THE RESPONSE OF THE GROWING PIG TO CHANGES IN ENERGY INTAKE ACHIEVED THROUGH CHANGES IN DIETARY ENERGY CONCENTRATION VERSUS RESTRICTION OF FEED INTAKE

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Saskatoon, Saskatchewan

By

Jennifer P. Marriott

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ABSTRACT

This study was undertaken to compare the effects of changing energy intake, either by restricting feed intake or by altering dietary energy concentration, on the growth performance of pigs. The relative abilities of the DE, ME and NE systems to predict pig growth performance were also evaluated. A total of 72 barrows, having initial body-weights of 30 ± 2 kg, were randomly assigned to one of nine dietary treatments. These treatments were organized in a 3 x 3 factorial arrangement consisting of three dietary energy concentrations (2.18, 2.29 and 2.40 Mcal NE/kg) and three levels of feed allowance (80, 90 and 100% of ad libitum). Actual feed allowances of 79, 91 and 100% of ad libitum were achieved. No interactive effects of feeding level and dietary energy concentration were observed ($P > 0.10$). Increases in feed allowance from 79 to 91 to 100% of ad libitum resulted in increases in daily intakes of feed ($P < 0.0001$) and energy ($P < 0.0001$). Improvements in the rate ($P < 0.0001$) and efficiency ($P < 0.0001$) of body-weight gain were also noted. Additionally, feeding level affected the amount of energy available for body-weight gain on a daily ($P < 0.0001$) but not on a total ($P > 0.10$) basis. The efficiency with which dietary energy was used for weight gain was unaffected by feeding level ($P > 0.10$). Increases in dietary energy concentration were accompanied by decreases in daily feed intakes ($P = 0.0016$); however, dietary energy concentration did not affect daily energy intakes ($P > 0.10$). Neither average daily gains nor feed conversion efficiencies were affected by changes in dietary energy concentration ($P > 0.10$). Additionally, there were no differences among energy concentration treatments in terms of the amount of dietary energy available for body-weight gain ($P > 0.10$) or the efficiency with which it was used ($P > 0.10$). No differences were observed between the DE, ME and NE systems in terms of their abilities to predict the growth performance of pigs. The present study demonstrates that the energy intake of pigs can be

effectively manipulated via adjustments in feeding level and that changes in dietary energy density, over the range studied here, are unable to affect changes in energy intake. This finding indicates that extreme caution should be used when extrapolating data obtained from studies in which feed allowance was manipulated to scenarios (e.g. commercial practice) in which energy density is to be altered, and vice versa.

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ADFI	Average daily feed intake	SD	Standard deviation
ADG	Average daily gain	SEM	Standard error of the mean
Ad Lib	Ad libitum	Wt	Weight
ATP	Adenosine tri-phosphate		
Avg	Average		
BW	Body-weight		
CVB	Centraal Veevoederbureau		
Conc	Concentration		
CP	Crude protein		
CV	Coefficient of variation		
d	Day		
DE	Digestible energy		
FCE	Feed conversion efficiency		
GE	Gross energy		
G:F	Gain-to-feed ratio		
h	Hour		
Mcal	Megacalorie		
ME	Metabolizable energy		
Med	Medium		
NE	Net energy		
PVC	Polyvinyl chloride		

1. LITERATURE REVIEW

1.1 INTRODUCTION

1.1.1 Importance of understanding energy metabolism in the pig

In his 1991 review, Taverner commented that the pork industry generally measures the success of research through its ability to generate significant cost savings via the development of widely-applicable, easily-adopted technologies. By this measure, research into the energy metabolism of pigs is poised for great success. It has been postulated that an improved understanding of how pigs metabolize energy will allow increased precision in the definition of their energy requirements across the various stages of production (Black et al., 1986; Whitney, undated). The formulation of rations that more accurately meet these requirements will also be facilitated (Black et al., 1986; Whitney, undated). As energy is the mostly costly nutrient in pig feed, which is itself the single largest expense in pork production (Patience et al., 1995; Saskatchewan Pork Development Board, 2006), a result of these advancements would be significant monetary savings for pork producers (Whitney, undated). Additionally, as increased global demand for the feed grains traditionally utilized in swine rations drives a more extensive utilization of novel feed ingredients in swine rations, a better understanding of energy metabolism is anticipated to be advantageous to the pork industry as a whole. Such an understanding will hasten the process of determining the optimal way in which to incorporate novel ingredients into diet formulations for swine (Seerley and Ewan, 1983).

1.1.2   General definitions of energy & metabolism

The first law of thermodynamics, which Rubner (1894) is credited with having validated in biological systems (Benzinger and Kitzinger, 1949; Webb, 1991), holds that energy cannot be created or destroyed, but can be converted from one form to another (Purves et al., 2001; Mayes and Botham, 2003). Energy is generally defined as the ability to do work; where work is defined as the mathematical product of a force (in Newtons) applied to an object and the distance (in meters) through which that object is moved (Hallett et al., 2002). The resultant unit in which work is expressed, the Newton*meter, is more commonly referred to as the "joule" (Hallett et al., 2002). In a nutritional context, the unit in which energy is expressed is either the joule or the calorie (Seerley and Ewan, 1983; NRC, 1998). Rather than being related to work, as previously defined, a calorie is defined as the quantity of energy required to elevate the temperature of 1 g of water by 1°C (Seerley and Ewan, 1983; Ewan, 2001).

The ultimate source of the energy that drives biological systems is the sun (Whitney and Rolfes, 1993). Photosynthetic organisms, such as plants (Horton et al., 2002), have the ability to harness solar energy as chemical potential energy by utilizing it to drive the synthesis of organic compounds (Whitney and Rolfes, 1993; Horton et al., 2002). When an animal feeds on plants or other photosynthetic organisms these organic compounds are broken down, making the chemical potential energy stored within them available for use by the animal (Whitney and Rolfes, 1993; Horton et al., 2002).

The term "metabolism" encompasses the processes just described, i.e. the processes involved in liberating, utilizing and/or storing energy from organic compounds (Whitney and Rolfes, 1993; Mayes and Bender, 2003). The various processes encompassed by the term "metabolism" can be further classified as being catabolic or anabolic (Horton et al., 2002; Mayes

and Botham, 2003). The former involves the breaking down of relatively large molecules into smaller ones and is accompanied by a release of energy (Horton et al., 2002; Mayes and Bender, 2003), while the latter refers to the synthesis of relatively large molecules from smaller constituents via reactions that consume energy (Mayes and Botham, 2003).

1.1.3   The energy-yielding nutrients

Pigs derive the energy that they require from the lipid, carbohydrate (Berdainer, 1995; NRC, 1998) and protein in their diets (Berdainer, 1995; Patience et al., 1995). Lipid is the most energy dense of the macronutrients with energy density estimates ranging from 8.0 (NRC, 1998) to 8.9 Mcal/kg (van Milgren and Noblet, 2003). Generally, the purpose of the addition of lipid to a swine ration is to boost its energy concentration (Bayley and Lewis, 1963; Cole et al., 1971).

The carbohydrate fraction of a swine ration consists of the readily digestible starches and sugars (Noblet and Henry, 1993; NRC 1998) that contribute the majority of the energy found in typical North American swine rations (NRC, 1998). However, the carbohydrate fraction also consists of structural carbohydrates or fibre, which is generally poorly utilized as an energy source by growing pigs (Ewan, 2001; Grieshop et al., 2001). In addition to its own poor utilization, dietary fibre has been reported to have a negative impact on the growing pig's use of the other energy-yielding macronutrients (Noblet and van Milgren, 2004) and is considered overall to act as an energy diluent in rations for growing pigs (NRC, 1998; Noblet, 2007).

The primary role of dietary protein is not to serve as an energy source, but rather it is to provide amino acids for the synthesis of body proteins and other amino acid-derived compounds (Patience et al., 1995). It is only amino acids that are provided in excess of this requirement that will be catabolized to provide energy (Patience et al., 1995; Ewan, 2001). However, a significant

concern associated with the use of dietary protein as an energy source is that the catabolism of amino acids generates ammonia, which must be detoxified by its incorporation into urea (Rodwell, 2003). The process of urea synthesis is an energetically expensive one, and thus is responsible for the relative inefficiency of using dietary protein as an energy source (Ewan, 2001; van Milgren, 2002).

1.1.4   Derivation of energy at a cellular level

The catabolic pathways for the release of energy from carbohydrates, lipids and proteins converge at the formation of acetyl-CoA (Mayes and Bender, 2003), which enters the TCA (also called the Citric Acid or Kreb's) cycle (Horton et al., 2002; Mayes and Bender, 2003), as depicted in Figure 1-1.
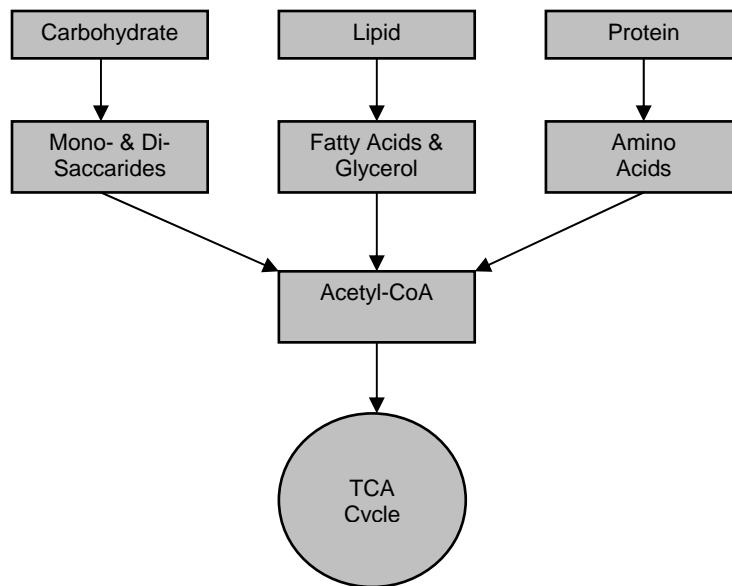
Figure 1-1:   Schematic overview of the metabolic pathways for releasing energy from the dietary macronutrients (adapted from Mayes and Bender, 2003)

Ultimately, the energy liberated from the catabolism of the energy-yielding macronutrients is captured in the ATP (Berdainer, 1995) which is generated via the TCA cycle and the reactions of the oxidative phosphorylation pathway (Horton et al., 2002; Mayes and Bender, 2003). The ATP thus formed is used to provide the energy required to drive a myriad of biochemical reactions (Berdainer, 1995; Horton et al., 2002).

1.2 ENERGY SYSTEMS

According to the definition of Noblet and Henry (1991, 1993), an energy system is the result of a combination of a single level of energy utilization (Figure 1-2) with a single method for the prediction of the pig's utilization of energy within a given energy level.
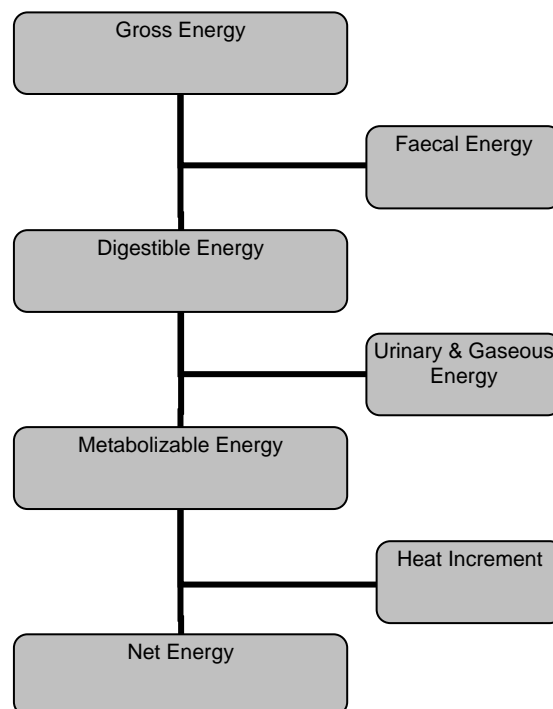
Figure 1-2: Levels of energy utilization (adapted from Ewan, 2001)

A major aim of energy systems in general is to provide a platform from which to formulate diets that allow pork producers to better meet their production objectives (de Goey and Ewan, 1975; Noblet, 2000) and vice versa; to provide a means of predicting growth performance at a given intake of a feed or feedstuff of interest (Just et al., 1983; Baldwin and Sainz, 1995). Other uses of energy systems have been identified as: providing a means of ascribing a fixed energy value to a given feedstuff and providing a basis for comparing one feedstuff to another as a means of determining the relative cost or value of feedstuffs (Oresanya, 2005).

1.2.1   Gross energy

Gross energy (GE) is a measurement of the energy released upon complete oxidation of a feed or feedstuff (Forbes, 1924; Ewan, 2001) to carbon dioxide and water (Seerley and Ewan, 1983). As such, it provides a measure of the total amount of energy contained within the feed or feedstuff (NRC, 1998; Ewan, 2001). Gross energy is commonly determined by measuring the heat energy released following the combustion of the feed or feedstuff of interest in a bomb calorimeter (Leveille and Cloutier, 1987). Alternatively, equations have been derived that permit the estimation of the GE content of a feedstuff from its chemical composition (NRC, 1998).

1.2.2   Digestible Energy

Digestible energy (DE) is defined as gross energy minus the energy lost in the faeces (NRC, 1998; Ewan, 2001). DE is, therefore, a measure of the amount of ingested gross energy which is absorbed from the lumen of the intestinal tract (Just, 1982). However, as several authors have pointed out, this measure may be more appropriately termed the "apparent digestible energy" owing to the presence of energy-yielding compounds of endogenous and microbial

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origin in the faecal material (Just, 1982; Adeola, 2001). The lack a suitable means of accounting

for these compounds means that they will, somewhat erroneously, be considered to be of dietary

origin for the purpose of determining DE (Noblet and Henry, 1991; Adeola, 2001).

DE can be measured by determination of the gross energy content of the faeces and

subtraction of this value from the gross energy intake (Noblet and Henry, 1991). As an

alternative to direct determination, there exist in the literature equations allowing the prediction

of the DE content of a given feed from its chemical composition (Just et al., 1983; Black et al.,

1986). When applied to whole feeds, determination of the DE content via the use of these

equations assumes that the DE values of the individual ingredients are additive and that no inter-

ingredient interactions occur (Noblet and Henry, 1993). It should, however, be borne in mind

that there is a certain amount of plasticity in the DE content of any given feed or feedstuff, as DE

content is subject to the effects of dietary, animal and environmental factors affecting

digestibility in general (Noblet, 2000; Noblet and van Milgren, 2004).

1.2.3   Metabolizable Energy

As described in the preceding section, DE differs from GE in that it accounts for faecal

energy losses. However, there are additional losses of energy that arise from the ingestion and

metabolism of a feed or feedstuff; that is, not all of the energy that is absorbed from the lumen of

the gastro-intestinal tract is available to the pig. A portion of this energy is lost through the

evolution of combustible gases, particularly methane (Just, 1982) and as energy-containing

compounds, most notably urea, excreted in urine (Seerley and Ewan, 1983). Measures of

metabolizable energy (ME) take both of these losses into account; therefore:

$$ME = DE - (\text{Urinary Energy} + \text{Gaseous Energy})$$

(NRC, 1998; Noblet, 2007)

Similar to DE, ME can be determined directly via metabolism trials (Adeola, 2001). Metabolism trails for the determination of ME are somewhat more complex than those for the determination of DE owing to the need for the quantitative collection of urine as well as faeces (Ewan, 1991). Additionally, energy lost via gas production is exceedingly difficult to quantify (NRC, 1998). The quantity of energy lost by the pig due to gas production has been found to vary depending on the animal's age/size and the composition, particularly in terms of fibre content, of the diet (Noblet, 2000; Noblet and van Milgren, 2004). In growing pigs, gaseous losses of energy have been ascribed a value of 0.4% of DE (Noblet and Henry, 1991; Noblet and van Milgren, 2004); however, these losses are more generally considered to be negligible in the overall scheme of energy utilization by the pig (Just, 1982; Seerley and Ewan, 1983).

The quantity of energy lost by the pig via the urinary excretion of combustible compounds is more variable than the gaseous losses of energy (Noblet and Henry, 1991; Noblet and van Milgren, 2004). The magnitude of these losses is primarily dependent on the magnitude of urea excretion by the pig (Seerley and Ewan, 1983; Noblet, 2000), which is itself related to dietary crude protein (CP) content (Noblet and Henry, 1991; Noblet, 2000). A ME:DE ratio of 0.96 has been proposed (Noblet and van Milgren, 2004), with the proviso that it be applied only to whole feeds whose CP content falls within the "typical" range (Noblet and Henry, 1993). In their 2004 publication, Noblet and van Milgren identify this range as being between 10 and 25% CP. This ratio of ME:DE allows the former to be determined from the latter, when it is known (De Goey and Ewan, 1975[a]). The poor applicability of this ratio to the ME and DE contents of

individual feedstuffs is emphasized in the related literature (Noblet, 2000; Noblet and van Milgren, 2004).

In addition to the approaches to calculating ME described above, there are a number of prediction equations that permit the estimation of the ME value of a feed/feedstuff based on its chemical composition (Just et al., 1983; Noblet and Henry, 1991).

1.2.4   Net Energy

Forbes (1924) pointed out that the net energy (NE) system most accurately quantifies the energy that is truly available to the pig from a given feedstuff. In addition to the energetic losses accounted for by the DE and ME systems, the very actions and chemical reactions of ingestion, digestion and nutrient metabolism result in losses of energy as heat (Kerr et al., 2003). Collectively, these losses are termed the "heat increment" (also known as the "specific dynamic action" or as "diet-induced thermogenesis" (Leveille and Cloutier, 1987)) and it is this heat increment that forms the difference between the ME and the NE value of a feed or feedstuff (Ewan, 2001; Noblet, 2007).

It is because the NE system accounts for energetic losses in the form of the heat increment in addition to energetic losses via excreta that its proponents claim it to be the truest estimation of the quantity of energy that the pig can derive from a given feed or feedstuff (Forbes, 1924; Noblet et al., 1994). Additionally, because measures of NE account for energy losses due to the ingestion, digestion and utilization of a given feedstuff, rankings of feedstuffs on an NE basis are deemed to be more accurate than rankings based on DE or ME (De Goey and Ewan, 1975[a]; Noblet and van Milgren, 2004). It is held that by failing to account for the heat increment the latter two energy systems provide an over-estimation of the energy content of

proteinaceous feedstuffs (De Goey and Ewan, 1975; Just, 1982), while under-estimating the energy content of feedstuffs high in lipid or starch (Noblet and van Milgren, 2004; Rijnen et al., 2004).

It should be noted that while NE systems may provide more accurate estimations of the energy available to the pig from a given feed or feedstuff than either the DE or ME systems, they are not without their limitations. More specifically, it has been deduced that the NE content of a given feed or feedstuff is affected by the productive outcome for which the energy is used (Noblet et al., 1994; Noblet and van Milgren, 2004). This is because the proportion of GE lost to the pig varies depending on the purpose for which the feed energy is utilized (Noblet and Henry, 1993). It has further been noted that the NE value of a given feedstuff will be somewhat dependant on the pig's gender (Just et al., 1983) and stage of development (Noblet and Henry, 1993). Finally, as previously noted, an energy system encompasses the combination of a single level of energy utilization and a single prediction method (Noblet and Henry, 1991). A number of methods exist that permit the estimation of NE (Rijnen et al., 2004), and accordingly the related literature is rife with warnings against assuming the interchangeability of NE values and requirements that were not estimated using the same technique (Noblet et al. 1994; Rijnen et al., 2004).

1.2.4.1 Use of calorimetry to determine net energy

Calorimetry provides a measurement of heat production (van Milgren et al., 1998; Adeola, 2001). As its name suggests, direct calorimetry measures heat production directly (Benzinger and Kitzinger, 1949; Adeola, 2001). In principle, this technique is analogous to the bomb calorimetry technique used to determine gross energy. The technique requires that the pig be housed in a specially-designed chamber and the heat lost by the pig is measured as the quantity of heat transferred from the pig to the insulating layer of the chamber itself (Benzinger and Kitzinger, 1949; Adeola, 2001).

The discovery and subsequent description of the relationship between heat production and oxidation rate gave rise to the technique of indirect calorimetry (Webb, 1991). In contrast to the direct method, indirect calorimetry involves the calculation of heat production from measurements of the rate of change in the concentrations of the substrates and products of oxidation (Webb, 1991; van Milgren and Noblet, 2003). These gas exchange values are then used as inputs into Brouwer's (1965) equation:

$$\text{Heat Production, kcal} = 3.866 * O_2 \text{ (in Litres)} + 1.2 * CO_2 \text{ (in Litres)} - 0.518 * CH_4 \text{ (in Litres)} - 1.431 * N_{urinary} \text{ (in grams)}$$

(Brouwer, 1965 as cited by Adeola, 2001).

In addition to the relative simplicity of measuring gas exchange versus measuring heat production (Benzinger and Kitzinger, 1949; Adeola, 2001), indirect calorimetry offers the advantage of lending itself to the use of portable instrumentation. Therefore, this technique allows experimental subjects greater freedom of movement that the direct method (Webb, 1991). It also permits the determination of the energy loss associated with specific activities (Webb, 1991; van Milgren et al., 1998).

1.2.4.2 Determination of net energy from retained energy

In growing pigs, net energy can be calculated as the sum of retained energy (RE) and

fasting heat production (FHP) (Noblet and Henry, 1993; Noblet et al. 1994). The growing pig

retains energy in the form of body stores of protein and lipid (Seerley and Ewan, 1983; Ewan,

1991). This energy can be quantified by use of the comparative slaughter technique (Mohn and

de Lange, 1998; Oresanya et al., 2008). The comparative slaughter technique involves the

determination of the protein (determined as N*6.25 (AOAC, 2005)), lipid and ash contents of the

carcass (Ross, 2009) following euthanasia of the pig and the subsequent removal of the contents

of the gastro-intestinal tract (De Goey and Ewan, 1975[a]; Mohn and de Lange, 1998) and of the

gall and urinary bladders (Ross, 2009). Once the quantity of retained energy is known, NE can

be calculated as the sum of retained and maintenance energies (Just, 1982).

1.2.4.3 Estimation of net energy from prediction equations

In this approach to estimating NE, the values corresponding to the chemical composition

of a given feed or feedstuff are used as inputs into one of the number of equations available for

the prediction of NE (Table 1-1; Noblet et al., 1994; Noblet and van Milgren, 2004). Noblet and

van Milgren (2004) place emphasis on the need to consider each prediction equation as a

separate NE system, citing their discovery of differences as great as 17% among net energy

values obtained using different predictive equations (Noblet and van Milgren, 2004).

The equations presented in Table 1-1 were derived from studies in which growing pigs

were fed experimental diets encompassing a range of ingredients (Just, 1982; Noblet et al.,

1994). The net energy values of these ingredients were determined via the use of the comparative

slaughter technique (Just, 1982) or via indirect calorimetry (Noblet et al., 1994) and regressed

back to their chemical composition (Noblet, 1994). The development of prediction equations such as these represents an important step toward the broader adoption of a net energy system for swine by providing a measure of net energy while avoiding the laborious processes involved in direct determination (Noblet et. al, 1994).

Table 1-1:   Sampling of equations for the prediction of the net energy value of feedstuffs and complete feeds, in growing pigs (adapted from Noblet and van Milgren, 2004)

Prediction Equation [1,2]	Reference
NE = 0.01133*DCP + 0.0350*DEE + 0.0144*Starch + 0.0000*DCF + 0.0121*DRes	Noblet et al. (1994)
NE = 0.0121*DCP + 0.0350*DEE + 0.0143*Starch + 0.0119*Sugar + 0.0086*DRes	Noblet et al. (2002)[3]
NE = 0.703*DE − 0.0041*CP + 0.0066*EE − 0.0041*CF + 0.0020*Starch	Noblet et al. (1994)
NE = 0.730*ME − 0.0028*CP + 0.0055*EE-0.0041*CF + 0.0015*Starch	Noblet et al. (1994)
NE = -1.88 + 0.75*ME	Just (1982)

[1] NE is calculated in MJ/kg dry matter, unless otherwise stated
[2] "D" denotes "digestible"; "Res" denotes "residue" which is defined as the digestible organic matter that is not accounted for by the other inputs into the equation (Noblet et al., 1994).
[3] As cited by Noblet and van Milgren (2004)

1.3   THE PIG'S REQUIREMENT FOR ENERGY

1.3.1   Energy partitioning

The pig prioritizes its energy demands such that absorbed energy is first used to meet its maintenance energy requirements. Only once these requirements have been met will dietary energy be used by the pig for productive purposes (Close et al., 1973; Weis et al., 2004). The term "energy partitioning" refers to the dividing of absorbed energy between the demands of maintenance and production (Whittemore et al., 2001[a]; Sandberg et al., 2005). It is generally held that there are both animal-related and feed-related factors that influence the process of energy

partitioning (Sandberg et al., 2005). However, in many cases it has yet to be firmly established on which side of a causal relationship a given variable belongs (van Milgren and Noblet, 2003). Although a set of rules to describe energy partitioning in the pig has yet to be realized (Sandberg et al., 2005), the scientific community's understanding of the nature of the relevant variables and their effects on energy partitioning by the pig continues to expand and evolve (Black et al., 1986; Sandberg et al., 2005).

1.3.1.1 Energy requirements for maintenance

Some authors have expressed the view that, while conceptually useful in understanding and describing the theory and the process of energy partitioning, "maintenance" as a state of being is a physiological impossibility (Whittemore et al., 2001). The NRC (1998) describes maintenance energy requirements as encompassing: "the [energy] needs of all body functions and moderate activity."; a description that is supported by de Lange and colleagues (2001). In a similar vein, Whittemore and colleagues (2001) commented that maintenance energy is "that [energy] which is not accountable elsewhere". The energy requirement for maintenance has also been defined as the energy intake required to affect an energy retention of zero (Pullar and Webster, 1977; van Milgren and Noblet, 2003). However, this quantity has proven to be something of an enigma, since even when overall energy retention is zero, the growing pig will continue to deposit protein, utilizing body reserves of lipid to do so (Ewan, 1991; van Milgren and Noblet, 2003).

The pervasive view in the related literature is that maintenance energy requirements are a function of body-weight, raised to some exponent (Pullar and Webster, 1977; Whittemore, 2006). However, some have argued that maintenance energy requirements are affected to a

greater extent by body composition than by body-weight itself (Black et al., 1986; de Lange et al., 2001). It has been postulated that this is primarily to do with the different metabolic activities of adipose versus lean tissue (de Lange et al., 2001; Whittemore et al., 2001).

1.3.1.2 Energy requirements for productive purposes

Productive demands for energy can include the energy requirements of growth, gestation or lactation (NRC, 1998; Ewan, 2001). However, the present discussion will be limited to the energy requirement of the pig for growth, which is itself comprised of the energy requirements for both protein gain and lipid gain (Close et al., 1973).

Just as there is a hierarchy among maintenance and productive energy requirements (Weis et al., 2004; Sandberg et al., 2005), there is also a hierarchy within the pig's use of energy for growth. This hierarchy is such that energy requirements for protein deposition will be given priority over energy requirements for lipid deposition (Seerley and Ewan, 1983). Protein deposition rates in the pig are generally considered to fit a linear-plateau model (Mohn and de Lange, 1998; van Milgren and Noblet, 2003); below the pig's maximum, an increase in energy intake is associated with an increased rate of protein deposition (Just, 1984; Whittemore, 1986). Only when the pig's maximal capacity for protein gain has been reached will ingested energy be utilized to deposit lipid (Quiniou et al., 1999; van Milgren and Noblet, 2003).

Some authors amend the hierarchy between energy use for protein and lipid deposition with the proviso that even during periods of sub-maximal protein deposition, a minimum quantity of lipid must be deposited (Whittemore, 1986; Mohn and de Lange, 1998). The reasons for this are thought relate to the need for a minimum amount of body lipid for the maintenance of cellular membrane integrity (Seerley and Ewan, 1983; Berdainer, 1995). Furthermore, it has been

reported that the relative rates of deposition of lean tissue and fat depend on, among other variables, the stage of maturity (van Milgren and Noblet, 2003) or body-weight (Pullar and Webster, 1977) of the pig.

1.4 RESEARCH MODELS FOR EVALUATING THE EFFECT OF ENERGY INTAKE ON PIG PERFORMANCE

As stated at the outset, dietary energy is the most significant cost in pork production (Patience et al., 1995; Saskatchewan Pork Development Board, 2006). Therefore, the potential exists to deliver millions of dollars in savings to the pork industry through improved feed formulation technology, which can be achieved via an enhanced understanding between energy intake and pig growth performance (Campbell et al., 1985).

Researchers have at their disposal two different means of manipulating the energy intake of pigs: 1) by restricting their feed intake and 2) by altering the energy density of the diet. A few researchers have recognized that it may be erroneous to assume that the effects of these two techniques are analogous and free from any interactions (Oresanya et al., 2008). Therefore, a very few studies have examined the combined effects of altering feed intake and dietary energy density on pig growth performance (Oresanya et al., 2008).

1.4.1 Manipulation of energy intake by feed restriction

Studies of this nature typically involve feeding a single ration at defined proportions of the ad libitum intake of a uniform group of conspecifics. It is therefore anticipated that the ADFIs of pigs on restricted feeding regimens will, as an inherent feature of the experimental design, be significantly different from ad libitum intake. The reports of Leymaster and

Mersmann (1991) and of Renaudeau et al. (2006) are in accordance with these expectations. A change in daily energy intake concomitant with changes in feeding regimen (Mohn and de Lange, 1998; King et al., 2004) or ADFI (Renaudeau et al., 2006) is reported. Therefore, in studies of this nature, the terms "feed intake" and "energy intake" become synonymous (King et al., 2004).

Possibly one of the most telling criticisms of this experimental approach to determining the effect of changes in energy intake on growth performance concerns the questionable commercial applicability of its outcomes (Stein and Easter, 1996). This is an issue because in commercial practice the pig is provided with ad libitum access to feed, and producers may lack the means to limit the feed intakes of growing-finishing swine (Oresanya et al., 2008). Nevertheless, experiments that have used feed restriction to alter pigs' energy intake have made huge contributions to the body of knowledge concerning energy metabolism in the pig (Oresanya, 2005).

1.4.1.1 Effects of feed restriction on body-weight gain & growth performance

The effect of altering feed allowance on the growth performance of pigs was put very succinctly by De Goey and Ewan (1975[a]), who remarked that: "Pigs that consumed more feed gained more rapidly"; a finding that has been borne out time and again in the related scientific literature (Fuller and Livingstone, 1978; Campbell et al., 1985; Quiniou and Noblet, 1997; King et al., 2004; Weis et al., 2004).

In looking at the effect of changes in feed allowance on the efficiency of body-weight gain in pigs, Leymaster and Mersmann (1991) observed an inverse relationship between feed intake and feed conversion efficiency (FCE). Conversely, Bikker et al. (1995) and King et al.

(2004) found that the relationship between energy intake and FCE was positive. The findings of Fuller and Livingston (1978) and of Campbell et al. (1985) were that the relationship between energy intake and FCE takes an inverse parabolic form, with a vertex at 7.9 Mcal DE/day (Campbell et al., 1985).

1.4.1.2 The confounding effect of reduced amino acid intake

The issue of the effects of feed-intake mediated reductions in energy intake potentially being confounded by concomitant feed-intake mediated reductions in amino acid intake occasionally arises in the literature (Nyachoti et al., 2000; Oresanya et al., 2006). Energy is thought to limit growth when amino acid nutriture is (at least) adequate (Seerley and Ewan, 1983; Kyriazakis and Emmans, 1992). If energy intake is to be reduced by reducing the pig's feed intake then the pig's protein intake will be simultaneously reduced (Ewan, 2001; Oresanya et al., 2006). Therefore, questions may arise as to whether any resultant changes in growth performance are attributable to changes in energy intake, to changes in protein intake, or to some combination thereof (Oresanya et al., 2006). However, following investigations aimed at clarifying this issue, it was concluded that amino acid nutriture does not confound the effects of feed intake on the growth performance of weanling barrows, provided that feed allowance is not less than 70% of ad libitum (Oresanya et al. 2006). Similarly, Nyachoti et al. (2000) found that in growing barrows, reductions in amino acid intake resulting from restriction of feed intake to as little as 63% of ad libitum do not confound the effects of the simultaneous reduction in energy intake on growth performance.

1.4.2 Manipulation of energy intake by altering dietary energy density

As a generalization, the objective of studies of this nature is to use ingredient manipulations to generate diets having different energy densities. Typically, these ingredient manipulations take the form of either altering the relative proportions of the main dietary ingredients (Beaulieu et al., 2006; Beaulieu et al., 2009) or the incremental addition of lipid to a basal formulation (Bayley and Lewis, 1963; Campbell and Taverner, 1986; Wu et al., 2007). Less commonly, a nutritionally inert energy diluent is used to affect decremental changes in dietary energy concentration (Baker et al., 1968). Once prepared, the experimental diets are then provided, generally on an ad libitum basis, to groups of pigs and the effects of energy density on their growth performance is determined.

1.4.2.1 Effect of energy density on daily intakes of feed and energy

The results of an experiment conducted in 1923 by Smith and Carey demonstrated that rats fed diets with energy concentrations ranging from 4.2 to 7.4 Mcal/kg will adjust their feed intakes such that their daily energy intakes are essentially constant. The conclusions of a number of authors agree with these findings and hold that pigs, like the rats used in the study conducted by Smith and Carey (1923), eat to achieve a target, constant energy intake. Therefore they will adjust their feed intakes up or down in response to changes in the energy density of their diets (Roth et al., 1999; Smith et al., 1999) This phenomenon is given as an explanation for the plateau in energy intake seen in Figure 1-3.

In addition to illustrating the ability of pigs to regulate their energy intakes over a range of dietary energy densities, Figure 1-3 indicates that at very low dietary energy densities, the pig

will be unable to consume enough feed to prevent a decline in energy intake (Baker et al., 1968; Black et al., 1986). Conversely, at very high energy densities, other factors, such as those thought to be related to a need to achieve a minimum level of gut fill (Cole et al., 1971), will attain primary significance and the result will be a feed intake level that fails to fully attenuate an increase in the pig's energy intake (Ferguson et al., 1999; Oresanya et al., 2007). Black et. al. (1986) suggested that pigs weighing less that 50 kg are unable to fully compensate for reductions in dietary energy concentration below 3.3 Mcal/kg. Conversely, Beaulieu et. al. (2009) fed diets ranging in energy concentration from 3.1 to 3.6 Mcal/kg to pigs initially weighing approximately 30 kg without observing any differences in energy intake. What is agreed upon is that the specific energy concentrations associated with the inflection points seen in Figure 1-3 will be influenced by factors including: the size/age, gender and genetic make-up of the pig, as well as the ingredient and nutrient compositions of the diet, particularly with respect to dietary fibre content (Ellis and Augspurger, 2001).
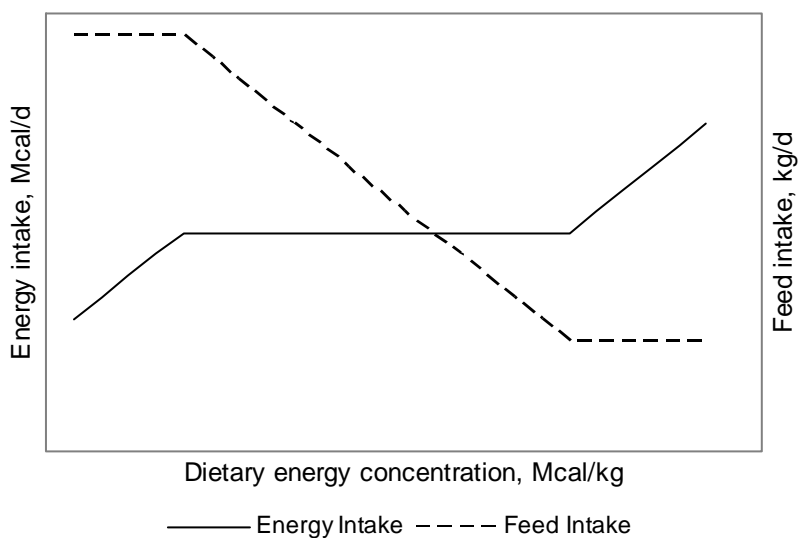
Figure 1-3:   Illustration of the general relationships between the energy concentration of the diet and intakes of feed and energy (adapted from Cole et al., 1971)

In contrast to the previously cited studies, instances in which pigs did not alter their ADFIs in response to changes in dietary energy concentration are also reported (Campbell and Taverner, 1986; Wu et al., 2007). In these studies, it was reported that the pigs' daily energy intakes were affected by the energy concentration of their diets (Patterson, 1985; Stein and Easter, 1996).

1.4.2.2 Effect of energy density on the rate and efficiency of body-weight gain

In the related literature, the reported effects of changes in dietary energy on growth performance in pigs span the breadth of possibilities. At one extreme are the studies that report improvements in both the rate and efficiency of body-weight gain with increased dietary energy density (Campbell and Taverner, 1986; De la Llata et al., 2001). At the other extreme are studies in which no changes in growth performance resulted from changes in energy concentration of the diet (Bayley and Lewis, 1963; Beaulieu et al., 2009). Additionally, a number of studies occupy the middle ground, reporting that dietary energy density affects the efficiency, but not the rate, of body-weight gain (Smith et al., 1999; Oresanya et al., 2007).

Understanding the effects of energy density on performance has implications for pork production in terms of the likelihood of successful manipulation of pig growth performance. Such an understanding also has application to human and to companion animal nutrition in terms of the development of nutritional strategies to combat the obesity epidemic that plagues these species (Donahoo et al., 2008; Rolls, 2009).

1.4.2.3 The confounding effect of changes in dietary composition

One of the most significant challenges in studying energy metabolism is that changes in dietary energy concentration can never occur independently of changes in dietary ingredient composition (Leveille and Cloutier, 1987; Beaulieu et al., 2009). Therefore, there is always some room for doubt as to whether the observed effects are strictly due to changes in energy density or whether they are due to the underlying changes in ingredient composition (Rolls et al., 1999; Donahoo et al., 2008). While preceding sections examined the effects of energy density of the diet on intakes of feed and energy and on growth performance, the ability to affect changes in these parameters has also been attributed to dietary macronutrient composition (McCargar et al., 1989; Pettigrew and Moser, 1991). Given the existence of evidence that both energy density and macronutrient composition affect energy intake, a logical next step may be to study their interactive effects in a systematic way.

1.5 SUMMARY

Seerley and Ewan (1983) speculated about the evolution of a Brave New World of swine energy metabolism in which researchers will have developed the means to repartition energy which would otherwise be dissipated as heat, and thus lost to the pig, back for use for productive purposes. While this is not yet within the realm of possibility, significant advances have been, and continue to be, made in understanding how pigs metabolize energy and how this can be manipulated to the greatest advantage of the pork industry. It is generally understood that energy intake has a significant impact on pig growth and that dietary energy concentration can have a significant impact on energy intake. What is less clear is the nature of these impacts and the potential interactive effects of the macronutrient composition of swine rations. Nevertheless, the huge contribution of the provision of dietary energy to the overall costs of swine production, and the potential applicability of swine-based findings to other species, more than justify the continued devotion of a significant portion of research resources to the field of swine energy metabolism.

2.   INTRODUCTION

Dietary energy has been identified as the most significant cost in pork production (Patience et al., 1995; Saskatchewan Pork Development Board, 2006). Therefore, the potential exists to deliver millions of dollars in savings to the pork industry through improved feed formulation technology, which can be achieved via an enhanced understanding between energy intake and pig growth performance (Campbell et al., 1985).

There are two approaches to manipulating the energy intake of pigs. They are: 1) by restricting their feed intake and 2) by altering the energy density of the diet. Previous work aimed at discerning the effect of feed intake on pig growth performance found that increases in energy intake (King et al., 2004; Renaudeau et al., 2006) and in average daily gain (De Goey and Ewan, 1975[a]; Weis et al., 2004) result from increases in feed allowance. However, there is markedly less consensus among studies with respect to the effect of feed intake on feed conversion efficiency. Some authors report a negative relationship between feed intake and feed conversion efficiency (Leymaster and Mersmann, 1991), while others report the opposite (Bikker et al., 1995; King et al., 2004). A third group of studies report that the relationship between these parameters takes an inverse parabolic form (Fuller and Livingston, 1978; Campbell et al., 1985).

An oft-stated criticism of studies in which energy intake was manipulated by altering feed allowance is its poor applicability to commercial practice (Stein and Easter, 1996; Oresanya et al., 2008). In a typical commercial situation pork producers are equipped to provide their herds with ad libitum access to feed. They are therefore limited to manipulating dietary energy density to affect changes in energy intake (Stein and Easter, 1996; Oresanya et al., 2008).

Studies conducted to elucidate the effect of changes in dietary energy density on pig growth performance have yielded conflicting outcomes. Investigations such as those of Black et al. (1986) and of Beaulieu et al. (2009) support the notion that over a range of energy densities, pigs will adjust their ADFIs to maintain a constant energy intake. In investigations such as these, it is reported that no changes in growth performance result from changes in dietary energy density (Bayley and Lewis, 1963; Kerr et al., 2003).

In contrast to the aforementioned studies, a number of previously conducted experiments demonstrated that ADFI was unaffected by dietary energy concentration (Campbell and Taverner, 1986; Stein and Easter, 1996) and that energy intake was therefore increased as energy concentration increased (Stein and Easter, 1996; Wu et al., 2007). Additionally, a number of studies have reported improvements in growth performance with increases in dietary energy density (Ferguson et al., 1999; De la Llata et al., 2001)

Understanding the pig's response to changes in feed intake and dietary energy density has important implications for pork production in terms of the likelihood of successful manipulation of pig growth performance. Clearly there is a lack of consensus in the literature with respect to the individual effects of each of these parameters. Additionally, a few researchers have recognized that it may be erroneous to assume that the effects of manipulating feed intake and the effects of manipulating energy density are analogous and free from any interactions (Oresanya et al., 2008). Therefore, the objective of the present experiment was to compare the pig's response to changes in energy intake brought about by changes in feed intake with the pig's response to changes in energy intake brought about by changes in dietary energy concentration. Concurrently, the abilities of the DE, ME and NE systems to predict the growth performance of pigs were evaluated.

3. EXPERIMENTAL

3.1 MATERIALS & METHODS

3.1.1 Animals & housing

This experiment used a total of 72 growing barrows. They were selected for inclusion in the experiment firstly on the basis of body-weight (30 ± 2 kg (mean ± SD) on experimental day 0), and secondly on the basis of uniformity of ADG during the previous two week period. This selection process ensured that the most uniform group of pigs was included in the experiment. For the entirety of the experiment, the pigs were individually-housed in pens measuring 1.67 m^2 (0.91 m wide by 1.83 m deep) and consisting of fully-slatted concrete floors and PVC siding. Each pen was equipped with a nipple drinker and a single-space dry feeder. Additionally, a gap of approximately 7 cm running from the top to the bottom of the back wall of each pen afforded each pig visual and nose-to-nose contact with a conspecific.

The animal care protocol adhered to throughout this study was evaluated for compliance with the guidelines of the Canadian Council on Animal Care (CCAC; 1993) and was approved by the University of Saskatchewan's University Committee on Animal Care and Supply (UCACS; Protocol No. 2008-0070).

3.1.2 Data Collection

All pigs were weighed on a weekly basis. Additionally, feed that was offered to, but not consumed by, the ad libitum-fed pigs was weighed each week to permit the calculation of the feed intake (disappearance) of these animals. On the basis of these two parameters, the feed allowances of pigs receiving restricted feed were adjusted weekly (see section 3.1.3 for more details). Feeder weigh-backs were only performed on the restricted-fed pigs in the event that

their entire daily feed allowance was not consumed within a 24 h period. Pigs were removed from the growth experiment when they attained a body-weight of 60 ± 2 kg (mean $\pm$ SD).

3.1.3 Dietary Treatments & Experimental Design

Treatments were arranged in a 3 x 3 factorial design with 3 feeding levels (80, 90 and 100% of ad libitum intake) and 3 levels of dietary energy density (2.18, 2.29 and 2.40 Mcal NE/kg), for a total of 9 dietary treatments. Each set of 9 treatments was considered to be a "block" and the experiment encompassed a total of 8 such blocks. The ingredient and nutrient compositions of the experimental diets are given in Tables 3-1 and 3-2, respectively. The dietary macro-ingredients that were used in this study were selected for their relevance to the swine industry of the Prairie provinces of western Canada. They were sourced by, and purchased from, Federated Co-operatives Ltd. (Saskatoon, SK). Celite was included in the diets as an indigestible marker.

The low, medium and high energy diet formulations were obtained by shifting the relative proportions of the main energy-yielding ingredients. This approach was taken in order to minimize any confounding of the effects of energy concentration by the effects of changes in dietary ingredient composition. In so doing, this approach to diet formulation will lend credence to the attribution, if appropriate, of changes in growth performance to changes in dietary energy density.

Table 3-1: Ingredient composition of experimental diets

Ingredient, % as-fed	Low Energy	Med Energy	High Energy
Barley	55.450	31.328	6.800
Soybean Meal	24.000	22.200	20.400
Wheat	15.000	39.548	64.505
Canola Oil	1.000	2.250	3.500
Mono-Di Cal/P	1.300	1.325	1.350
Limestone	0.850	0.825	0.800
PSCI Vitamin Premix[1]	0.600	0.600	0.600
PSCI Mineral Premix[2]	0.600	0.600	0.600
Salt	0.500	0.500	0.500
Celite	0.400	0.400	0.400
Lysine-HCl	0.190	0.270	0.350
L-Threonine	0.060	0.093	0.125
DL-Methionine	0.045	0.058	0.070
L-Tryptophan	0.005	0.005	0.000

[1]Provides (per kg diet): Vitamin A: 9900 IU, Vitamin D_3: 990 IU, Vitamin E: 48 IU, Vitamin K: 4.8 mg, Vitamin B_{12}: 0.03 mg, Thiamin: 1.2 mg, Riboflavin: 6.0 mg, Pantothenic Acid: 18 mg, Niacin: 42 mg, Folacin: 2.4 mg and Biotin: 0.24 mg.
[2]Provides (per kg of diet): Ca: 4.9 g, P_{Avail}: 0.6 mg, Na: 3.6 mg, Cl: 3 mg, K: 7.8 mg, Mg: 7.2 mg, S: 94.8 mg, Zn: 120.4 mg, Mn: 30.4 mg, Fe: 96.3 mg, Cu: 60.0mg, I: 0.6 mg, Co: 0.36 µg and Se: 0.12 mg

Table 3-2: Calculated nutrient composition of experimental diets

Item	Low Energy	Med Energy	High Energy
DE, Mcal/kg	3.23	3.37	3.51
ME, Mcal/kg	3.03	3.16	3.28
NE, Mcal/kg	2.18	2.29	2.40
Dry Matter, %	89.16	89.53	89.89
Crude Protein, %	21.34	20.89	20.44
Crude Fat, %	2.75	3.97	5.18
ADF, %	6.27	5.27	4.26
Total Lysine, %	1.15	1.15	1.15
TID Lysine, %	0.95	0.97	0.98
g D-Lys/Mcal NE	4.34	4.21	4.09

3.1.3.1 Determination of feed allowance

In this experiment the feed allowances of pigs on restricted feeding regimens were calculated on a weight-matched basis with their ad libitum-fed counterparts. This was done in the following manner: first, and solely for the purpose of determining feed allowances, 10 weight ranges of 3 kg each (i.e. 30.1 – 33.0, 33.1 - 36.0 . . . 57.1 - 60.0 kg) were defined within the total weight range over which the pigs were studied. On a weekly basis the ADFI of each ad libitum-fed pig was incorporated into the average ADFI for the weight range(s) in which he fell during the previous week. The daily feed allowance for any given restricted-fed pig was then calculated as the appropriate percentage (80 or 90 %) of the average ad-libitum ADFI for the weight-range into which the restricted-fed pig in question fell at the time of determination.

The approach to determining feed allowance described above was necessary to address the issues of anticipated differences in growth rate between the ad libitum and restricted-fed pigs and expected differences in feed intake related to size/body-weight. In addition to addressing these issues, the procedure for determining feed allowance followed in the present study offers the advantage of mitigating the impact of fluctuations in feed intake by a single ad libitum-fed pig on the feed allowances of the restricted-fed pigs.

As this experiment had generated no feed intake data prior to the commencement of the first block of animals, it was necessary to consult with colleagues at the Prairie Swine Centre to obtain estimates, based on previously generated data, of the voluntary feed intakes of individually housed pigs of a similar size on which to base the feed allowance calculations for the first week of feeding for the first three blocks of animals. The daily feed allowance of the restricted-fed pigs was provided in two equally-sized meals per day. All pigs had ad libitum access to water throughout.

3.1.4 Statistical Analysis

Growth performance and energy intake and utilization data were analyzed using the MIXED procedure of SAS (SAS Institute Inc., 1996) where the individual pig was the experimental unit and where the statistical model examined the fixed effects of feeding level, energy concentration and the interaction between them. The correlation procedure of SAS (Proc CORR; SAS Institute, 1996) was used in the evaluation of the relative predictive capabilities of the DE, ME and NE systems. In all instances, statistical significance was declared when $P < 0.05$.

3.2   RESULTS

Overall, the health of the pigs throughout the experiment was satisfactory. It was necessary to remove 2 out of 72 animals from the experiment due to their having developed clinical signs of illness which, critically, included anorexia. Consequently, their data were removed from the data-set. These pigs were receiving the Med-100 and High-90 dietary treatments; however, there was no reason to implicate the experimental treatments in the aetiology of illness in either animal.

It should be noted that for the purposes of this thesis the terms "feeding level" and "feed allowance" are used synonymously, as are the terms "energy concentration" and "energy density". Additionally, all net energy values given in this thesis were obtained from CVB values.

No interactive effects between feeding level and dietary energy concentration were found; therefore, only the main effects of feeding level and energy concentration are presented.

Feeding levels of 80, 90 and 100% of ad libitum were targeted. As shown in Table 3-3, the actual feeding levels achieved were 79, 91 and 100% of ad libitum; demonstrating that the feed restriction protocol followed in this experiment was highly effective.

Table 3-3: Targeted and actual feeding levels as a percentage of ad libitum intake

	Feed Intake Level, % Ad Libitum		
Targeted Intake	80	90	100
Actual Intake	79	91	100

As expected, ADFI, expressed on both a kg/d basis and as a percentage of that predicted by the NRC (1998) significantly increased with increasing feeding level (P < 0.0001). A significant improvement in both the rate and efficiency of body-weight gain was observed (P < 0.0001), while the number of days required for the pigs to reach a body-weight of 60 kg was significantly reduced with increased feeding level (P < 0.0001; Table 3-4).

Table 3-4: The effects of feed allowance on the performance of growing barrows

Feed Intake Level, % Ad Lib	79	91	100	SEM	P-Value[1]
N	24	23	23	-	-
Initial Wt., kg	30.4	30.4	29.6	0.35	0.0654
Final Wt., kg[2]	59.6	60.3	60.2	0.31	0.2305
No. Days on Test[2]	41^a	35^b	29^c	0.83	<0.0001
ADG, kg	0.72^a	0.85^b	1.06^c	0.02	<0.0001
ADFI, kg	1.61^a	1.87^b	2.05^c	0.03	<0.0001
ADFI, % NRC[3]	76^a	87^b	96^c	1.48	<0.0001
G:F, kg/kg	0.45^a	0.46^a	0.52^b	0.02	0.0006

[1] Means in a row without a common superscript differ (P < 0.05)
[2] Pigs were grown to a constant final weight of 60 ± 2 kg
[3] Compares measured ADFI to that calculated from NRC (1998) as: DE Intake (kcal/d) = 13 162*$(1 - e^{-0.0176*BW})$ where BW was taken to be the average of the initial and final weights

Table 3-5 illustrates the effects of feeding level on the pigs' intake and utilization of dietary energy on a daily basis. Not surprisingly, the pigs' DE, ME and NE intakes were all significantly increased as feeding level increased from 79 to 100% of ad libitum (P < 0.0001). The estimated daily maintenance energy requirements of the pigs were unaffected by feed intake level, while the estimated amount of energy available to them, on a daily basis, for body-weight gain was significantly increased (P < 0.0001). The efficiency with which the pigs used dietary energy for body weight gain on a daily basis was not significantly affected by feeding level.

Table 3-5: The effects of feed allowance on daily energy utilization by growing barrows

Feed Intake Level, % Ad Lib	79	91	100	SEM	P-Value[1]
DE Intake, Mcal/d[2]	5.44[a]	6.28[b]	6.89[c]	0.11	<0.0001
DE Maintenance, Mcal/d[3]	1.91	1.92	1.91	0.01	0.5524
DE Gain, Mcal/d[4]	3.53[a]	4.36[b]	4.98[c]	0.10	<0.0001
DE Efficiency, Mcal/kg[5]	5.00	5.16	4.78	0.02	0.3440
ME Intake, Mcal/d[2]	5.10[a]	5.88[b]	6.46[c]	0.10	<0.0001
ME Maintenance, Mcal/d[6]	1.84	1.85	1.84	0.01	0.5509
ME Gain, Mcal/d[4]	3.25[a]	4.04[b]	4.62[c]	0.10	<0.0001
ME Efficiency, Mcal/kg[5]	4.61	4.78	4.43	0.20	0.3659
NE Intake, Mcal/d[2]	3.69[a]	4.26[b]	4.68[c]	0.07	<0.0001
NE Maintenance, Mcal/d[7]	1.36	1.37	1.36	0.01	0.4955
NE Gain, Mcal/d[4]	2.33[a]	2.92[b]	3.32[c]	0.07	<0.0001
NE Efficiency, Mcal/kg[5]	3.30	3.43	3.19	0.12	0.3867

[1] Means in a row without a common superscript differ (P < 0.05)
[2] Calculated from ADFI and the calculated energy concentration of the diet
[3] Calculated as: $DE_{Maintenance} = 110 * BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[4] Calculated as $E_{Intake} - E_{Maintenance}$
[5] Calculated as: E_{Gain}/ADG
[6] Calculated as: $ME_{Maintenance} = 106 * BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[7] Calculated as: $NE_{Maintenance} = 0.74 * ME_{Maintenance}$ (Noblet, 2007)

Table 3-6 summarizes the effects of feed intake level on the intake and utilization of energy by the pigs over the entire experimental period. As anticipated, increasing the pigs' feed allowance was accompanied by a significant increase in their energy intake (P = 0.01). Over the whole experimental period, there was a significant reduction in the estimated quantity of energy required by the pigs for maintenance as feeding level increased (P < 0.0001). This observation can likely be explained by the reduction in the number of days pigs spent on the experiment, as feeding level increased (P < 0.0001). However, feed intake level did not significantly affect either the estimated quantity of energy available to the pigs for body-weight gain or the efficiency with which the available energy was used.

Table 3-6: The effects of feed allowance on the total energy utilization of growing barrows

Feed Intake Level, % Ad Lib	79	91	100	SEM	P-Value[1]
DE Intake, Mcal[2]	223.45[a]	222.42[a]	201.05[b]	5.72	0.0100
DE Maintenance, Mcal[3]	78.50[a]	68.08[b]	55.70[c]	1.49	<0.0001
DE Gain, Mcal[4]	144.95	154.34	145.35	4.62	0.2590
DE Efficiency, Mcal/kg[5]	5.00	5.16	4.78	0.18	0.3440
ME Intake, Mcal[2]	209.47[a]	208.52[a]	188.46[b]	5.36	0.0100
ME Maintenance, Mcal[6]	75.64[a]	65.60[b]	53.68[c]	1.44	<0.0001
ME Gain, Mcal[4]	133.82	142.92	134.79	4.30	0.2453
ME Efficiency, Mcal/kg[5]	4.61	4.78	4.43	0.17	0.3659
NE Intake, Mcal[2]	151.81[a]	151.08[a]	136.61[b]	3.88	0.0100
NE Maintenance, Mcal[7]	55.98[a]	48.55[b]	39.72[c]	1.07	<0.0001
NE Gain, Mcal[4]	95.84	102.54	92.89	3.10	0.2485
NE Efficiency, Mcal/kg[5]	3.30	3.43	3.19	0.12	0.3867

[1] Means in a row without a common superscript differ (P < 0.05)
[2] Calculated from ADFI, calculated energy concentration of the diet and number of days on test
[3] Calculated as: $DE_{Maintenance} = 110*BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[4] Calculated as $E_{Intake} - E_{Maintenance}$
[5] Calculated as: $E_{Gain}/$ (Final BW – Initial BW)
[6] Calculated as: $ME_{Maintenance} = 106*BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[7] Calculated as: $NE_{Maintenance} = 0.74*ME_{Maintenance}$ (Noblet, 2007)

Increasing the energy concentration of the diet resulted in a significant reduction in the quantity of feed consumed by the pigs on a daily basis (P = 0.0016); however, dietary energy concentration had no effect on feed intake expressed as a percentage of the intake predicted by the NRC (1998). Similarly, neither the rate nor the efficiency of body weight gain responded to changes in dietary energy concentration (Table 3-7). However, differences among diets in terms of cost per tonne (of diet) translated into an increase in the monetary cost of body weight gain from $0.66 per kg of body weight on the low energy diet to $0.70 and $0.71 per kg of body weight gain on the medium and high energy diets, respectively.

Table 3-7: The effects of dietary energy concentration on the performance of growing barrows

Relative Energy Concentration	Low[1]	Med[2]	High[3]	SEM	P-Value[4]
N	24	23	23	-	-
Initial Wt., kg	30.2	30.2	30.0	0.35	0.7498
Final Wt., kg [5]	60.3	59.7	60.0	0.31	0.3379
No. Days on Test[5]	35	35	35	0.83	0.9775
ADG, kg	0.89	0.85	0.88	0.20	0.4667
ADFI, kg	1.93[a]	1.81[b]	1.78[b]	0.04	0.0016
ADFI, % NRC[6]	86	85	87	1.51	0.6542
G:F, kg/kg	0.46	0.47	0.50	0.02	0.2072

[1] DE = 3.22, ME = 3.03 and NE = 2.18 Mcal/kg
[2] DE = 3.37, ME = 3.16 and NE = 2.29 Mcal/kg
[3] DE = 3.51, ME = 3.28 and NE = 2.40 Mcal/kg
[4] Means in a row without a common superscript differ (P < 0.05)
[5] Pigs were grown to a constant final weight of 60 ± 2 kg
[6] Compares measured ADFI to that calculated from NRC (1998) as: DE Intake (kcal/d) = 13 162*$(1 - e^{-0.0176*BW})$ where BW was taken to be the average of the initial and final weights.

The nature of the effects of dietary energy concentration on the daily intake and utilization of energy by the pigs was consistent across the energy systems evaluated in the present study. These effects can be summarized as: the energy concentration of the diet had no effect on the pigs' daily energy intake, nor did it affect the estimated quantity of energy required by the pigs for maintenance or available to them for body-weight gain, on a daily basis. In addition, the efficiency with which dietary energy was utilized for gain did not respond to changes in dietary energy concentration (Table 3-8).

Table 3-8: The effects of dietary energy concentration on the daily energy utilization of growing barrows

Relative Energy Concentration	Low	Med	High	SEM	P-Value
DE Conc., Mcal/kg	3.22	3.37	3.51	-	-
DE Intake, Mcal/d[1]	6.22	6.09	6.26	0.11	0.6087
DE Maintenance, Mcal/d[2]	1.92	1.91	1.91	0.01	0.4171
DE Gain, Mcal/d[3]	4.30	4.18	4.35	0.10	0.5964
DE Efficiency for Gain, Mcal/kg[4]	4.93	4.99	5.02	0.02	0.9262
ME Conc., Mcal/kg	3.03	3.16	3.28	-	-
ME Intake, Mcal/d[1]	5.85	5.71	5.85	0.10	0.6188
ME Maintenance, Mcal/d[5]	1.85	1.84	1.84	0.01	0.4734
ME Gain, (Mcal)[3]	4.00	3.87	4.01	0.10	0.6272
ME Efficiency for Gain, Mcal/kg[4]	4.58	4.62	4.63	0.20	0.9755
NE Conc., Mcal/kg	2.18	2.29	2.40	-	-
NE Intake, Mcal/d[1]	4.20	4.14	4.27	0.07	0.4908
NE Maintenance, Mcal/d[6]	1.37	1.36	1.36	0.01	0.5302
NE Gain, Mcal/d[3]	2.83	2.78	2.91	0.07	0.4732
NE Efficiency for Gain, Mcal/kg[4]	3.24	3.31	3.36	0.12	0.7768

[1] Calculated from ADFI and the calculated energy density of the diet
[2] Calculated as: $DE_{Maintenance} = 110*BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[3] Calculated as: $E_{Gain} = E_{Intake} - E_{Maintenance}$
[4] Calculated as: $E_{Efficiency} = E_{Gain}/ADG$
[5] Calculated as: $ME_{Maintenance} = 106*BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[6] Calculated as: $NE_{Maintenance} = 0.74*ME_{Maintenance}$ (Noblet, 2007)

When the whole experimental period was considered, no effect of dietary energy concentration on total energy intake was seen. There were also no effects of energy concentration on the estimated quantities of energy required for maintenance and available for gain. The efficiency of energy utilization for gain over the entire experimental period was similarly unaffected by the energy concentration of the diet. The pattern of these responses (or lack thereof) of energy intake and utilization to dietary energy concentration persisted irrespective of which of the three energy systems was being considered (Table 3-9).

Table 3-9: The effects of dietary energy concentration on energy utilization by growing barrows

Relative Energy Concentration	Low	Med	High	SEM	P-Value
DE Conc., Mcal/kg	3.22	3.37	3.51	-	-
DE Intake, Mcal[1]	215.68	213.96	217.62	5.72	0.8533
DE Maintenance, Mcal[2]	67.87	67.65	67.22	1.49	0.9446
DE Gain, Mcal[3]	147.82	146.31	150.40	4.62	0.7833
DE Efficiency for Gain, Mcal/kg[4]	4.93	4.99	5.02	0.18	0.9262
ME Conc., Mcal/kg	3.03	3.16	3.28	-	-
ME Intake, Mcal[1]	202.81	200.55	203.39	5.36	0.8797
ME Maintenance, Mcal[5]	65.40	65.19	64.78	1.44	0.9447
ME Gain, Mcal[3]	137.40	135.36	138.61	4.30	0.8346
ME Efficiency for Gain, Mcal/kg[4]	4.58	4.62	4.63	0.17	0.9755
NE Conc., Mcal/kg	2.18	2.29	2.40	-	-
NE Intake, Mcal[1]	145.74	145.39	148.64	3.89	0.7564
NE Maintenance, Mcal[6]	48.40	48.24	47.94	1.07	0.9447
NE Gain, Mcal[3]	97.34	97.15	100.71	3.10	0.6227
NE Efficiency for Gain, Mcal/kg[4]	3.24	3.31	3.36	0.12	0.7768

[1] Calculated from ADFI, calculated energy density of the diet and number of days on test
[2] Calculated as: $DE_{Maintenance} = 110 * BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[3] Calculated as: $E_{Gain} = E_{Intake} - E_{Maintenance}$
[4] Calculated as: $E_{Efficiency} = E_{Gain} / (Final\ BW - Initial\ BW)$
[5] Calculated as: $ME_{Maintenance} = 106 * BW^{0.75}$ (NRC, 1998) where BW is the average of the initial and final BWs
[6] Calculated as: $NE_{Maintenance} = 0.74 * ME_{Maintenance}$ (Noblet, 2007)

The combined effects of feeding level and dietary energy concentration on the growth performance of the pigs are illustrated in Figure 3-1. This figure corroborates the statement made at the outset - that there are no significant interactive effects of feeding level and dietary energy concentration on any of the parameters investigated in this study.

(i)

(ii)

(iii)
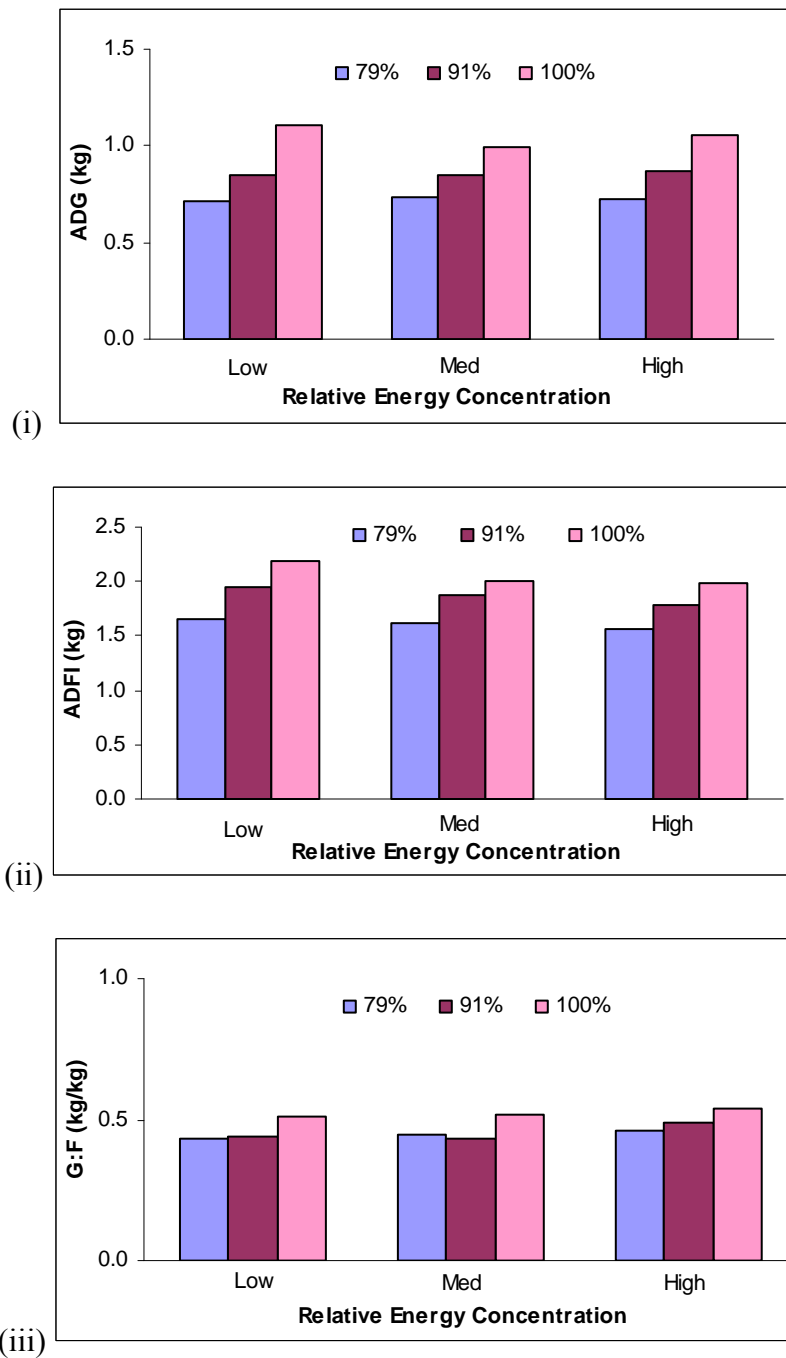
**Figure 3-1:** The effects of dietary energy concentration (Low: DE = 3.22, ME = 3.03 and NE = 2.18Mcal/kg; Med: DE = 3.37, ME = 3.16 and NE = 2.29 Mcal/kg; High: DE = 3.51, ME = 3.28 and NE = 2.40 Mcal/kg) and feeding level (79 versus 91 versus 100 % of ad libitum) on: ADG (Fig 4-1(i); pooled SEM = 0.20), ADFI (Figure 4-1(ii); pooled SEM = 0.04) and G:F ratio (Figure 4-1(iii); pooled SEM = 0.02)

Under the conditions of the present study, no differences were observed between the correlation co-efficients obtained when energy intake, as determined using each of the DE, ME and NE systems was correlated with a given performance outcome (Table 3-10).

Table 3-10: Comparison of the correlation between DE, ME and NE intake with measures of growth performance in 30 to 60 kg barrows[1]

Item		Performance Parameter		
		ADG	ADFI	G:F
Overall	n = 70			
	DE	0.61 (<0.0001)	0.96 (<0.0001)	-0.05 (0.6840)
	ME	0.61 (<0.0001)	0.97 (<0.0001)	-0.05 (0.6616)
	NE	0.60 (<0.0001)	0.95 (<0.0001)	-0.04 (0.7259)
100% Ad Lib	n = 23			
	DE	-0.09 (0.6930)	0.93 (<0.0001)	-0.79 (<0.0001)
	ME	-0.08 (0.7166)	0.94 (<0.0001)	-0.79 (<0.0001)
	NE	-0.10 (0.6522)	0.91 (<0.0001)	-0.78 (<0.0001)
91% Ad Lib	n = 23			
	DE	-0.08 (0.7050)	0.93 (<0.0001)	-0.66 (0.0006)
	ME	-0.09 (0.6922)	0.94 (<0.0001)	-0.67 (0.0004)
	NE	-0.08 (0.7293)	0.91 (<0.0001)	-0.64 (0.0009)
79% Ad Lib	n = 24			
	DE	-0.10 (0.6547)	0.66 (0.0005)	-0.26 (0.2141)
	ME	-0.10 (0.6423)	0.70 (0.0001)	-0.28 (0.1843)
	NE	-0.09 (0.6816)	0.58 (0.0031)	-0.23 (0.2781)
High E	n = 23			
	DE	0.59 (0.0031)	1.00 (<0.0001)	-0.08 (0.7304)
	ME	0.59 (0.0031)	1.00 (<0.0001)	-0.08 (0.7306)
	NE	0.59 (0.0031)	1.00 (<0.0001)	-0.08 (0.7304)
Med E	n = 23			
	DE	0.41 (0.0528)	1.00 (<0.0001)	-0.30 (0.1615)
	ME	0.41 (0.0528)	1.00 (<0.0001)	-0.30 (0.1617)
	NE	0.41 (0.0527)	1.00 (<0.0001)	-0.30 (0.1619)
Low E	n = 24			
	DE	0.72 (<0.0001)	1.00 (<0.0001)	0.16 (0.4692)
	ME	0.72 (<0.0001)	1.00 (<0.0001)	0.16 (0.4691)
	NE	0.72 (<0.0001)	1.00 (<0.0001)	0.16 (0.4691)

[1]Co-efficients of correlation between daily energy intake as determined using each energy system and performance parameter are presented. The P-value associated with each co-efficient is provided in parentheses

3.3 **DISCUSSION**

3.3.1 **The DE, ME & NE systems as predictors of growth performance**

One of the objectives of this experiment was to compare the DE, ME and NE systems in terms of their respective ability to predict the growth performance of pigs. The aforementioned energy systems were compared by determining the co-efficient of correlation for each combination of energy system and performance outcome. The extent to which the correlation coefficients differed between energy systems, within a given performance parameter, was then evaluated. This approach is analogous to that taken by Oresanya et al. (2008) in a study of the growth and body composition of weanling pigs. As in that study (Oresanya et al., 2008), the correlation coefficients within each of ADG, ADFI and F:G were found to be similar across energy systems in the present investigation. It was on the strength of this observation that the present study concluded that there is no difference in the abilities of the DE, ME and NE systems to predict the growth performance of pigs, expressed in terms of ADG, ADFI or G:F. This conclusion suggests that when using ingredients typical of the Prairie provinces of western Canada to formulate diets to meet specified growth performance targets, there is no advantage to be gained by choosing to work with any one of the DE, ME or NE systems over the two.

The conclusion reached in the present study may seem to be somewhat counter-intuitive if one considers that the NE system most accurately quantifies the energy available to the pig (Leveille and Cloutier, 1987; Noblet and Henry, 1993; Noblet et al., 1994). It is also in stark contrast to the conclusion of Noblet (2007) that: "unlike the NE system, the DE and ME systems are relatively unable to predict the performance of pigs". Similarly, Noblet and Henry (1993), Noblet and van Milgren (2004) and Rijnen et al. (2004) determined that, as a predictor of growth performance in pigs, the NE system is superior to both the DE and ME systems. The

independence of the NE system, relative to the DE and ME systems, from the influence of diet- and/or ingredient-specific factors, together with its ability to account for the metabolic cost to the pig of using a given ingredient/compound for energy have been emphasized in discussions of its predictive superiority (Noblet, 1996; Rijnen et al., 2004; Noblet, 2007). In a similar vein, Wu et al. (2007) found that when diets differing in fat content were fed to growing pigs, the NE system most accurately predicted their growth. In contrast, changes in the composition of the diets used in the present study were consciously minimized, thus providing a possibility, albeit tenuous, to reconcile the findings of the present study with the previously-drawn conclusions of other research groups. One might hypothesize that, in the absence of dramatic shifts in diet composition, there are no differences among the predictive capabilities of the DE, ME and NE systems. However, further research is indicated in order to test the validity of the aforementioned hypothesis, as well as to ascribe, if appropriate, quantitative values to the notion of "dramatic shifts" in the context of diet composition.

In addition to the findings of comparisons of the DE, ME and NE systems presented above, comparisons of various NE systems, namely those proposed by Schiemann et al. (1972), Just (1982), Central Veevoederbureau (CVB; 1993) and Noblet et al. (1994), have been undertaken (Noblet, 1996; Noblet, 2000). Noblet (1996) reported differences between NE systems with respect to their relative abilities to predict pig growth performance, while Noblet and Henry (1993) and Noblet (1996) reported inequalities among NE systems with respect to the extent to which they are influenced by diet and/or ingredient changes. For the most part, these differences are attributed to the manner in which the various NE systems account for fasting heat production (Noblet and van Milgren, 2004). In the literature concerning the prediction of growth performance by the various energy systems, the NE system to which the DE and ME systems are

compared varies among studies. However, it is unlikely that differences among studies in terms of which measure of NE is used in the energy system comparison can be held responsible for the reported discrepancy between the finding of this study and the findings of studies conducted previously. The reason for this being that the vast majority of reviews of the accuracy and precision of predictions of pig performance made using various NE systems, as well as the DE system report that, as a collective, the NE systems are superior to the DE system (Noblet and Henry, 1993; Noblet, 1996).

3.3.2   Energy concentration & intakes of feed and energy

This study provides evidence that an inverse relationship exists between dietary energy concentration and ADFI ($P = 0.0016$). This observation is in accordance with previous findings, such as those of Beaulieu et al. (2009). These researchers observed that pigs weighing 30 to 50 kg reduced their ADFIs, thereby maintaining a constant energy intake, as the energy concentration of their diets increased. Additionally, Baker et al. (1968), Smith et al. (1999) and Beaulieu et al. (2006) observed that pigs reduce their ADFIs in response to increasing dietary energy concentration.

In contrast to ADFI, it was observed in the present study that the pigs' energy intakes were unaffected by changes in dietary energy concentration. Together the responses of feed- and energy intake are compatible with reports in the literature that pigs eat to achieve a target energy intake and therefore will adjust their feed intakes up or down according to the energy density of their diet (NRC, 1998; Ellis and Augspurger, 2001; Noblet and van Milgren, 2004).

As demonstrated above, there are a number of previously published studies whose findings are corroborated by those presented herein. Conversely, there exist in the literature a number of reports of the effect of energy density on feed and energy intake whose findings are contradicted by those of the present study. In a number of experiments it was observed that, in contrast to the increase reported here, ADFI did not change with increased dietary energy density (Campbell and Taverner, 1986; Stein and Easter, 1996; Wu et al., 2007; Oresanya et al., 2008). In accordance with having reported that there were no reductions in ADFI, these studies also reported that increases in the energy density of the diet were accompanied by increases in energy intake (Campbell and Taverner, 1986; Stein and Easter, 1996; Wu et al., 2007; Oresanya et al., 2008).

Clearly, there are disparities between the findings of the present study and those of a number of previously published studies. However, recognition that control of voluntary feed intake is highly complex and multi-faceted is ubiquitous in the related literature (Ellis and Augspurger, 2001; Nyachoti et al., 2004; Kyriazakis and Whittemore, 2006). For instance, several authors have observed that the macronutrient composition of the diet affects energy intake (Leveille and Cloutier, 1987; Ellis and Augspurger, 2001; Stubbs et al., 2000). Specifically, higher energy intakes have been reported with an increased contribution of fat, versus carbohydrate, to the energy density of iso-caloric diets (Ellis and Augspurger, 2001; Stubbs et al., 2000). It has been postulated that this effect may be due, at least in part, to there being a lower heat increment of feeding associated with the digestion and utilization of dietary fat versus dietary carbohydrate (Leveille and Cloutier, 1987; Azain, 2001; Ewan, 2001). This reduced heat increment has itself been suggested to contribute to reduced feelings of satiety associated with intake of dietary fat versus intake of carbohydrate (Stubbs, 1998; Stubbs, 1999).

These observations indicate a possibility that the pig's ability to adjust his/her feed intake in response to changes in dietary energy density may be affected by the manner in which these changes are brought about. That is, the pig's response, in terms of feed intake, to the addition (or removal) of fat (or oil) to a basal formulation may not be analogous to his/her response to changes in energy density brought about by shifts in the proportions of the main dietary ingredients. It therefore becomes potentially relevant that a number of those studies reporting an effect of energy density on energy intake but not on feed intake (Patterson, 1985; Campbell and Taverner, 1986; Stein and Easter, 1996) are also studies in which energy density was increased by the addition of fat to a basal formulation. Generally, those studies in which energy density was changed by shifting the proportions of the main dietary ingredients were also those studies in which an effect of energy density on feed, but not on energy, intake was observed (Beaulieu et al., 2006; Oresanya et al., 2006; Beaulieu et al., 2009; present study).

However, evidence also exists that refutes the suggestion that dietary lipid is relatively un-satiating. Indeed, increased dietary lipid has been linked to a decrease in the rate of passage of digesta through the gastro-intestinal tract (Azain, 2001), which has in turn been suggested to contribute to increased satiety and reduced feed intakes with increasing inclusion of lipid in the diet (Azain, 2001; Oresanya et al., 2008). Additionally, the work of Halas et al. (2010) provides compelling evidence that, when studied on an iso-energetic basis, there is no effect of dietary fat versus dietary starch on the rate or efficiency of body-weight gain by growing-finishing pigs. Clearly, further investigation of the effects of changes in the macro-nutrient composition of iso-caloric diets on pig growth performance and energy intake is warranted.

The possibility also exists that at least a portion of the observed differences among experiments as far as the reported effects of energy density on feed and energy intake can be explained in terms of the energetic basis on which these studies are compared. (Noblet and van Milgren, 2004). The information available necessitated that the outcomes of this study and those conducted previously be compared on the basis of dietary DE concentration. However, it has been demonstrated that the NE system provides a more accurate estimation than either the DE or ME systems of the quantity of energy which is actually available to the pig (Noblet and Henry, 1993; Noblet et al., 1994). It has also been demonstrated that by not accounting for the energetic costs to the animal of metabolizing a particular ingredient, estimates of DE and ME will systematically underestimate the amount of energy that is available to the pig from ingredients which are high in lipid and/or starch. Concurrently, the amount of energy available to the pig from ingredients which are high in protein will be systematically over-estimated (Noblet and Henry, 1993; Noblet et al., 1994; Noblet and van Milgren, 2004). Therefore, even when presented with dietary DE concentrations that are similar among studies (Patterson, 1985; Campbell and Taverner, 1986; Stein and Easter, 1996; Beaulieu et al., 2009; present study), differences in the ingredient compositions of these diets (Azain, 2000; Wu et al., 2007) and in the abilities of the pigs to use them for energy (Noblet and Henry, 1993) may result in widely different NE concentrations. This may, in turn, contribute to the discrepancies seen among the pigs' responses to changes in dietary energy concentration.

Thirdly, the age/size of the pigs in whom the response to dietary energy concentration is studied has the potential to influence the outcome. It has been reported that the ability of weanling pigs to adjust their ADFIs in response to energy concentration is impaired relative to older/larger pigs (Black et al., 1986; Ball and Aherne, 1987; Oresanya, 2005). However, there is

conflicting information in the literature, with the results of a number of studies indicating that it is possible for weanling piglets to maintain a constant energy intake when faced with changes in dietary energy concentration (Roth et al., 1999; Beaulieu et al., 2006; Oresanya et al., 2007). Furthermore, it has been suggested that until a pig reaches approximately 50 kg in body-weight s/he will be unable to increase ADFI sufficiently to fully compensate for diets containing less than 3.35 Mcal DE/kg (Black et al., 1986). However, the findings of the present study demonstrate that pigs between 30 and 60 kg body-weight can increase their ADFIs to compensate for energy concentrations as low as 3.22 Mcal DE/kg. These inconsistencies indicate that the effects of age and size or body-weight, together with their interactions, on the pig's intakes of feed and energy have yet to be fully elucidated and that further investigation in this area could prove useful.

3.3.3 Energy concentration & body-weight gain

The only growth performance parameter that was found to be affected by dietary energy concentration in the present study was ADFI. Both the rate and efficiency of body-weight gain were unaffected by changes in energy concentration. Roth et al. (1999) and Beaulieu et al. (2009) reported the same response. The growth performance results presented herein can potentially be explained by the fact that growth performance is heavily dependant on energy intake (Smith and Carey, 1923; Quiniou et al., 1999; Nyachoti et al., 2004). Therefore, changes in growth performance result from changes in energy intake, with feed being the vehicle by which energy is delivered to the pig (Rijnen, et al., 2004). Given that in the present experiment the pigs' energy intakes did not differ with dietary energy concentration, changes in either the rate or in the efficiency of body-weight gain would not be expected.

By contrast, in the case of studies reporting that a change in energy concentration was accompanied by a change in energy intake (Patterson, 1985; Campbell and Taverner, 1986; Stein et al., 1996; Wu et al., 2007; Oresanya et al., 2008), it would be reasonable to hypothesize that changes in other growth performance parameters would also occur. Increases in the rate of gain were reported by Patterson (1985), Campbell and Taverner (1986), Stein and Easter (1996) and Wu et al. (2007); while Campbell and Taverner (1986), Stein and Easter (1996) and Wu et al. (2007) also reported increases in the efficiency of body-weight gain. In contrast, Oresanya et al. (2008), despite having reported an increase in energy intake with changes in energy density, observed no change in ADG. The opposite scenario: no change in energy intake, mediated by a reduction in ADFI, accompanied by improvements in both ADG and ADFI, was reported by Smith et al. (1999).

3.3.4 Feeding level & growth performance

The extent to which previous studies are in agreement with each other as far as the reported effects of feeding level on pig growth performance is much greater than that which was observed among the reported effects of energy concentration. In the present study, increasing the pigs' feed allowance resulted in increases in daily gain ($P < 0.0001$) and daily feed intake ($P < 0.0001$), an improvement in feed conversion efficiency ($P < 0.0006$) and a reduction in the time taken for the pigs to grow from 30 to 60 kg ($P < 0.0001$).

The observed increases in ADFI with increasing feeding level were expected to occur as an inherent characteristic of the feeding level treatments. Such increases have also been noted by the authors of a number of previous studies (Ball and Aherne, 1987; Bikker et al., 1995; King et al., 2004; Oresanya et al., 2008; Halas et al., 2010). Although expected, observing the differences

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in ADFI between dietary treatments confirms that the feeding levels selected are, in fact, appropriately spaced to be helpful in answering the research question posed.

The observed reduction in the number of days on test could be postulated to be concomitant with the increase in ADG that was observed, as feed allowance increased. The latter is itself consistent with the findings of a number of previous studies (Bikker et al., 1995; Quiniou et al., 1996; King et al., 2004; Weis et al., 2004; Oresanya et al., 2008; Halas et al., 2010). These observations suggest that as the level of feed restriction becomes increasingly severe, the extent to which energy intake limits pig growth becomes greater. Therefore, as reported herein, an increased growth rate is observed with the provision of more energy (Lovatto et al., 2006) via the provision of more feed. However, the finding of Leymaster and Mersmann (1991), that ADG did not respond to changes in feed allowance, conflicts with the finding of this study.

The improvement in feed conversion efficiency that was observed in this study speaks to an increase in body-weight gain from one feeding level to the next that is of greater magnitude than the increase in feed intake (Ball and Aherne, 1987). The effects of feeding level on feed conversion reported by Bikker et al. (1995) and by King et al. (2004) are in agreement with the results of the present study. By contrast, the research of Quiniou et al. (1996), Oresanya et al. (2008) and Halas et al. (2010) did not reveal changes in feed conversion efficiency among feeding levels. The observations of Campbell and colleagues (1985) are different again, in that these authors reported that increases in feed allowance up to approximately 80% of ad libitum intake result in improved feed conversion efficiency. However, further increases in feed allowance were observed to have a detrimental effect on feed conversion efficiency (Campbell et al., 1985). Finally, the findings of both Ball and Aherne (1987) and Leymaster and Mersmann (1991) are the antithesis of those reported herein. These authors obtained an inverse relationship

between feed conversion efficiency and feeding level when feeding level was incrementally

increased from 85 to 100 percent of ad libitum intake.

3.3.5 Feeding level & energy utilization

Whether expressed on a daily or on a total basis, the pigs' energy intakes were observed

to increase with increasing feeding level ($P = 0.0001$ and 0.01, respectively). This is an important

and very much desired outcome of providing graded levels of feed. The effect of energy intake

on growth performance cannot be determined if the dietary treatments do not cause energy intake

to change. Previously published studies have also reported successful manipulation of energy

intake via the provision of feed at graded intake levels (Bikker et al., 1995; Quiniou et al., 1996;

Quiniou and Noblet, 1997; King et al., 2004; Weis et al., 2004; Oresanya et al., 2008).

Feed intake level was observed to have no effect on the pigs' estimated daily energy

requirements for maintenance (DE: $P = 0.5524$, ME: $P = 0.5509$, NE: $P = 0.4955$). This finding

supports that of Oresanya et al. (2008) and is consistent with the means by which estimated

maintenance energy requirements were calculated, this being as a function of metabolic BW

(NRC, 1998). In this instance "BW" was taken to be the average of the initial and final body-

weights of each pig. As these endpoints had been defined within the experimental protocol as 30

± 2 and 60 ± 2 kg, respectively, the variation in average bodyweight across treatments was small.

Consequently, no differences in estimated daily maintenance energy requirement were seen. In

contrast to the estimated maintenance energy requirement expressed on a daily basis, the pigs'

estimated total maintenance energy requirement over the entire experimental period was affected

by feeding level ($P < 0.0001$). The inverse relationship, reported herein, between feeding level

and the estimated amount of energy required for maintenance over the whole experimental

period can be explained as a function of the reduction in the number of days taken to reach 60 kg as feed intake level increased (P < 0.0001).

Concomitant (Ewan, 2001; Kyriazakis and Whittemore, 2006) with the combined increase in energy intake and constancy of estimated maintenance energy requirement is an increase in the estimated amount of energy available for gain, on a daily basis, as feeding level increased (P < 0.0001). This observation concurs with that reported by Oresanya and colleagues (2008). In addition, although determination of the effect(s) of feeding level on carcass composition was not a part of this study, the finding that the calculated quantity of energy available for gain increases along with feeding level is in accordance with reports of increases in feed allowance leading to increasing retention of energy in the carcass (Campbell et al., 1985; Kyriazakis and Emmans, 1992; Bikker et al., 1995; King et al., 2004). On a total basis, the observation that feeding level does not affect the estimated quantity of energy available for gain is a consequence of including defined body-weight end-points in the experimental design. It is likely that a difference would be observed if time on test, rather than body-weight, was chosen as the experimental end-point. However, it is equally likely that other outcomes would shift accordingly.

Whether evaluated on a daily or on a total basis, no effect of feeding level on the efficiency with which pigs used energy for gain was observed in the present study. This finding is analogous to those of Quiniou et al. (1996), Oresanya et al. (2006) and Renaudeau et al. (2006). In contrast, Oresanya et al. (2008) reported that the efficiency of body-weight gain was reduced with increased feeding level. These researchers went on to report a decreased rate of protein deposition and an increased rate of lipid deposition as feeding level increased (Oresanya et al., 2008). They postulated that these differences in deposition rates were related to their

findings vis-à-vis the effect of feeding level on the efficiency of energy utilization for body-weight gain. Deposition of protein results in a greater body-weight gain than deposition of an equal mass of lipid because of the significant deposition of water that accompanies protein, but not lipid deposition (Quiniou et al., 1999; de Lange et al., 2001; Ewan, 2001) and therefore results in more efficient body-weight gain (de Lange et al., 2001; Whittemore and Kyriazakis, 2006). Although the present study is not concerned with measurements of body composition, it could be inferred from the observed lack of an effect of feed allowance on the efficiency of energy utilization for body-weight gain, that rates of protein and lipid deposition were similar across feeding levels.

3.3.6 Comparison of approaches to alter energy intake

As stated at the outset, the main objective of this experiment was to compare the response of the pig to changes in energy intake, brought about by restriction of feed intake, with the response of the pig to changes in energy intake brought about by changes in dietary energy concentration. In the present study, changes in feed allowance brought about changes in energy intake while changes in dietary energy concentration did not. Therefore, it must be concluded that there is no comparison to be made. In order to meet the main objective, it would be necessary to feed diets with energy densities that fall outside the range over which the pigs in question are able to fully compensate for changes in energy density. This would ensure that changes in both feed allowance and energy density bring about changes in energy intake, the pigs' responses to which could then be compared. It could be argued that this outcome is indicative of a need for further research aimed at quantifying the range of energy densities over

which pigs can maintain a constant energy intake, as well as identifying and characterizing the factors that affect this.

It should perhaps be acknowledged that an unstated objective of this experiment was to maintain commercial relevance to the greatest extent possible. Accordingly, the range of dietary energy densities used here represents the greatest range that could be achieved with formulations that utilize ingredients typical of the Prairie provinces and that are practical commercially (Patience, 2009 – personal communication). Therefore, to observe the effects of a wider range of energy densities, while potentially highly informative, may become an academic exercise in that the diet formulations necessary to achieve an energy concentration range which results in changes in energy intake would likely prove to be impractical in a commercial setting. As such, any positive effects of such dietary energy densities on pig growth would be unattainable by pork producers.

If subsequent studies were to find that the diet formulations required to achieve energy concentrations that affect changes in energy intake are poorly applicable in a commercial setting, and this finding was to be evaluated in light of the outcomes of the present study, it could be concluded that changing dietary energy concentrations within a range that is practical in a commercial setting does not result in changes in the growth performance of pigs. However, the discrepancies already described (please see section 5.2) both between and among studies in which dietary energy concentration is changed, either by shifting the relative proportions of the main ingredients or by the addition of lipid to a basal formulation, suggest that the means by which energy concentration is manipulated may affect the pigs' response and therefore warrants further investigation.

The findings presented herein indicate that the results of studies in which energy intake has been manipulated by restricting feed intake should be extrapolated to commercial scenarios with caution. Taken together with the fact that typical commercial feeding practice involves the ad libitum provision of feed (Patience et al., 1995; Ellis and Augspurger, 2001) these findings suggest that any improvements in pig performance reported in studies where energy intake is altered by changing feed allowance, while very real, may be unattainable in commercial practice, simply because pork producers do not have the necessary means to alter energy intake at their disposal.

4. IMPLICATIONS

The present study demonstrated that the energy intake of growing pigs can be successfully manipulated by the provision of feed at graded intake levels. Improvements in pig growth performance resulted from increases in feed allowance from 79 to 100 % of ad libitum intake. This is a positive finding for pork producers, who generally lack the means to provide growing/finishing pigs with feed at anything less than ad libitum intake. Realistically, the only tool by which pork producers could alter the energy intake of their herd is by manipulation of dietary energy concentration. The present study, in which diets with NE concentrations ranging from 2.18 to 2.40 Mcal/kg were formulated, using ingredients typical of the Prairie provinces of western Canada, demonstrates that growing pigs will alter their feed intakes, thereby maintaining constant energy intakes across a commercially-relevant range of dietary energy concentrations. Therefore, altering dietary energy concentration via gradual shifts in ingredient composition and within a commercially-relevant range of energy concentrations is an ineffective tool for manipulating the energy intake, and thus the growth performance, of pigs.

It should be noted that the response of the growing pig to changes in dietary energy concentration observed in the present study may not apply universally. For instance, in commercial production situations exist in which, for a plethora of reasons, feed intakes are sub-optimal. In this scenario increases in feed intake in response to reductions in dietary energy concentration may not be of sufficient magnitude to fully attenuate a decline in energy intake, or, may not occur at all. This example illustrates the need to take individual circumstances into account when applying the principles of energy metabolism by pigs.

When the findings of the present study are examined in combination with the findings of previous studies, it becomes apparent that the pig's response to changes in dietary energy concentration is at least somewhat dependant on the source of the energy. More specifically, it can be seen that the pig's response to changes in dietary energy brought about by the addition of fat to the ration may differ from the response seen when energy concentration is altered by shifting proportions of high- and low-energy dietary ingredients.

In addition, this study demonstrated that when formulating diets to meet specified growth performance targets, there is no advantage to be gained by the use of any one of the DE, ME or NE systems over the other two energy systems.

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