 21.
5. Feed UltraWean 21 for the first seven days post weaning after which switch feed to CO-OP GI Max 21.

WARNING
Treated swine must not be slaughtered for use in food for at least 24 hours after the latest treatment with this medicated feed.

APPENDIX B

Manufacturer's label for CO-OP GI MAX 21 (Phase II)

CO-OP® GI MAX 21 (Diet for Starting Piglets)
CLAIM
Medicated with 0.0022 % (22 mg/kg) lincomycin from lincomycin hydrochloride monohydrate and 0.0022 % (22 mg/kg) spectinomycin from spectinomycin sulfate tetrahydrate as an aid in prevention of Swine Dysentery (Vibrionic Dysentery, Bloody Scours) in growing swine only.

This feed contains added selenium at 0.300 mg/kg.
GUARANTEED ANALYSIS

Crude Protein	Min.	19.00 %
Crude Fat	Min.	6.00 %
Crude Fibre	Max.	1.80 %
Calcium	Act.	1.00 %
Phosphorous	Act.	0.88 %
*Sodium	Act.	0.40 %
Zinc	Act.	300 mg/kg
Copper	Act.	120 mg/kg
Vitamin A	Min.	12,000 IU/kg
Vitamin D_3	Min.	1,500 IU/kg
Vitamin E	Min.	50 IU/kg

*Equivalent to approximately 1.00 % salt.

INGREDIENTS
A list of ingredients used in this feed may be obtained from the manufacturer or the registrant.
FEEDING DIRECTIONS

1. Feed this medicated feed as sole ration to growing swine up to 57 lb bodyweight.
2. Feed CO-OP GI MAX 21 as the second feed post weaning to piglets weaned at 21 days of age, GI MAX 21 should follow this feeding of CO-OP Ultrawean 21 having been fed in the first seven days post weaning.
3. Provide piglets with an adequate, continuous source of good quality water after which switch feed to CO-OP GI Max 21.
4. Feed as the sole ration beginning on day 8 post weaning to pigs weaned at 21 days until piglets attain 10 – 15 kg bodyweight.
5. When piglets achieve 10 –15 kg body weight switch feed to CO-OP PD MAX.

WARNING
Treated swine must not be slaughtered for use in food for at least 24 hours after the latest treatment with this medicated feed.

APPENDIX C

Table C1. Allocation of pen to treatments[a]

13	12
14	11
15	10
16	9
17	8
18	7
19	6
20	5
21	4
22	3
23	2
24	1

[a]External pens #1, 12, 13 and 24 were not used in the study. Pens were grouped into blocks of 5 pens as follows: block 1, pens 2 to 6; block 2, pens 7 to 11; block 3, pens 14 to 18; and block 4, pens 19 to 23. Within location, blocks 1 and 3 were randomly assigned to the 5 LDE treatments, while blocks 2 and 4 were randomly assigned to the 5 HDE treatments.

APPENDIX D

Table D1. Residual sum of square (RSS) and r-square statistic of quadratic and linear plateau models[a]

	RSS		R^2	
Criteria	Quadratic	Linear Plateau	Quadratic	Linear Plateau
ADG d 0 to 14	0.1329	0.3417	0.64	0.09
ADG d 0 to 28	0.0477	0.1456	0.68	0.08

[a]The R^2 was taken from the contemporary GLM models as the maximum likelihood techniques used by proc MIXED do not allow an R^2 statistics.

APPENDIX E

Factorial Estimate of Lysine Requirement

Growing pigs require amino acids to meet obligatory losses (maintenance) and for tissue protein accretion (Fuller and Wang, 1987). It is therefore possible to estimate the lysine requirement (g/d) with the factorial approach by combining the requirement for these two functions. In this regard, the lysine requirement is taken as the sum of the two elements, and the greater the rate of protein accretion, the greater the requirements for amino acids.

The method is based on the following equation:

$R = aM + bcG$

Where R = requirement for a particular amino acid e.g. lysine; M is the maintenance requirement; G is the protein gain; c is the proportion of the particular amino acid in the protein gain; a and b are coefficients describing the efficiency with which the amino acid is utilized for maintenance and protein deposition, respectively.

Provided that other nutrients are supplied in adequate amounts, the efficiency of utilization for maintenance can be taken as close to 1 (Fuller and Wang, 1987). The lysine requirement for maintenance equal to 36 mg per kg metabolic body weight per day (Fuller et al., 1989) is widely adopted.

The biggest factor in the estimated requirement with the factorial method is a precise estimate of the efficiency of utilization for body protein accretion. Since there is no theoretical basis from which this can be established (Fuller and Wang, 1987), it implies that the factorial method is largely dependent on the description of the relationships between amino acid supply and animal response generated from

empirical data similar to a dose response study. Reported efficiency for utilization varies widely (0.58 to 0.75 e.g. in Bikker et al., 1993; Langer and Fuller, 1996; Möhn et al., 2000). Equations applicable to factorial estimates of lysine requirement are reported in the NRC (1998). Several models were used to estimate the lysine requirement based on the present performance data (Table E1).

Table E1. Estimated digestible lysine requirement, intake and balance in weaned pigs fed diets at two levels of digestible energy concentration and five lysine:DE ratios over a 28 d period

	Lysine:DE ratio, g/Mcal					
	3.7	4.0	4.3	4.6	4.9	
Item, g/d			d 0 to 14			SEM
Total lysine intake[a]	6.71	7.59	8.17	8.86	8.33	0.33
TID intake[b]	6.27	6.99	7.48	8.01	7.82	0.22
ADG	342	375	396	419	386	37
Protein gain[c]	55.0	60.3	63.6	67.6	62.3	1.9
Close[d]						
TID for maintenance	0.203	0.208	0.211	0.215	0.210	0.004
TID for protein gain	6.06	6.60	6.93	7.34	6.81	0.26
Lysine requirement	6.26	6.81	7.14	7.55	7.02	0.27
Intake/requirement	1.01	1.03	1.05	1.06	1.13	0.01
Fuller and Wang (updated with Bikker et al., 1993)[e]						
TID for maintenance	0.200	0.204	0.206	0.209	0.205	0.003
TID for protein gain	4.90	5.38	5.67	6.03	5.56	0.23
Lysine requirement	5.10	5.58	5.88	6.24	5.77	0.23
Intake/requirement	1.26	1.26	1.27	1.29	1.38	0.02
NRC[f]						
TID for protein gain	6.60	7.23	7.63	8.11	7.48	0.30
Lysine requirement	6.80	7.44	7.84	8.32	7.69	0.31
Intake/requirement	0.94	0.95	0.96	0.97	1.04	0.02
			d 15 to 28			
Total lysine intake[a]	14.53	16.14	17.19	18.46	18.97	0.28
TID intake[b]	13.56	14.85	15.74	16.70	17.83	0.24
ADG	687	687	700	689	705	13
Protein gain[c]	110.6	108.4	112.5	111.0	114.5	2.2
Close[d]						
TID for maintenance	0.371	0.379	0.389	0.396	0.389	0.009
TID for protein gain	12.40	12.20	12.65	12.51	12.86	0.28
Lysine requirement	12.78	12.58	13.04	12.91	13.25	0.28
Intake/requirement	1.06	1.18	1.21	1.29	1.35	0.02
Fuller and Wang (updated with Bikker et al., 1993)[e]						
TID for maintenance	0.302	0.307	0.313	0.317	0.313	0.005
TID for protein gain	9.86	9.67	10.04	9.90	10.21	0.20
Lysine requirement	10.17	9.98	10.35	10.22	10.54	0.20
Intake/requirement	1.34	1.49	1.53	1.64	1.69	0.03
NRC[f]						
TID for protein gain	13.27	13.02	13.50	13.32	13.74	0.27
Lysine requirement	13.58	13.32	13.82	13.64	14.05	0.27
Intake/requirement	1.00	1.12	1.15	1.23	1.27	0.03

[a]Calculated from determined dietary lysine content (g/kg) and weekly ADFI.
[b]True ileal digestible lysine intake. Calculated from ADFI and estimated dietary TID lysine content (g/kg) based on lysine digestibility coefficient of individual ingredient (NRC, 1998).

[c]Estimated assuming that 16.1% of daily weight gain is protein based on data of body protein content analysis in experiment 2 (Chapter 4).
[d]Close (1994) based on the following assumptions and calculations: Lysine for maintenance = 0.091 × 0.5 × [(initial empty body protein wt + final empty body protein wt)/0.65].Where daily maintenance cost per kg of protein is 91 g, assuming that protein turnover rate is 4 g/kg and a lysine content of replacement protein of 22.7 g/kg. Initial and final empty body protein content was assumed as 150.8 and 169.9 g/kg, respectively, based on the measured protein content of weaned pigs of similar body weight and age (Chapter 4). The initial empty body weight was predicted as: 0.98liveweight – 0.32, R^2 = 0.98; and the final empty body weight was predicted as: 0.92liveweight + 0.22, R^2 = 0.95 (data from experiment 2; Chapter 4). Net efficiency of lysine utilization was assumed at 65% (Close, 1994).
Lysine for protein deposition = 70 × [(initial empty body protein wt + final empty body protein wt)/0.65] × 14. Where 70 is g lysine per kg of protein (ARC, 1981) and 14 is the test period in days.
Protein deposition, g/d = (final protein wt, g – initial protein wt, g)/14.
[e]Fuller and Wang (1987) based on the following assumptions and calculations: TID for maintenance estimated as 0.036g × kg $BW^{0.75}$ per day; lysine content of protein = 0.066g/g; efficiency with which ileal digestible lysine is retained = 0.74 (Bikker et al., 1993).
[f]NRC (1998) based on the following assumptions and calculations: TID for maintenance estimated as 0.036g × kg $BW^{0.75}$ per day; TID for protein gain estimated as 0.12 × whole body protein gain.