FACTORS INFLUENCING THE RATES OF LIPID DEPOSITION AND WITHDRAWAL IN GROWING PIGS

ROWENA SEWJEE

BSc. Agric. University of Natal, Pietermaritzburg

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DECLARATION

We hereby declare that the research reported in this thesis does not contain material which has been accepted for the award of any other degree or diploma in another University and, to the best of our knowledge, does not contain material previously published or written by another person, except where due reference is made in the text.

R. Y. Sewjee

R.M. Gous
(Supervisor)

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ABSTRACT

This study was conducted to determine the influence of factors on the efficiency of protein utilization and the rate of lipid deposition and withdrawal in growing pigs. Two experiments were conducted in total.

The first experiment involved fifty-two crossbred entire Large White x Landrace male pigs, individually penned, which were used to test the proposition that the efficiency of protein utilisation is influenced by the body composition of the pig at the start of the trial. The experiment was divided into two phases: in the first period, starting at 20kg liveweight, when 3 pigs were slaughtered to determine the initial body composition of the pigs on the trial, the remaining 48 pigs were divided into three groups, two of which were fed *ad libitum,* with 11 pigs being offered a feed high in crude protein (HP, 197g CP/kg) and 19 pigs being offered a low CP (LP, 166g/kg) feed. The remaining 19 pigs were fed HP on a restricted basis; the daily allowance being 0.7 of the mean intake of those pigs fed HP *ad libitum.* The objective of this initial period was to create three groups of pigs differing in body lipid content. As each pig achieved a protein weight of approximately 5.9kg, predicted to occur when the pigs on the three treatments reached live weights of 35, 39 and 34kg respectively, the pig entered phase 2 of the trial. At this stage three pigs from each treatment (a total of 9 pigs) were slaughtered for carcass analysis, the protein contents being approximately 5.9kg, and lipid contents being 85, 98 and 87g/kg for the 3 treatments respectively. During phase 2, the 8 pigs fed HP in phase 1 continued to be fed HP in phase 2; 8 pigs were chosen at random from those fed LP in phase 1 and were allocated the high CP basal feed, while the remaining 8 were given LP; and 8 of the pigs feed-restricted in phase 1 were randomly chosen and fed HP, while the remaining 8 were given LP. All pigs were fed *ad libitum* during phase 2. Four pigs from each treatment in phase 2 were slaughtered after 1 week and the remaining 4 a week later for analysis of body composition. In the first week of the second phase of the trial protein gain was highest (264g/d) on the pigs previously restricted and then fed HP, followed by those previously fed LP and then HP (242g/d), with pigs previously restricted and then fed LP depositing the least amount of protein (192g/d). Pigs fed LP or HP throughout, had protein gains of 217 and 210g/d, respectively. Efficiencies of utilization of dietary protein did not differ significantly between treatments, however, the highest being measured in pigs fed LP throughout (461g/kg), followed in order by those fed LP and then HP (457g/kg), those fed

HP throughout (404g/kg), those previously restricted and then fed LP (394g/kg), with those previously restricted and then fed HP being the least efficient (372g/kg).

The second experiment involved twenty-six male and twenty-six female crossbred Large White x Landrace pigs, individually penned, which were used to determine the maximum rate at which growing pigs can gain lipid. The experiment was divided into three phases: In the first, starting at 20kg live weight (56 days old), when two males and 2 females were slaughtered to determine the initial body composition of the pigs on the trial, the remaining 24 males and 24 females were randomly allocated to their various treatments. The treatments consisted of a feed high in crude protein (H, 197g/kg), a feed low in CP (L, 166g/kg) and three blends, namely 50H/50L (180g/kg) (male diet), 30H/70L (167g/kg) (both male and female diets) and 20H/80L (162g/kg) (female diet). Six pigs from each sex were allocated to each treatment. The EFG Pig Growth Model was used to determine the fat contents (lipid index) on the two feeds available and the three blends, to estimate the best times to sample pigs. It was estimated that phase 1 would terminate at 63 d, phase 2 at 70 d and phase 3 at 77 d of age. At the end of each phase two pigs from each sex and treatment were slaughtered. The lipid contents differed significantly between treatments at the end of phase 2 for the male pigs, with the highest being measured in pigs fed L (108g/kg), followed in order by those fed 70L/30H (86g/kg), those fed 50L/50H (74g/kg), and those fed H (68g/kg) with the least lipid content. The lipid contents of the female pigs were highly significantly different at the end of phase 3, with the highest being measured in pigs fed L (147g/kg), followed in order by those fed 80L/20H (124g/kg), those fed 70l/30H (116g/kg) and the least lipid content from those fed H (115g/kg). As estimated by the EFG Pig Growth Model, the male and female pigs fed L treatment had the highest lipid content and those fed H treatment, achieving their target rate of lipid deposition, with the lowest lipid content.

This study indicates that the response in protein gain and in efficiency of utilization of protein of pigs to a given feed is dependent on the amount and quality of the feed given to the animals previously. Also, the maximum rate of lipid deposition can be achieved by monitoring the changes in lipid deposition over a period of time, which enables an enhanced understanding of the theory of food intake regulation in a growing pig. As a result, accurate changes can be made when designing a phase-feeding program for growing pigs.

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

The growing pig's capacity for protein accretion is the major factor determining growth performance and dietary amino acid requirement. Rate of lean growth is mostly a function of the pig's genotype but it is modified by the quantity and quality of food that the pig eats and the environment (including health status) in which the pig is kept. By measuring the pig's potential for lean growth, it is possible to set dietary specifications according to genetic potential so that returns are maximised.

It has been accepted by many researchers (Kielanowski, 1969; Whittemore *et al.*, 1988; Moughan, 1999; Schinckel, 2001), that an animal has a natural potential rate of protein deposition, but little concern has been given to the possibility that animals also have a target rate of lipid deposition. For example, if a growing pig has been given free access to an unbalanced food or has its intake restricted for a period of time, it will fail to achieve its potential for growth (Kyriazakis *et al*, 1991). At the end of the period of inadequate nutrition the pig will usually have a lower protein weight, it's lipid weight may be lower or higher than that of a similar pig treated in a non-limiting way at the same protein weight (Kyriazakis *et al*, 1991). The normal consequence of growth limitation following access to an unbalanced feed is the rate of protein deposition being less than the potential or the rate of lipid deposition being less than or greater than required to achieve the preferred lipid to protein ratio in the body. According to Kyriazakis and Emmans (1992), the rate of lipid deposition is dependent on the rate at which an animal attempts to return to its normal protein weight in a non-limiting environment. If the animal has both a protein and lipid deficit, then the correction of one usually assists the other. An attempt to overcome a protein deficit will usually result in an increased food intake and a consequential increase in lipid retention rates due to the over-consumption of energy (Kyriazakis and Emmans, 1991; Ferguson and Gous, 1997; Ferguson *et al.*, 2000). Experimental evidence indicates that animals, which are fatter than their desired level, show a reduction in lipid gain once the dietary protein deficiency is removed (Kyriazakis and Emmans, 1991; Kyriazakis *et al.*, 1991; Stamataris *et al.*, 1991; Ferguson and Theeruth, 2002). It is proposed that this response will continue until the level of fatness has returned to levels similar to those observed in animals that have been unrestricted or followed normal growth.

The response of growing pigs to feeds of increasing nutrient content has been extensively researched, and it is now possible to determine with accuracy the daily intakes of many of the essential nutrients required to enable the pig to grow at its potential at that stage of its life. However, evidence is lacking on how the initial state of these animals influences the efficiency with which they utilize dietary protein.

By virtue of the way in which growing pigs are fed, they will undergo periods during which they will become fatter than their genetically-determined degree of fatness, when the feed offered is limiting in an amino acid, and they will then make use of those lipid reserves as an energy source when the feed is no longer limiting. This theory has been incorporated into a simulation model that predicts voluntary food intake by pigs on each day of the growing period, when subjected to a given feed in a given environment.

The research reported in this thesis explores this theory in two ways: by ascertaining whether the initial state of the pig influences the amount of food consumed, and the efficiency with which it utilizes this food; and by following the rate of lipid deposition and withdrawal in growing pigs subjected to feeds differing in their protein:energy ratio, on the assumption that the more unbalanced the feed, the greater the rate of lipid gain, but in all cases, that body lipid reserves would be utilized as an energy source once the feed had become less-limiting in essential nutrients.

CHAPTER 2

LITERATURE REVIEW

2.1 THE REQUIREMENT FOR AMINO ACIDS

2.1.1 Essential amino acids

Proteins are made up of many amino acids. Pigs do not have a protein requirement as such, but dietary protein provides the amino acids that cannot be synthesized sufficiently rapidly to permit normal growth. These are known as the essential amino acids, which need to be provided in the feed in order to meet the requirements of the animal for maintenance and growth. The nonessential amino acids are those that can be made in the body from other amino acids or other nutrients in the diet. The ten essential amino acids that are required for maximum growth are shown in Table 2.1 (Cunha, 1977).

Table 2.1. *Amino acid classification for the pig*

Essential amino acids	Nonessential amino acids
Lysine	Glycine
Tryptophan	Serine
Methionine	Alanine
Valine	Norleucine
Histidine	Aspartic acid
Phenylalanine	Glutamic acid
Leucine	Hydroxyglutamic acid
Isoleucine	Cystine
Threonine	Citrulline
Arginine*	Proline
	Hydroxyproline
	Tyrosine

* Arginine is not essential for the growing pig above 20 kg (Whittemore *et al.*, 2001)

It is therefore imperative that pigs are supplied with a regular intake of protein because they continually make use of this protein either to build new tissues, as in growth and

reproduction, or to repair worn-out tissue. If adequate protein is lacking in the diet, the pig will suffer a reduction in growth, or body gain will be of abnormal composition compared with an animal that receives the required levels of protein (Kyriazakis *et al.*, 1991). Ultimately, protein will be withdrawn from certain tissues to maintain the functions of the more vital tissues of the body as long as possible.

2.1.2 Balance of amino acids

Protein is a costly item in pig diets, so maximizing efficiency of amino acid utilization is very important. Therefore, diets containing amino acids at minimally required levels (for maximal lean growth) with minimal excesses is a critically important factor. A major advance in the understanding of amino acid requirements is the concept that there is an 'ideal' protein for the pig, (Cole, 1978) which contains all the essential amino acids in the correct balance or proportions, and the correct ratio of essential to non-essential amino acids. This balanced protein means that the proportion of essential amino acids should remain constant but the amount may vary depending on factors such as weight, sex and breed. The idea of an 'ideal' protein had greater application for maintaining a minimum balance of amino acids, relative to lysine because lysine is required in major proportions for lean deposition, and is normally the first and major limiting amino acid in cereal-based diets. The first-limiting amino acid is that which is present in the least amount in the feed relative to its requirement by the pig and it is the extent to which this amino acid is adequate that will determine the performance of the pig. Therefore, pig diets are usually formulated to a specific lysine, rather than a protein, level. In certain situations, depending on the availability of ingredients, it may not be possible to achieve an optimum balance of amino acids to provide ideal protein. For instance, an individual amino acid may be under- or over-supplied when attempting to meet the nutrient specifications of a diet from a particular range of ingredients.

Three factors need to be established when studying the response to an individual amino acid (Figure 2.1):

1. The supply of amino acids at which the optimum response is achieved (point B). The combination of these values for individual amino acids will give the optimum balance needed for the ideal protein.

2. The consequence of undersupply of an amino acid (an increase in dietary supply of amino acid will result in an increase in the slope of the response from point A to B).
3. The consequence of oversupply of an amino acid (the change in response when dietary supply exceeds the optimum).

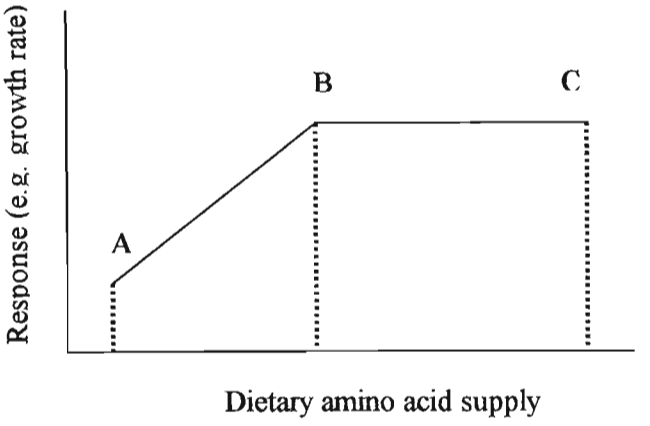

Figure 2.1. *Response in changes to undersupply (A to B), optimal supply (B) and oversupply (B to C) of dietary amino acid (Cole and Haresign, 1985)*

In maintaining a minimum ratio of amino acids relative to lysine, it was assumed that a surplus of one or several other essential amino acids would not affect pig response (ARC 1981). Chung and Baker (1992) suggested that by using chemically defined diets containing an almost perfect balance of amino acids as a sole source of dietary nitrogen, a 13.6 kilogram pig is capable of converting 87% of its absorbed nitrogen above maintenance to carcass protein. This does not mean that each of the amino acids found in dietary protein are utilized at 87% efficiency for protein accretion.

Table 2.2 shows the change, over the years, with respect to the proportion of essential amino acids in a balanced diet for growing pigs.

Table 2.2. *The ratio of essential amino acids in the ideal protein for growing pigs*

Amino acid	Yen *et al.* (1986)	Wang and Fuller (1989)	Chung and Baker (1992)*
Lysine	100	100	100
Methionine and cystine	50	63	62.5
Threonine	57	72	67
Tryptophan	20	19	19
Isoleucine	55	60	60
Leucine	100	110	100
Phenylalanine and tyosine	100	120	95
Histidine	35	-	32
Valine	70	75	68

*Ideal patterns of essential amino acids for pigs in the weight range of 20 to 50 kg

2.1.3 Energy : Protein interaction

The provision of protein and energy is what determines the consequences for the rate of growth and composition of the pig as it grows, rather than a determinant of the requirement. Energy in the diet can be regarded as a fuel source for the body, excess consumption of energy is stored as fat, whilst protein is the material used for lean tissue growth, excess is deaminated and the nitrogen proportion is excreted in the urine. Pigs eat to meet their lysine requirement, so the concentration of lysine in the diet greatly influences the amount of feed a pig will eat; therefore, energy and other nutrients should be in proportion to lysine in order for the pig to meet its daily nutrient requirement and to maximise protein and minimise fat deposition. Protein is energy rich, but when the respective amino acids are used for body protein retention, energy is not released. Therefore, ingested protein only contributes to the available net energy if it is not retained for body protein (Whittemore and Fawcett, 1976). A high-energy diet should have a high concentration of other nutrients, while a lower energy diet could have a reduced concentration of nutrients; but it is impractical in some cases, to lower the concentration of some nutrients, even when the energy concentration of the diet is low.

Figure 2.2 illustrates the relationship between protein and energy according to Cole (1985). At first there is a linear response to protein intake until energy becomes limiting. There is no further response to increasing protein intake until energy intake is increased, thereafter, once energy intake is increased, protein deposition again responds in a linear manner, until energy intake again becomes limiting. Where protein intake is limiting, protein deposition will not increase with additional energy intake (Whittemore and Fawcett, 1976). This indicates that there is a balance between protein and energy, which is affected by factors such as growth phase, sex, environment, genotype, rate of feeding and growth hormones.

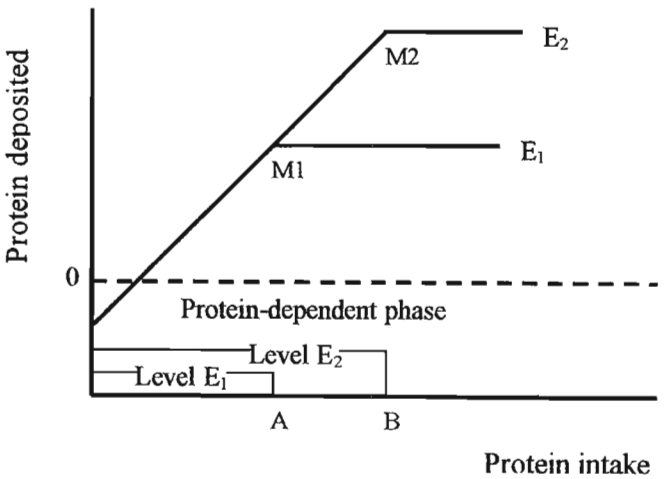

Figure 2.2. *Relationship between protein deposition and protein intake with energy concentration, where A is the protein intake at the first energy level (E_1) and B is the protein intake at the second energy level (E_2), M_1 and M_2 represent the optimum level of protein deposition at energy levels E_1 and E_2, respectively. (Taken from Cole, 1985).*

Kyriazakis and Emmans (1992) suggested that at low levels of protein intake the rate of protein deposition is dependent only on the rate of protein supply, whereas, at high levels of protein intake protein deposition depends only on the energy supply.

2.2 NUTRITIONAL VALUE OF PROTEINS IN PIG DIETS

2.2.1 Quality of protein

Protein quality refers to the amino acid content of the feed ingredient. Feeds that supply the essential amino acids in the correct proportion needed by the pig, supply good quality protein. The more closely a protein conforms, in the balance of its amino acids, to the protein requirements of the animal, the higher its quality or biological value. If any one amino acid is lacking in the correct amount, it will limit the utilization of the other amino acids in the diet (Cunha, 1977). This means that one serious amino acid deficiency will cause the entire diet to be inadequate. Therefore, diets or, more commonly, ingredients that are low in one or more of the essential amino acids, should not be fed alone; otherwise, pigs will make poor use of the protein supplied by that feed in performing the body functions which require protein. For optimum efficiency of lean deposition, all of the constituent amino acids must be available in their correct amounts at the sites of protein synthesis. The essential amino acid that is in least relative supply will determine the rate at which protein synthesis proceeds. The presence of anti-nutritional factors in plant proteins may also decrease the quality of protein supplied to the animal due to these factors decreasing protein digestibility (Sarwar and Sepehr, 2003).

2.2.2 Availability and digestibility of amino acids in feed ingredients

It should be emphasized that amino acid availability and digestibility are not the same. According to the NRC (1998) in most pig diets, a portion of each amino acid that is present is not biologically available to the animal. This is because most proteins are not fully digested and the amino acids are not fully absorbed, and also because not all absorbed amino acids are metabolically available. The ARC (1981) defined available amino acids as the proportions of dietary amino acids, which are digested, absorbed and utilized to sustain life and/or the growth of new tissue. Digestibility, otherwise known as absorbability of amino acids is the amount of amino acid, which is present that is broken down by the digestive process into a suitable form. Most of the amino acids are absorbed in the ileum of the pig. Although a substantial amount of microbial fermentation occurs in the hind gut of pigs, the nitrogenous compounds absorbed are of insufficient nutritive value to the animal (Whittemore, 1993). Batterham (1992) demonstrated that not all the lysine absorbed up to

the distal ileum is completely utilized, probably due to some structural change in the absorbed amino acid molecule.

A review by Meade (1972) stated that severe overheating of protein supplemental feeds results in seriously depressed availability of all amino acids of which lysine appeared to be more heat sensitive than some of the other essential amino acids. In this situation the amino acids were digested, but were unavailable for utilization. Pigs and chickens (monogastrics) have digestive systems that are unable to utilize poor quality protein, heat damaged protein, and significant amounts of fibre as efficiently as ruminants. Although the feed ingredient may be high in protein content, the amino acids may not be available to the animal. An example is lucern meal, which has a relatively high protein content but this protein is unavailable to the pig due to the high fibre content of the feed.

Bioavailability estimates based on animal performance provide relative information on the capacity of a feed ingredient to provide a specific limiting amino acid for maintenance and growth. These estimates differ among feed sources and can be helpful in choosing between alternative food sources. The higher the bioavailability of a particular amino acid in a feed ingredient, the less of that feed ingredient will be required and the less wasted. Different proteins vary with respect to their digestibility. Proteins that have a lower digestibility must be supplied in greater quantities in the diet, to meet the requirements of the animal; however, the efficiency with which protein is utilized may decrease with increasing protein supply. Therefore, reliable prediction of the digestibility of amino acids in different dietary proteins is of great importance in order to prevent the oversupply of protein.

2.2.3 Factors influencing digestibility of proteins in ingredients

Protein digestibility is a useful indicator of feed value but it is greatly affected by both extrinsic and intrinsic factors. These factors are:

a. ***Damage by heat treatment***

   Digestibility is greatly reduced if the proteins, from animal and plant origin, are heat damaged due to overcooking during the production process. Heat damage alters the protein structure and consequently reduces its digestibility. The greater the degree of heating, the higher the loss in digestibility. Specific amino acids may be bound on heating. An example is the binding of lysine to sugar compounds; this

reduces the digestibility and utilization of lysine. If the lysine is unavailable, then the other amino acids in the protein, even though utilizable, cannot be utilized (Whittemore, 1993). Sarwar and Sepehr (2003) conducted an experiment on rats and found that protein digestibility of skim milk powder was significantly reduced by heating in both old and young rats.

b. Anti-nutritional factors

Most, if not all, plant proteins are associated with anti-nutritional factors. For example, tannins which are usually associated with brown sorghum, but are also present in rape seed, sunflower and some bean varieties; disrupt digestion, reduce digestibility and are difficult to destroy. Protease, or specifically trypsin and chymotrypsin, inhibitors act as anti-enzyme factors, reducing protein digestibility in the gut. These anti-enzyme factors are present in raw soya, field beans and potato and can have digestibilities lower than 30% (Whittemore, 1993). Goitrogens, tannins, saponins, gossypols and alkaloids are heat stable, but lectins, protease inhibitors and other poisonous amino acids are destroyed by heat. Heat treatment requires careful control in order to achieve adequate cooking to detoxify but to avoid overcooking and heat damage. The most common method of reducing heat-stable poisons is to breed improved strains of plants not carrying the offensive material (Whittemore, 1993). Proper processing (autoclaving) significantly increased protein digestibility in raw soyabean meal, raw black beans and fava beans (Sarwar and Sepehr, 2003).

c. Rate of passage

High feeding levels of liquid diets of low dry matter based on by-products or liquid waste, reduces protein digestibility by increasing the rate of passage through the intestine, thereby decreasing digestive enzyme activity (Whittemore, 1993).

d. Size of particles in the feed material

Enzymes activity is most efficient if they have a large surface area to act upon. Therefore, large fragments and coarsely ground feed material will decrease digestibility. Grinding , milling , biting or chewing are processes that rupture the cell wall exposing the protein for enzyme attack and thereby increasing protein digestibility (Whittemore, 1993).

e. ***Age of the animal***

Sarwar and Sepehr (2003) found that protein digestibility values as determined in old rats was lower than those obtained in young rats. The possible reason may be due to the under development of the digestive system and the associated enzymes.

These factors should be adequately managed in order to maximize digestibility and hence supply the animal with the required quantities of amino acid.

2.3 BODY COMPOSITION AND POTENTIAL GROWTH

2.3.1 Composition of the body at maturity

The four main chemical components in the pig's body are water, protein, lipid and ash. Only minor amounts of carbohydrates (in the liver) are present. Table 2.3 illustrates the changes that take place in the chemical composition of a pig as it grows and demonstrates the increase in fatness and decrease in water:protein ratio.

Table 2.3. *Changes in the chemical composition of the pig as it grows (g/kg) (Whittemore, 1993).*

	0 days	28 days	100kg		150 kg
			ad. libitum fed	feed-restricted	
Water	770	660	600	680	630
Protein	180	160	150	170	160
Lipid	20	150	220	120	180
Ash	30	30	30	30	30

The change in composition is a result of the growth that occurs through the accretion of bone, fatty tissue and lean tissue in the body. It is best expressed in the form of an allometric relationship $Y= aX^b$ where Y is the component weight, X is the body weight and a and b are growth parameters. Table 2.3 also shows the effect that feed restriction has on the fat content of the body. The fat content is a less stable proportion of the total body than the protein content, which remains relatively constant (Whittemore, 1993).

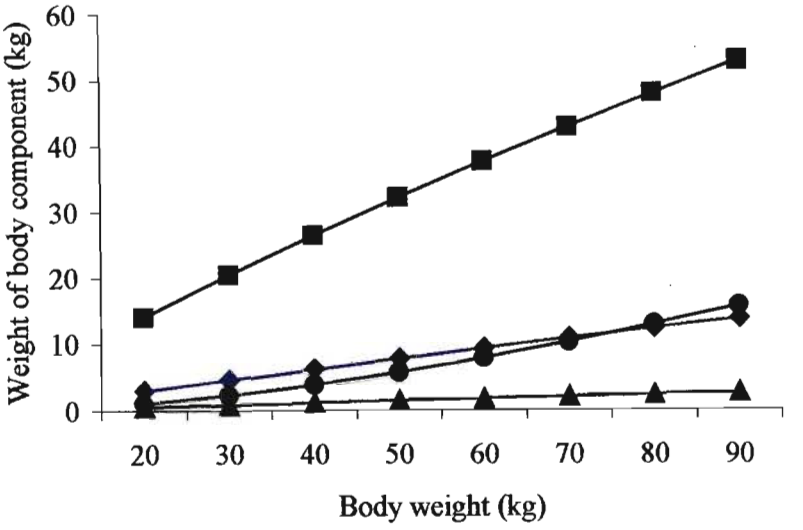

Figure 2.3. *Body component weights (■ moisture; • lipid; ♦ protein; ▲ ash) of ad. libitum-fed pigs (Large White x Landrace entire males) in relation to increases in body weight. Pigs were fed 14.5 MJ/kg energy, 197g/kg crude protein and 13.55g/kg total lysine (the feed was balanced for all required nutrients). The genetic parameters used where:*
Rate of maturing (/d): 0.0107
Mature protein weight (kg): 39.0
Lipid:Protein at maturity: 2.6
(Simulated data from the Pig Model)

Figure 2.3 represents the changes in the chemical composition of the body with the progression of body weight. Notice that there is a relative constancy of the lipid:protein ratio between 20 and 75 kg. The rate at which each of the chemical components varies is dependent on the sex, genotype and the quantity and quality of the feed supplied to the animal.

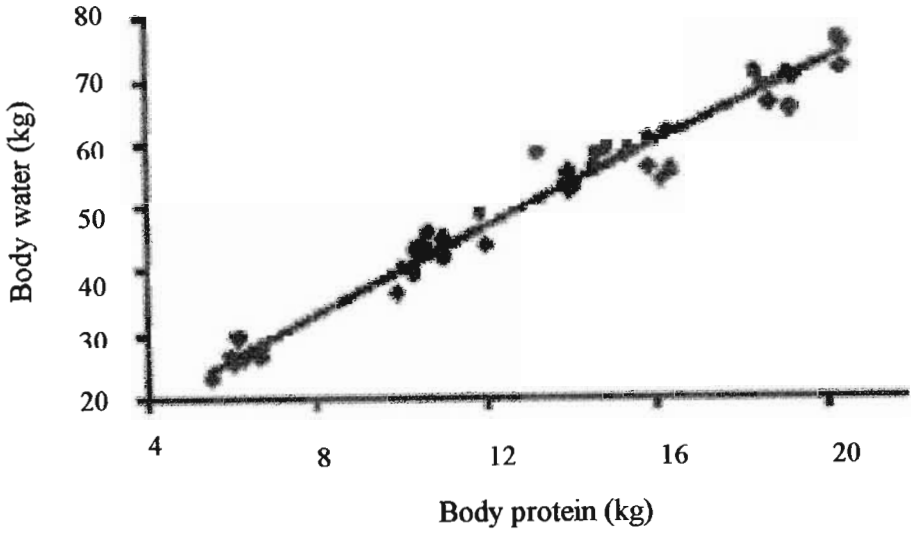

Figure 2.4. *The relationship between body water mass and body protein mass in intact male Yorkshire pigs between 50 and 125 kg body weight. Pigs were offered four energy intake levels ($Y = 5.5513\ X^{0.8592}$; $n = 50$, $r^2 = 0.8912$). (Taken from de Lange et al., 2003).*

Muscle tissue usually contains 700-750 g water / kg (can be as high as 800 g water / kg in young pigs and less than 700 g water / kg in mature animals), 50-150 g lipid / kg and 200-250 g protein / kg. Fatty tissue contains 100-250 g water / kg, 20 g protein / kg and 700-800 g lipid / kg. Due to the allometric relationship that exists between body water and body protein, water can be predicted from protein with reasonable accuracy using the relationship: Wa (kg) = a x P (kg)^b where Wa is body water, P is body protein and a and b are the scaling parameters (Figure 2.4).

This expression allows for the reduction in the amount of water associated with each unit of protein as the animal grows. It also implies that the relationship between water and protein is independent of nutritional factors. Conversely, fat is poorly predicted from either muscle mass or live weight due to the variation in its growth, which is a result of the nutrient supply (the more food consumed, the fatter the pig). However, when the animal is feed-restricted, lipid accretion in relation to lean is much more predictable and may be represented as a stable proportion of protein over much of the growth period. The point at

which fattening begins in the normal growth of the pig is dependent on sex, genotype and feeding level (Whittemore, 1993).

The distribution of the total body protein and body lipid can be manipulated by nutrition and the amount of feed the animal consumes. Bikker (1994) clearly illustrated the effect of nutrition on the composition of protein in the pig's body (Table 2.4). At higher levels of energy intake, the protein content deposited in lean tissue is reduced. Furthermore, the intra-muscular lipid content is increased when feed intake levels are increased.

Table 2.4. *Composition of lean tissue in pigs at approximately 85kg body weight when fed two levels of energy intake (Bikker, 1994).*

	Feeding level	
	2.2 x Maintenance	3.7 x Maintenance
Composition of lean tissue, %		
Protein	20.2	19.1
Lipid	7.9	10.3

The conversion of nutrients, supplied by various feed ingredients, into good quality pork products, includes the relationship between nutrient intake and chemical body composition, and between physical and chemical body composition of growing pigs (Walstra, 1980). The amount of protein deposited and its distribution is what determines the quantity and quality of pork that can be derived from a pig's carcass. The total body protein and body lipid contents are important determinants of the physical carcass characteristics and hence carcass value.

2.3.2 Potential growth

2.3.2.1 Potential protein deposition

Möhn and de Lange (1998) describe the protein deposition (PD), i.e. lean growth, as the gain of the valuable parts of the pig's body. The rate of protein deposition is the gain of body protein with time. The maximum potential protein deposition (PD_{max}) can be defined as the highest possible level at which protein is deposited, it is determined by the genetic

potential of the animal and is influenced by factors such as genetic capacity for growth or environmental conditions (Whittemore and Fawcett, 1974; Black *et al.*, 1986; Moughan *et al.*, 1987; Pomar *et al.*, 1991; de Lange, 1995).

In order to verify that the observed PD is the PD_{max}, it has to be established that the amino acid intake is adequate and that an additional increase, or minor decrease in energy intake, does not alter the PD (van Milgen *et al.*, 2000).

Different nutritional conditions (e.g. a limiting supply of protein or energy) and environmental stresses (e.g. pig density and exposure to disease) can prevent pigs from expressing their true PD_{max}. For example, the data in Figure 2.5 illustrate that the level of amino acid intake sufficient for some pig genotypes will limit the expression of lean growth potential in other improved pig genotypes. In other words, there are very clear interactive effects between dietary protein (lysine) levels and pig genotypes on PD and other aspects of animal performance (Campbell and Taverner, 1988; Stahly *et al.*, 1988; Bikker, 1994).

The idea that environmental stresses can significantly reduce lean growth rate in grower-finisher pigs, is supported by findings from Williams *et al.* (1993) and Dionissopoulos *et al.* (1997). Since it is not yet possible to predict the degree to which the true PD_{max} is reduced due to these stresses, the expression "operational PD_{max}" was introduced. It represents the maximum potential protein deposition that pigs can achieve under practical conditions (de Lange and Schreurs, 1995; Moughan *et al.*, 1995). The operational PD_{max} may differ for a particular pig genotype depending on the environment to which these pigs are exposed.

According to Emmans and Kyriazakis (1999, 2001), the inherent potential for protein deposition rate (dPd) is assumed to follow the derivative of a Gompertz growth function (Equation 2.1)

$$\mathbf{dPd = B \times Pt \times \log_e (Pm/Pt)} \qquad \textit{(2.1)}$$

where B is the mature rate constant, Pm is the mature total body protein and Pt is the body protein mass at a given time .

The potential rate of protein deposition is estimated from two parameters, i.e. B and P_m that is assumed specific to each pig, and from its current protein weight. A suggestion is that compensatory protein growth is inadmissible, any protein deposition below the PD_{max} will decrease the deposition of the other body constituents (lipid, ash and water) and will delay the attainment of the body's mature size. Whittemore and Fawcett (1976) excluded compensatory protein growth when developing a computer model to predict growth responses to nutrient input, based on the hypothesis that the potential rate of protein deposition for a particular genotype at a given protein weight cannot be exceeded, irrespective of the feeding level.

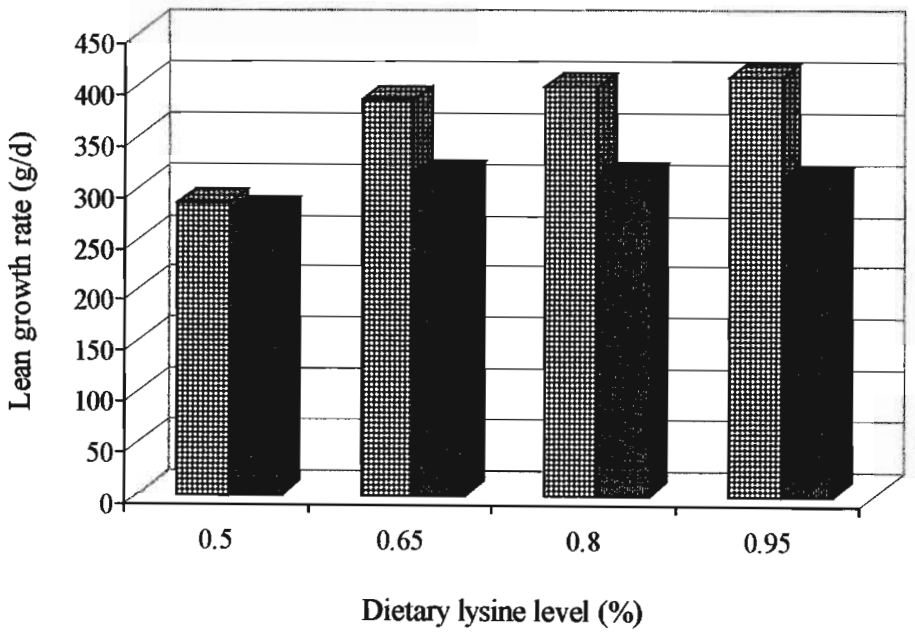

Figure 2.5. *Interactive effects of pig genotype (*solid bars: *high lean, grey bars: medium lean) and dietary lysine level on lean growth rates in pigs (Stahly, 1988).*

2.3.2.2 Target lipid deposition

According to Whittemore (1993), target fat is defined as the minimum level of fatness at which, having achieved that target, the animal feels sufficiently physiologically comfortable to partition available nutrients and to maximize metabolic effort toward the primary aim of reaching the potential for lean tissue growth rate. At levels below the

target, the achievement of target lipid levels will divert from the achievement of potential rates of protein deposition, as the physiological priority would be to restore lipid levels until the target is reached. Whittemore *et al.* (1988) referred to the target level of fatness as a means of explaining the minimum quantity of lipid relative to protein that a growing pig can deposit, because protein gains will be restrained until target levels of fat are achieved. At all times prior to lean-tissue growth rate reaching its maximum potential, the ratio of fat to lean will reflect directly the proportion of fat in the gain which is the target level (Figure 2.6) (Whittemore, 1993).

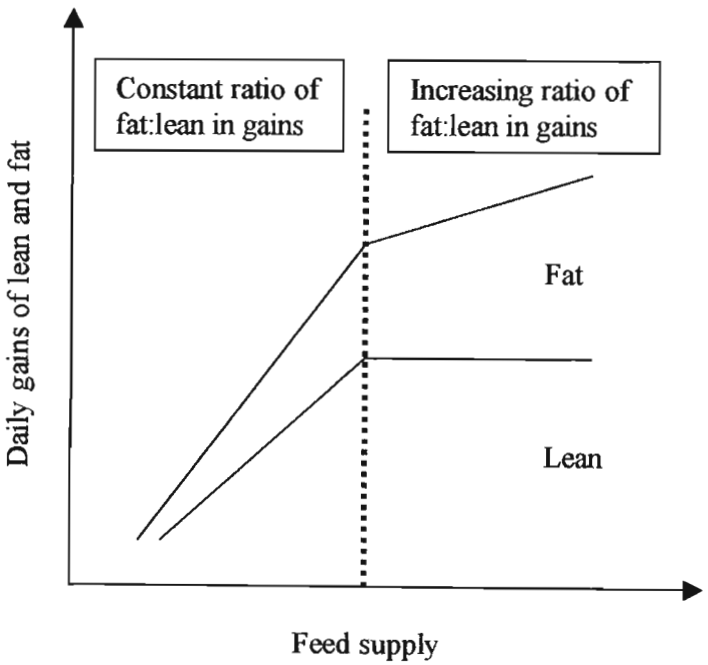

Figure 2.6. *The ratio of lean to fat in gain will tend to be constant until maximum potential lean growth rate is achieved.*

This minimum lipid:lean ratio is highly dependent upon genotype and sex (Whittemore *et al.*, 1988). Genetically fat pigs (for example the Meishan pig) and female pigs will tend always to have lower lean growth rate potentials, higher minimum lipid ratios, or both, compared to a genetically leaner pig (for example the Landrace pig) and intact male pigs. The ability for a pig to achieve its desired normal fatness depends on the quantity and quality of feed ingested by the animal and its capacity to lose heat (Tullis *et al.*, 1986; Kyriazakis *et al.*, 1991).

Fattening usually occurs under the following conditions (Whittemore, 1993):

a. ***When the diet is unbalanced or is deficient in protein (at any pig weight).***
   This can be observed in experiments by Ferguson and Theeruth (2002) in addition to Kyriazakis *et al.* (1991), who deliberately fattened pigs by providing them with a protein-deficient diet during the initial stages of the experiment. These pigs attempted to satisfy their requirements of normal protein deposition by consuming more food. However this resulted in an oversupply of energy and consequently an increase in lipid retention.

b. ***When energy intake exceeds the requirement for protein deposition and maintenance (at any pig weight).***
   Kyriazakis and Emmans (1992) reported that the rate of lipid deposition can be increased by increasing the level of feeding, and hence, energy intake. Table 2.5 illustrates the effect of energy intake on the rate of fat deposition in male and female pigs.

Table 2.5. *Effect of energy intake between 48 and 90 kg on the rate of lipid deposition in male (M) and female (F) pigs (Campbell et al., 1985).*

		Energy intake (Mcal DE/d)			
		5.39	6.31	7.57	8.60
Body lipid	M	203	249	257	315
(g/kg)	F	293	332	353	368

These conditions indicate that fatness can be effortlessly controlled because the association between pig fatness and pig weight is not primarily a function of weight itself but a function of feed intake. Feed intake control determines the attainment of any required level of fat at any required carcass weight. The literature states that if an animal has been previously fattened (Ferguson and Theeruth, 2002) or feed-restricted (Stamataris *et al.*, 1991) for a period of time, the animal will return to a state that is consistent with that of a non-limited animal, when provided with a diet adequate in protein and energy.

2.4 DEVIATIONS FROM POTENTIAL GROWTH

2.4.1 Effects of underfeeding

There are two types of underfeeding:

a. Where the animal is supplied with a carefully balanced ration, but not enough of that ration is provided to the animal. If a pig does not get enough feed, it is guaranteed to lack energy, as well as protein, minerals, and vitamins (Cunha, 1977) as a result the animal will fail to achieve its potential for growth.
b. Using unbalanced diets is another form of underfeeding. Diets that do not supply the required levels of protein, energy and other nutrients, but that are fed *ad libitum*, result in the animal not attaining its potential for growth.

A growing animal that has been given *ad libitum* access to an unbalanced feed or has had its intake restricted for a period of time, will usually have a lower protein weight; it lipid weight may be lower or higher than that of a similar pig treated in a non-limiting way at the same protein weight. Campbell (1977) and Kyriazakis (1989) fed pigs a diet deficient in crude protein and found that these pigs had a reduced growth rate, the length of time and quantity food needed to reach a given weight were both increased and the fatness at that weight were greater than normal. At the end of such a period of underfeeding, the pig is therefore older, fatter and has lower protein stores than it would have on a balanced diet at the same weight (Tullis, 1981). Similar results were obtained by Kyriazakis and Emmans (1991), Ferguson and Gous (1997), Ferguson *et al.* (2000) and Ferguson and Theeruth (2002).

Cole *et al.* (1968) and Owen *et al.* (1971) subjected pigs to a period of feed restriction found that these pigs had reduced growth rates and the degree of fatness at the end of the period of feed restriction was less than normal. According to Pàlsson and Vergés (1952) and Elsley *et al.* (1964) the food processing organs would also be less developed in relation to the growth of the remaining lipid-free empty body, since these animals are able to show a truly adaptive ability to grow these organs at a slower rate than the rest of the lipid-free empty body when food is scarce. These results correspond with results by Stamataris *et al.* (1991), where the restricted pigs had a lower lipid:protein ratio, which reflected their smaller lipid stores, and they had less gut fill, which reflected their reduced

growth of the food processing organs. Prince *et al.* (1983) restricted growing pigs to 70% and 85% of *ad libitum* fed pigs. They found that the average daily gains during the restriction period were decreased for the restricted pigs and that pigs fed 70% *ad libitum* grew slower than those fed the 85% level. There were no significant differences in feed efficiency but the restricted pigs were more efficient than the *ad libitum* fed pigs (2.48 vs 2.59).

The severity and the duration of the period of underfeeding, will determine whether the animal is capable of achieving its potential growth when the cause of the retardation is removed. This phenomenon is discussed in a later section entitled compensatory growth.

2.4.2 Physical and environmental constraints

2.4.2.1 Gut capacity

Animal appetite is the desire for nutrients expressed in terms of feed intake (Whittemore, 1993). By definition it is a function of the pig's requirements for nutrients, and is reduced by various constraints imposed on the animal (Black et al., 1986; Emmans & Kyriazakis, 1989). These constraints relate to diet characteristics (bulk density, nature and rate of digestion of fiber, water holding capacity, nutrient and anti-nutrient contents) and the pig's physical capacity of the gut, i.e. gut size together with the rate of passage of feed along it.

Whittemore (1993) explains that gut size is a more important variable than rate of passage; because the rate of outflow is relatively constant for much of the total dry matter moved and is not greatly affected by the absolute amount of feed ingested. Therefore gut size is the most important factor controlling the physical limits of feed intake in the pig, and it may be confidently believed that the physical limits to feed intake is related to some function of body weight.

According to Black *et al.* (1986) the pig's physical capacity to ingest feed (gut fill) is likely to limit performance in growing pigs up to approximately 40 kg body weight. In these pigs, an increase in the nutrient density of the diet will consequently not affect feed intake but it will increase the daily nutrient intake. At body weights higher than approximately 40 kg, the daily energy intake is more likely to determine feed intake; in this situation pigs tend to

compensate for changes in diet energy content with changes in feed intake in such a manner that the daily energy intake is constant.

Stamataris *et al.* (1991) found that pigs that were feed restricted had less gut fill and lower weights of the food processing organs that were appropriate to the imposed rate of feed intake of 300g/day. This reflected the adaptive ability of the animals to grow their food processing organs at a slower rate than the rest of the lipid-free empty body when food is scarce (Pàlsson and Vergés, 1952 and Elsley *et al.*, 1964). When these animals are realimentated, to be able to process the greatly increased intake they would need to expand their gut capacity rapidly, this can be achieved by providing the animal with a bulkier diet. The greatly increased daily feed intake would lead to a substantial increase in gut fill, which would be seen as an increase in live weight (Thornton *et al.*, 1979).

The ability of the pig to adjust appetite in response to progressive decreases in diet nutrient density (especially energy) has its limits when ultimate gut capacity is reached. A solution to the problem of reduced performance when pigs have maximised their gut fill but failed to maximise their productivity due to inadequate energy intake, is to supplement the diet with fats and oils which provide maximum energy for minimal diet space.

2.4.2.2 Heat loss

A high ambient temperature is just one of the environmental factors that affect the animals' expression of lean growth potential, as well as the relationship between energy intake and lean growth, by reducing feed intake in pigs. The reduction in feed intake is not constant and heavier pigs appear more sensitive to high temperatures than smaller pigs (Quiniou *et al.*, 2000). Growing pigs typically do not need energy as heat. In most situations, the heat that is released as a result of ATP utilization (i.e., maintenance) or as inefficiencies of growth will be sufficient to maintain a constant body temperature. The animal will use a greater proportion of energy intake to maintain body temperature as the temperature declines or heat loss increases. If the use of this 'waste heat' is inadequate to sustain body temperature, energy has to be diverted from growth to generate heat (or pigs have to eat more). This also implies that heat production becomes an essential process to maintain body temperature. The heat that is considered a loss under thermoneutral conditions then becomes a useful 'product'.

Consumed nutrients that have been used for metabolic work, together with energy not deposited in products, are actively lost as heat (Whittemore, 1993). This heat must be dissipated if stress and rise in body temperature are to be avoided. The literature states that feed, which has a high heat increment, such as protein and fiber, can be used with a greater efficiency (for thermogenesis) under cold conditions (Quiniou *et al.*, 2001), however, these feeds may potentially limit growth in a situation where the heat release by the animal is impaired (e.g., under heat stress). Le Bellego *et al.* (2001) demonstrated that the decline in Net Energy (NE) intake resulting from exposure to high ambient temperature was less significant for low heat increment diets than for standard diets.

As the lean growth potential in pigs increases, pigs are more prone to heat stress. There is more heat production associated with protein deposition (Pd) than with lipid deposition (Ld), therefore, pigs with high lean growth potentials will perform better when environmental temperatures are reduced (towards the low end of the thermoneutral zone), in addition, the more productive the pig, the greater its nutrient need, and consequently the greater the need to lose heat (Whittemore, 1993). It is noteworthy that animals realimented on high protein diets will dissipate more heat. This concept is supported by Ferrell (1988) who found that the heat loss associated with maintenance requirement may increase in pigs offered diets high in amino acids. If environmental temperature is too high, then feed intake will not be maximized. It was thought that the feed intake of the pigs in this particular experiment may have been limited by the ambient temperature (22°C).

2.5 COMPENSATORY GROWTH

Compensatory growth is the catch-up growth that follows a period of feed nutrient restriction imposed by either physical feed restriction or the feeding of diets very low in nutrient density.

The ability of animals to compensate for prior under-nutrition is affected by:

a. *The length and severity of the period of undernutrition*

   During the period of undernutrition the animal is usually fed above or below maintenance energy requirements or a low dietary protein level. Kyriazakis *et al.* (1991) demonstrated a situation where the restriction imposed was not too severe to prevent compensatory growth from occurring. They conducted trials on weaning

pigs using diets with low (L, 16% CP), medium (M, 27% CP) and high (H, 40% CP) levels of protein but with constant digestible energy content. The L diet was formulated to be deficient in protein and would therefore limit the animal from attaining its potential growth. According to the NRC (1988) pigs from 5-10kg require 20% CP. It was concluded that when pigs were given the L diet they had reduced protein stores, but when realimentated with a high protein diet they replenished those protein stores very rapidly. As the stores contain water as well as protein the repletion is seen as rapid compensatory gain in live weight. On the contrary Prince *et al.* (1983) restricted pigs to 70% or 85% of *ad libitum* intake for either 2 or 4 weeks. It was found that those restricted to 85% for 4 weeks performed the best whereas those restricted to 70% for 4 weeks were unable to fully compensate. This suggests that the restriction was either too severe and/or too prolonged. Upon realimentation, the pigs restricted to 70% for 2 weeks showed average daily gains and feed conversion efficiencies similar to the control and the pigs restricted to 85%. If the period of undernutrition is severe enough then the previously-restricted pig will only completely recover lost production if fed for a longer period, otherwise for a given age the pig will be slaughtered at a lighter weight. Many studies (Plavnik & Hurwitz, 1991 and McMurthry *et al.*, 1988) have shown that complete compensation is possible provided the restriction is not too severe.

b. *The stage of development (relative to maturity) of the animal*

Undernutrition in the earlier stages of growth is more detrimental to the animal than restriction at a later stage (Wilson & Osbourn, 1960). With previous research (Wahlstrom & Libal, 1983; Prince *et al.*, 1983), the body weight at which feed restriction is usually applied is between 15-25kg. Stamataris *et al.* (1985) restricted pigs to300 g/d of feed over the range of 6-12kg live weight. Once the pigs were realimentated, they were found to exhibit compensatory growth. However, the restricted pigs took 19.1 days longer than the *ad libitum*-fed pigs, to reach 12kg. At the end of the realimentation phase, the restricted pigs took 5.5 days less to reach 24kg (from 12kg), than the pigs fed *ad libitum*. Although compensatory growth did occur in this experiment, the time lost in growth during the period of restriction could not be regained. This suggests that the restriction was imposed at too early an age causing a deficit from which the pigs could not recover.

c. *Genotype and sex*

de Greef *et al.* (1992) found that two strains of pigs responded similarly to realimentation. The two strains had different ratios of fat to lean deposition rates during restriction and realimentation, however, at 105 kg live weight the body composition for the two strains was similar. The partitioning of energy and other nutrients into protein and lipid tissues changed with live weight and was different for the two strains of pigs, emphasizing the importance of designing feeding strategies for different genotypes (de Greef *et al.*, 1992). McMurtry *et al.* (1988) and Plavnik & Hurwitz (1991) demonstrated how male broiler chickens have a greater ability to exhibit compensatory growth than females. This is likely due to the higher natural rate of growth of male broilers and their lower deposition rate of body fat (Fisher, 1984).

d. *Level of feed intake during re-alimentation*

Increases in feed intake and daily gain after a period of feed-restriction have been reported by many researchers (Ratcliffe & Fowler, 1980 and Stamataris *et al.*, 1991). Contrary to this, de Greef *et al.* (1992) found that pigs fed low protein diets had reduced feed intakes during the restriction period, which carried over into the realimentation phase. Similar results were obtained by Pond & Mersmann (1990). According to Stamataris *et al.* (1991), previously-restricted pigs would increase their feed intake, when realimentated, in order to attain their potential growth rate and to attempt to eliminate their lipid deficit.

e. *Diet nutrient content during re-alimentation*

The quality and quantity of the diet eaten during the realimentation period has a significant effect on the ability of an animal to demonstrate compensatory growth (Yu and Robinson, 1992). Kyriazakis *et al.* (1991) found that pigs previously fed a low protein diet and then realimentated with a diet sufficiently high in protein, showed a substantial increase in growth rate. However, when pigs were offered a low protein diet free-choice, they were found to have less protein and a lipid excess compared to the pigs fed a diet adequate in protein. Ferguson & Theeruth (2002) found no significant differences in average daily gain for pigs fed a high or medium protein feed after a period of fattening. The lipid: protein ratio decreased, for pigs

fed high protein after a period of fattening, to a similar level as to those fed high protein throughout.

Figure 2.7 illustrates the theory used by Emmans & Kyriazakis (1989) to describe how body composition changes according to the way in which the pig is fed, always attempting to return to the desired, or genetically-determined lipid:protein ratio.

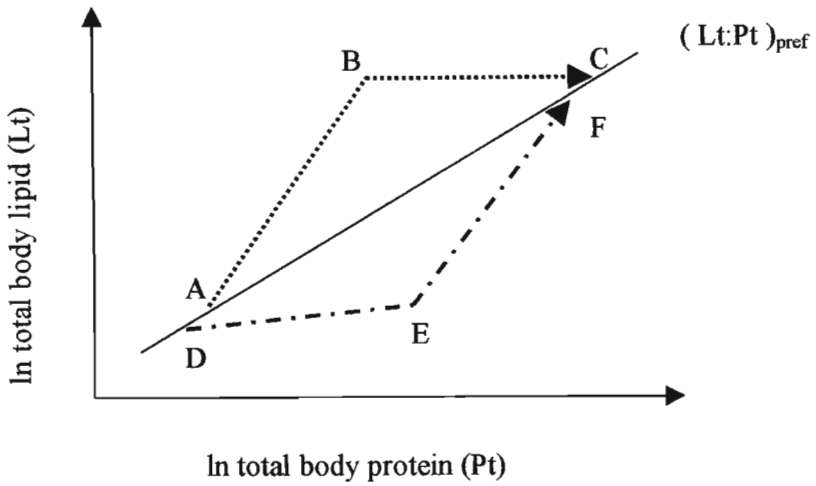

Figure 2.7. *The influence of prior feeding on body compositional changes, where A and D represent the start of the period of underfeeding with a low protein diet and feed restriction, respectively, B and E represent the point of feed change to a high protein diet fed ad. Libitum, C and F represent the points of achieving the preferred lipid: protein ratio ($(Lt: Pt)_{pref}$).*

From point A to B, the animal is offered a low protein feed, and as a result the animal gains excess lipid due to the over-consumption of energy.

From B to C, the realimentation period, during which the animal is fed a diet higher in protein, the animal decreases lipid retention and increases protein deposition. The excess lipid may be used to provide energy for protein deposition.

From point D to E, feed intake is quantitatively restricted e.g. 70% of the *ad libitum* intake, and as a result the animal deposits insufficient lipid.

From E to F, again a realimentation period, the animal is fed ad libitum and body lipid content returns to the desired level.

If the theory of Emmans (1981) is correct, then the pig will always attempt to revert to its desired, or genetically-determined ratio of lipid: protein, which means that the pig will respond differently to a feed depending on its state when the feed is introduced: a pig with excess lipid reserves will utilize these reserves as an energy source, where possible, and in so doing would make more efficient use of a high protein feed than would a pig that had no such reserves, thus having to consume more of the feed to obtain sufficient energy.

Where nutrient restriction is so severe that body protein gain is reduced, then during realimentation the pig may attempt to increase protein deposition in an attempt to compensate for the deficiency. However, the potential rate of protein deposition for a given genotype at a given body protein content cannot be exceeded, irrespective of the feeding level (Whittemore & Fawcett, 1976), so the protein gain can never be sufficient to enable the pig to 'catch-up' to its adequately-fed counterparts. It would be possible, however, for the pig to make up the deficiency in lipid reserves by consuming more food.

2.6 THE NEED FOR FURTHER RESEARCH

The aim of this chapter was to review the literature pertaining to the factors that influence the efficiency of protein utilization and the rates of lipid deposition and withdrawal in growing pigs.

According to the literature one of the major factors influencing the productivity of growing pigs is the nutrition of the animal, particularly the protein and energy content of the feed. Previous research has shown the influence of under-feeding growing pigs by either imposing feed restriction for a period of time or feeding the animal an unbalanced diet with respect to protein content, on performance characteristics and body composition.

It is evident that the ability of growing pigs to achieve their genetic potential depends to a large degree on the quality and quantity of the feed offered. In attempting to meet these requirements, nutritionists generally provide feeds of which the protein (amino acid) contents decrease over time, to match the changing requirements of the pig as it grows.

But such a practice (phase feeding) necessarily results in periods of under- and over-supply of essential amino acids, and the way in which the pig responds to such feeding is of considerable interest when modelling the food intake and growth of a pig. During periods when the amino acid supply is below the requirement, which could be regarded as being a period of nutritional limitation, the pig over-consumes energy in an attempt to obtain the required amount of amino acid to sustain growth (Emmans & Kyriazakis, 1989). Such periods of under-supply are followed by periods in which the amino acids are in excess of requirement, such that the amount of food that the pig would need to consume would be dependent on its energy requirement. If excess energy, in the form of body lipid, is available for such purposes, the amount of food consumed could be considerably reduced, depending on the amount of protein in the feed and the amount of excess lipid in the body. By drawing on these lipid reserves the pig would make very efficient use of the feed on offer, and possibly overcome the inefficiency of overconsuming energy during the period of under-supply of protein.

Much of the research reviewed above centered on the ability of growing pigs to compensate in growth following a period of nutritional limitation. However, information is lacking on how the state of the animal on a given day influences the efficiency with which the pig utilizes the food on offer. This information is of considerable interest when modelling the food intake and growth of pigs as accurately as possible, so that efficient feeding programmes may be developed for growing pigs, considering both biological and economic aspects of the production process. The two trials reported here attempt to address some of these issues.

CHAPTER 3

THE INFLUENCE OF PRIOR FEEDING ON THE EFFICIENCY OF PROTEIN UTILIZATION IN GROWING PIGS

3.1. INTRODUCTION

The rate at which growing pigs grow, and the body composition of growth, is determined in a large part by their intakes of protein and energy. It is logical to assume that when an animal is placed under non-limiting conditions, it is able to achieve its potential growth rate, considered to be normal growth, but when these animals are placed under nutritional limitation, either by being given an unbalanced feed or having their feed intake restricted, they will fail to grow as fast as they can, their body gain will be of abnormal composition, or both (Kyriazakis & Emmans, 1991).

Whittemore & Fawcett (1976) proposed that dietary protein would be preferentially used for protein deposition, unless energy availability or other factors (genotype or environment) became limiting. The key assumption is that, where protein intake is limiting, protein deposition rate will not increase with additional energy intake. The consequence of growth limitation following a period of inadequate nutrition is that the protein weight may be less than the potential or the lipid weight may be lower or higher than that of a similar pig treated in a non-limiting way at the same protein weight.

Various authors have reported that the rate of protein gain, in previously feed- restricted pigs, would increase immediately after the non-limiting conditions were restored (Robinson, 1964; Cole, Duckworth, Holmes & Cuthbertson, 1968; Tullis, 1981). They suggested that the animal was able to regain a proportion of the lost protein growth. Ferguson & Theeruth (2002) reported that previously fattened pigs would attempt to rectify their lipid to protein ratio by reducing their rate of lipid retention when the cause of the fattening is eliminated. Kyriazakis *et al.* (1991) also reported that pigs fed a diet low in protein content would result in a reduced protein:ash and an increased lipid:ash ratio in the body, but when these pigs are given a diet sufficient in protein content the protein:ash and lipid:ash ratios return to normal.

The literature indicates (Kyriazakis *et al.*, 1991) that when previously mis-fed pigs were given *ad libitum* access to an unbalanced diet they would be able to return to normal growth provided non-limiting conditions were removed, but evidence is lacking on how efficient previously fattened and previously restricted animals are at utilizing the protein provided during phase 2 and how the composition of the body is affected depending on the quality and quantity of the diet fed prior to phase 2.

The aim of the experiment reported here was to produce three groups of pigs at the same protein weight but differing in lipid content, then to compare the efficiencies with which these pigs utilized dietary protein during a two-week period (phase 2), the objective being to determine whether the initial state of the animal would influence its subsequent ability to utilize dietary protein.

3.2 MATERIALS AND METHODS

3.2.1 Animal Description

Fifty-two crossbred Large White x Landrace entire males were obtained at eight weeks of age and housed in individual pens. On arrival, four pigs were randomly selected for slaughter at 20kg live weight to provide the chemical composition of the empty body weight (EBW) at the start of the experiment. The remaining 49 pigs were fed a commercial pig grower until they reached 20kg live weight, at which time they were randomly assigned to one of three dietary treatments.

3.2.2 Trial Facilities

The trial took place at Ukulinga research farm. The pigs were placed in individual pens (48 individual pens), and one pig was placed in an outside pen, for a period of two weeks. Each pen contained two plastic self-feeding bins (Big Dutchman ®) and a nipple drinker. The outside pen contained one large plastic feed bin (Big Dutchman ®) in the center of the pen with 2 nipple drinkers and 2 food dispensers, activated by touch. An additional nipple drinker was provided on the side of the pen. These facilities allowed for free and continuous access to food and water for all pigs. The house contained light timers, which were set at 16L: 8D (16 hours light and 8 hours darkness). The pigs were weighed weekly

and the food was checked daily. Food weighed in was recorded and each time a pig was removed from the pen the food remaining in the feeder was weighed.

3.2.3 Design of the experiment

Two feeds were formulated to contain similar energy contents but with one having a higher crude protein (CP) content than the other (Table 3.1). The high CP diet (HP) was formulated to supply CP in excess of the requirement during the period 20 to 45 kg live weight while the low CP (LP) was to be deficient in protein. The objective was to create three groups of pigs with the same protein weight but with different body lipid weights. Pigs fed LP *ad libitum* were expected to have the highest body lipid contents; pigs fed HP *ad libitum* were assumed to have the desired (or normal) lipid contents, indicative of their genetic potential; and the third group (FR), fed restricted amounts of HP each day, were expected to have the lowest lipid content. Estimates of CP requirements were based on the dietary protein concentration (200g/kg) that produced the optimum response from previous studies conducted with this genotype (Ferguson & Gous, 1997; Ferguson *et al.*, 2000; Ferguson *et al.*, 2001). Dietary amino acids were balanced according to the ideal protein balance, with lysine as the reference amino acid (Wang & Fuller, 1989). All foods were intended to be non-limiting in minerals and vitamins.

At the start of phase 1 of the experiment (when pigs were 20 kg live weight), all pigs were ear-tagged, and then 19 pigs were allocated to the LP treatment, 11 to HP and 19 to FR. For the first three days of the trial the feed intake of all pigs receiving HP was monitored, and for each of the remaining four days of that week, pigs on FR received 0.70 of the mean daily *ad libitum* intake measured over the previous three days. Thereafter, these pigs received 0.70 of the food consumed by the *ad libitum*-fed pigs during the previous week. Food intake by the *ad libitum*-fed pigs on HP was monitored weekly in order to determine the feed allocation (for each week) for the restricted pigs.

Phase 1 ended when the pigs from each treatment reached a protein weight of approximately 5.9kg. The body weights at which the pigs on each of the three treatments were expected to reach this protein weight were estimated, by means of the EFG Pig Growth Model, to be 39 kg (in approximately 66 d), 35 kg (34 d) and 34 kg (50 d) for LP, HP and FR, respectively. The mature body protein weight of the simulated genotype was

33 kg, the rate of maturing was 0.0125 /d and the lipid: protein ratio at maturity was 6 g/g. The growth and food intake of this genotype was simulated using the two feeds and three feeding programs applied in phase 1. Three pigs were randomly selected from each treatment, before the start of the experiment, to be slaughtered once they reached their respective target body weights at the end of phase 1 (Figure 3.1).

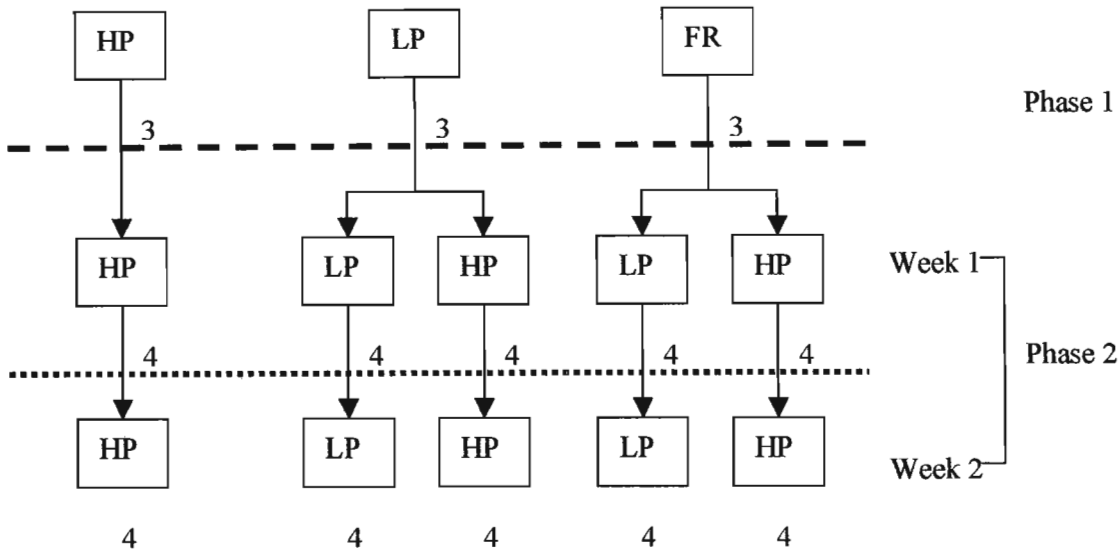

Figure 3.1. *Diagrammatic representation of the treatments imposed during Phases 1 and 2 of the trial (where HP is high protein, LP is low protein and FR is feed restriction), and the number of pigs slaughtered from each treatment at the end of Phase 1 and after 1 and 2 weeks of Phase 2.*

In Phase 2, eight of the remaining pigs fed LP in Phase 1 were placed on HP while the rest remained on LP. The pigs initially on HP remained on HP. Eight of the FR pigs in Phase 1 were placed on LP for Phase 2, while eight continued on HP. All pigs feed-restricted in Phase 1 were given *ad libitum* access to food in Phase 2. Pigs were then slaughtered at weekly intervals, four pigs from each treatment at the end of the first week, and the remaining pigs at the end of the second week (Figure 3.1), also according to a pre-determined schedule.

3.2.4 Feed Ingredients and Composition

The ingredients and chemical composition (g/kg fresh weight) of the high (HP) and low (LP) protein feeds offered in Phases 1 and 2 are given in Table 3.1.

Table 3.1. *The ingredients and chemical composition (g/kg fresh weight) of high (HP) and low (LP) protein feeds offered in Phases 1 and 2.*

	Feeds	
Ingredient	HP	LP
Yellow maize	553	687
Maize gluten 60	23.6	12.3
Soya bean meal	115	
Full fat soya	250	250
Limestone	10.8	10.6
Monocalcium phosphate	30.0	32.2
Salt	2.50	2.50
Vit and Min Premix	5.00	5.00
dL-methionine	2.53	
l-Threonine	2.25	
Tryptophan	0.32	
l-Lysine HCl	4.79	0.380
Analyzed Composition:		
DE (MJ/kg)[1]	14.5	14.5
CP (Nx6.25) (g/kg)	197	166
Total lysine (g/kg)	13.6	8.09

[1] Calculated as 3.8 - 0.019 NDF[a] + 0.76 GE[b] (Morgan *et al.*, 1984)

[a] NDF = Neutral detergent fibre

[b] GE = Gross energy

3.2.4 Slaughter Procedure

Four pigs were killed by injection of sodium pentobarbital once they had reached 20kg live weight, to determine the initial carcass composition of the pigs prior to being placed on the dietary treatments in Phase 1. The carcasses were then placed in a plastic bag and sealed to chill at 0°C overnight. The stomach and intestines were then removed and weighed full,

stripped of their contents and weighed empty. The empty stomach and intestines were added to the carcass weight to provide an estimate of the empty body weight. The viscera and carcass was cut into smaller pieces and placed into a mincer, homogenized and sub-sampled for chemical analysis. The remaining 49 pigs were killed by exsanguination at the commercial abattoir when they had attained their respective slaughter weights. After stunning, the blood from each pig was collected in two-liter plastic buckets. The pigs were eviscerated and the gastrointestinal tract, bladder, heart, liver and lungs were removed. Each empty carcass was then halved along the midline, with the right half of the carcass chosen for further analysis. The half carcass, organs and blood were stored overnight at 0^0C in a sealed plastic bag. The half-carcass was then portioned and together with the empty gastrointestinal tract, remaining organs and blood, was stored in a sealed plastic bag and frozen at -20^0C. The combined organs and blood were homogenized and then halved by weight. The frozen carcass portions and half the combined blood and organs were homogenized together in a mincer. Two samples were collected (in 500g containers) from each homogenate and submitted to the laboratory for proximate analysis according to AOAC (1984) methods, except for lipid, which was calculated from gross energy and protein content according to the method described by Ferguson *et al.* (2000) (Equation 3.1).

$$\textbf{Lipid} = (2.410 \times \textbf{GE}) - (0.5898 \times \textbf{protein}) \text{ [g/kg DM]} \qquad \textit{(3.1)}$$

where GE is the carcass gross energy expressed in MJ/kg DM and protein is the carcass protein content expressed in g/kg DM.

The duplicated results were averaged to provide a single result for each pig. The dry matter content of each sample was determined by freeze-drying the samples for 48 hours. The CP content was calculated as nitrogen x 6.25, where nitrogen content of the dry matter was determined on a LECO nitrogen analyzer (LECO Africa (Pty) Limited, P.O. Box 1439, Kempton Park, South Africa). The rates of retention were determined by subtracting the component weight at 20 kg from the final component weight and dividing by the time taken to grow between the two weights. Gross energy of the dry matter was determined by adiabatic bomb calorimetry.

3.2.5 Statistical analysis

During the initial phase the body weights and food intakes of all pigs from each treatment were pooled to determine the mean body weight and food intake for each treatment. The same was done for both weeks of phase 2, with the mean body weights and food intakes of the remaining pigs on trial, for each treatment, being used to calculate the required parameters. Carcass protein and lipid gains were calculated for each treatment and period using the mean carcass composition of all pigs sampled, from the given treatment at the appropriate slaughter periods, and the mean body weights of all pigs on that treatment. All results were then analyzed using the general analysis of variance in Genstat (1997) with dietary treatments as factors.

3.3 RESULTS

Phase 1 (from 20 kg Body Weight to 5.9 kg Protein Weight)

During the depletion phase, pigs receiving HP grew faster ($P<0.01$) and more efficiently ($P<0.01$) than those that received LP and those that were restricted. Pigs fed LP took more time ($P<0.01$) to reach 5.9 kg body protein (BP) than pigs fed HP or FR. Feed intakes were significantly higher ($P<0.01$) for pigs on LP than on HP. The pigs receiving HP and LP had greater water contents ($P<0.05$) than pigs on FR. There were no significant differences between the protein or lipid contents of pigs on the three treatments; however, pigs on LP tended to have a higher lipid content than pigs on HP or FR (Table 3.2).

Table 3.2. *Growth performance during, and body weight (BW) and body composition at the end of phase 1 (20kg BW to 5.9kg body protein) of the trial.*

Parameters	Dietary Treatment			RMS[d]	SED[e]
	HP[a] *ad lib.*	LP[b] *ad lib.*	FR Restricted[c]		
n	11	19	19		
BW, kg[f]	37	38	35	1.80	0.508
Days to reach 5.9kg BP[g]	24	38	30	591	8.11
ADG, g/d[f]	734	546	470	1278757	63.2
ADFI, kg/d[f]	1.53	1.64	1.04	2.25	0.084
FCE, g gain/kg intake[f]	471	348	455	350100	33.1
Body composition, kg					
Water	26.4	26.4	24.3	478	0.564
Protein	5.74	5.97	5.97	21.6	0.120
Lipid	3.15	3.74	3.056	314	0.458
Body composition, g/kg					
Water	713	694	693	371	15.7
Protein	155	157	171	15.4	3.20
Lipid	85.1	98.3	87.3	243	12.7

BP: Body protein

ADG: Average daily gain

ADFI: Average daily feed intake

FCE: Feed conversion efficiency

[a]*197g CP/kg.*

[b]*166g CP/kg.*

[c]Pigs were restricted to 0.70 of the feed intake of those pigs fed HP *ad libitum.*

[d]Residual mean square.

[e]Standard error of differences.

[f]Means within a row differed significantly ($P<0.01$).

[g]Days to reach 5.9 kg body protein.

Phase 2

Throughout phase 2, the previously-restricted pigs grew faster ($P<0.05$) and consumed significantly more feed ($P<0.01$) than the pigs fed LP or HP *ad libitum* throughout the trial (Table 3.3). The pigs previously on FR, and then placed on HP, had the greatest water ($P<0.01$) and protein gains ($P<0.05$) for week 1 and the highest water gains ($P<0.05$)

throughout phase 2. Average daily lipid gains during week 1 were highest ($P<0.01$) for pigs on LP in both phases, followed by those pigs that were fed LP in phase 1 and HP in Phase 2 (Table 3.5). For the first week of the second phase, the protein content of pigs fed HP throughout both phases was the highest ($P< 0.05$), while the greatest lipid contents were measured in those pigs fed LP in both phases and in those that were fed LP and then HP. The water content was highest ($P<0.01$) in the pigs on FR in phase 1 and then placed on HP. During the second week of phase 2, the pigs fed HP throughout had the highest protein ($P=0.05$) and water ($P<0.01$) contents, compared with pigs on all the other treatments. Pigs fed LP in both phases had the highest ($P<0.05$) lipid content in the second week of phase 2 (Table 3.4).

Pigs on FR in Phase 1 and then fed HP in phase 2 consumed the greatest amount of protein during week 1 ($P<0.01$) and over the entire second phase ($P<0.01$). There were no significant differences in protein intake during week 2 of phase 2 (Table 3.6).

Table 3.7 illustrates the efficiency with which pigs utilized dietary protein, during phase 2. Although there were no significant differences observed, the highest efficiency of protein utilization was achieved by the pigs fed LP-HP (642g/kg), during the first week. However, during week 2 and throughout phase 2, pigs fed LP-LP had the highest protein efficiencies (336g/kg and 461g/kg, respectively). Pigs previously feed-restricted utilized protein less efficiently than those fed LP-LP, HP-HP and LP-HP, overall phase 2.

Table 3.3. *Average daily gain (ADG, g/d), average daily feed intake (ADFI, kg/d) and feed conversion efficiency (FCE, g gain/kg feed) of pigs at the end of the 1st and 2nd weeks, and over both weeks of phase 2.*

	Week 1			Week 2			Week 1 + 2		
Treatment[a]	ADG	ADFI	FCE	ADG	ADFI	FCE	ADG	ADFI	FCE
HP-HP	944	1.71	569	616	1.76	340	835	1.72	493
FR-HP	1434	2.45	585	937	2.66	359	1268	2.52	510
LP-HP	875	1.92	433	852	2.203	379	870	2.01	415
LP-LP	1082	2.24	475	896	2.54	359	1020	2.34	436
FR-LP	1230	2.30	542	1071	2.70	407	1177	2.43	497
RMS[b]	6.43[b]	5.025	1.95[b]	1.57[b]	2.41	0.273[b]	9.12[b]	8.45	2.59[b]
SED[c]	214	0.190	118	229	0.283	95.5	166	0.160	88.6

HP: High protein

FR: Feed restriction

LP: Low protein

[a] Pigs were fed HP or LP *ad libitum* in the two weeks following a period in which they were subjected to one of three feeding treatments (LP, HP or FR).

[b] Residual mean square, x 10^6

[c] Standard error of differences of means.

Table 3.4. *Chemical composition of pigs on five dietary treatments at the end of weeks 1 and 2 of phase 2.*

	Chemical Composition (g/kg) [a]							
	Week 1				Week 2			
Treatment[b]	Protein	Lipid	Water	BW (kg)	Protein	Lipid	Water	BW (kg)
HP-HP	172	92.5	697	42	170	95.2	712	45
FR-HP	166	80.9	708	47	161	103	683	53
LP-HP	163	123	684	47	160	115	672	53
LP-LP	159	123	668	47	157	128	664	54
FR-LP	163	86.2	705	45	161	103	687	51
RMS[c]	21.3	124	193	7.53	29.8	191	185	8.78
SED[d]	3.26	7.86	9.82	1.37	3.86	9.78	9.60	2.095

BW: Body weight

HP: High protein

FR: Feed restriction

LP: Low protein

[a]The chemical composition was calculated using carcass analyses of pigs at the end of one and two weeks of phase 2.

[b]Pig were fed HP or LP *ad libitum* in the two weeks following a period in which they were subjected to one of three feeding treatments (LP, HP or FR).

[c]Residual mean square.

[d]Standard error of differences between means

Table 3.5. *Average daily gain of chemical components of the body at the end of the 1st and 2nd week and over both weeks of phase 2.*

	Daily Gain of Body Components (g/d)[a]								
	Week 1			Week 2			Week 1 + 2		
Treatment[b]	Water	Protein	Lipid	Water	Protein	Lipid	Water	Protein	Lipid
HP-HP	412	210	105	394	63.4	57	403	137	81
FR-HP	1290	264	106	417	105	239	854	185	173
LP-HP	826	242	185	498	120	153	662	181	169
LP-LP	720	217	291	632	142	163	676	179	227
FR-LP	1067	192	118	474	126	193	770	159	156
RMS[c]	7888	903	5112	9625	1545	10851	77723	5125	9303
SED[d]	62.8	21.3	50.6	69.4	27.8	73.7	139	35.8	48.2

HP: High protein

FR: Feed restriction

LP: Low protein

[a]The daily gain of body components was calculated using carcass analyses of pigs after one and after two weeks, and using the combined data.

[b]Pig were fed HP or LP *ad libitum* in the two weeks following a period in which they were subjected to one of three feeding treatments (LP, HP or FR).

[c] Residual mean square.

[d]Standard error of differences of means.

Table 3.6. *Protein intakes by pigs during the 1st and 2nd weeks of phase 2.*

	Protein intake (g/d) [a]		
Treatment[b]	Week 1	Week 2	Week 1 + 2
HP-HP	336	346	339
FR-HP	484	524	497
LP-HP	377	434	396
LP-LP	371	422	388
FR-LP	382	448	404
RMS[c]	1.84	0.875	3.032
SED[d]	36.2	54.0	30.3

HP: High protein

FR: Feed restriction

LP: Low protein

[a] The protein intakes were calculated using the feed intakes and protein content of the diet during weeks one and two, and using the combined data.

[b] Pig were fed HP or LP *ad libitum* in the two weeks following a period in which they were subjected to one of three feeding treatments (LP, HP or FR).

[c] Residual mean square, x 10^5

[d] Standard error of differences of means.

Table 3.7. *Efficiency of protein utilization of pigs during the first and second weeks of phase 2.*

	Efficiency of Protein Utilisation (g/kg)		
Treatment [a]	Week 1 [b]	Week 2 [c]	Week 1 + 2 [d]
HP-HP	625	183	404
FR-HP	545	200	372
LP-HP	642	276	457
LP-LP	585	336	461
FR-LP	503	281	394
RMS [e]	30205	7824	50605
SED [f]	123	62.5	113

HP: High protein

FR: Feed restriction

LP: Low protein

[a]Pig were fed HP or LP *ad libitum* in the two weeks following a period in which they were subjected to one of three feeding treatments (LP, HP or FR).

[b]Protein efficiencies calculated using the protein gains and protein intakes from the end of phase 1 to the end of the first week of phase 2.

[c]Protein efficiencies calculated using the protein gains and protein intakes from the end of the first week to the end of the second week of phase 2.

[d]Protein efficiencies calculated using the protein gains and protein intakes for phase 2 (mean of weeks 1+2 combined).

[e] Residual mean square.

[f]Standard error of differences of means.

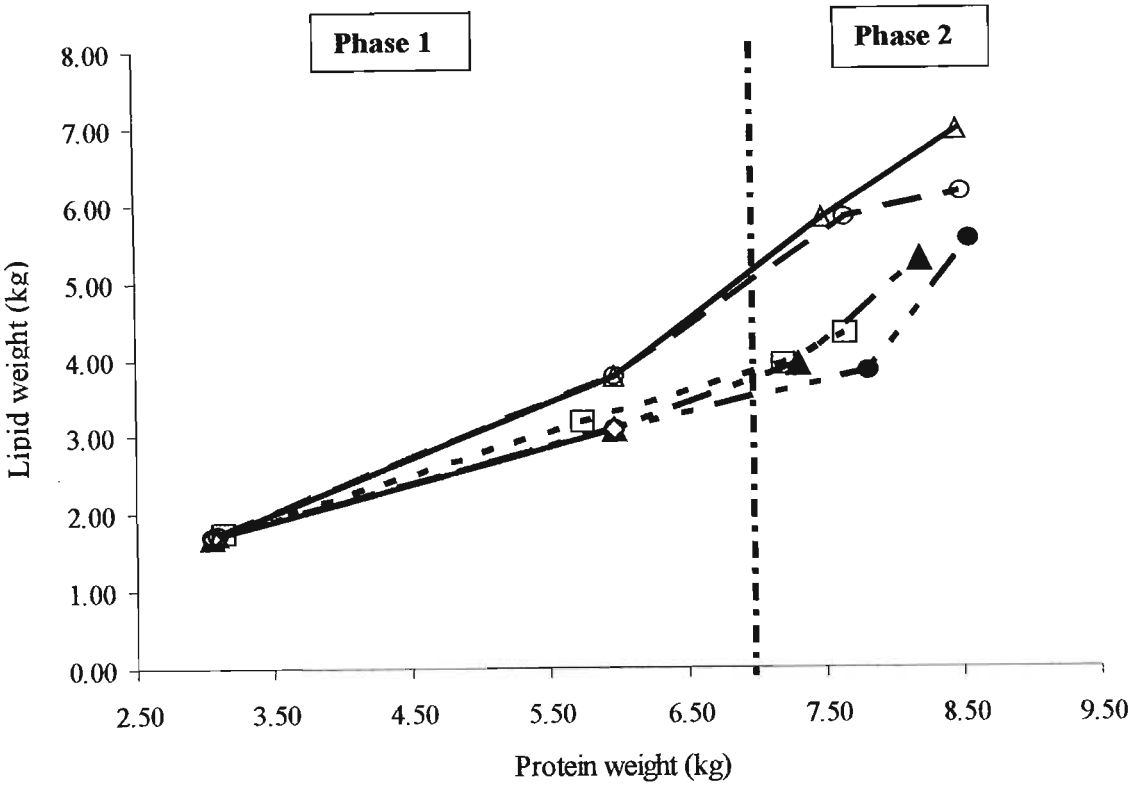

Figure 3.2: *The relationship between body lipid and body protein weights for the (a) restricted (◊), high protein (□) and low protein (△) treatments during the first phase and (b) the FR-HP (●), FR-LP (▲), LP-HP (○), LP-LP (△) and HP-HP (□) treatments in the second phase.*

3.4 DISCUSSION

This experiment was conducted to determine the extent to which the state of the animal influences the efficiency with which it subsequently utilizes dietary protein. The aim was to create three groups of pigs differing in body lipid content by the end of phase 1, but the resultant lipid contents, although different, did not differ significantly one from the other (Fig. 3.2). Possible reasons for this may be that the amount of protein in the LP treatment was too close to the requirement of the growing pig or the number of pigs sampled at this stage was too small. The pigs placed on the LP treatment did consume the greatest amount of feed and this should have resulted in an over-consumption of energy and hence an

increase in lipid deposition and consequently a high body lipid content, as reported in previous experiments, by Kyriazakis & Emmans (1991; 1992), Kyriazakis *et al.* (1991), Ferguson & Gous (1997) and Ferguson & Theeruth (2002). According to Kyriazakis & Emmans (1991), if pigs are fed a non-limiting food and are maintained in an ideal environment they deposit protein and lipid at their genetic potential, which they define as the normal rate of growth. In this experiment HP was formulated to meet the protein requirements of the pig from 20 to 45kg live weight, and it was assumed that the rates of protein and lipid deposition of the pigs fed HP throughout the experiment would be close to their normal levels of deposition (Figure 3.2). The efficiency of utilization of protein tended to be higher ($P=0.056$) for those pigs fed LP-HP than for pigs fed a normal diet (HP-HP) during phase 2 (Table 7). Since these animals were more efficient in utilizing the ingested protein, their protein gains were consequently higher than for the HP-HP animals. They also consumed significantly ($P<0.01$) less feed and deposited less lipid than pigs on LP throughout, and as a result they appeared to rectify their current state by utilizing the excess body lipid as a source of energy to sustain normal protein growth, and in so doing, restored the lipid: protein ratio to the desired level (Figure 3.2). Similar results were obtained by Whang *et al.* (2003), who fed a 90 g CP/kg diet during a depletion phase, and a higher CP diet, ranging from 118 to 218 g CP/kg, during the realimentation phase. The extent to which animals return to the desired lipid: protein ratio is dependent on the extent of the reserves of body lipid and the protein: energy ratio of the feed (Kyriazakis *et al.*, 1991). It would also be dependent on the prevailing environmental temperature, the reduction in lipid content being higher in cold than in hot conditions.

During phase 2 the previously-restricted (FR) pigs had higher daily gains and consumed more feed than the animals on the other treatments. Nielsen (1964) and Owen *et al.* (1971) suggested that such increased gains following restriction are due to parallel increases in daily feed intakes, and our results support this hypothesis. However, Vanschoubrek *et al.* (1965) and Zimmerman and Khajaren (1973) suggest that improved responses in performance after a period of restriction are not due to increased feed intakes, but rather reflect a change in metabolism. In this experiment there was no significant improvement in FCE following food restriction when compared with the other treatments, but food intake was significantly higher than in the other treatments receiving HP in phase 2. Pigs on FR-HP consumed significantly ($P<0.01$) more protein but were no more efficient in utilizing the ingested protein than pigs on the FR-LP treatment. If the pigs were attempting to

correct the lipid:protein ratio by increasing lipid content, they would be expected to overconsume protein on the HP treatment to a greater extent than on the LP treatment, and this is indeed what occurred. Efficiency of protein utilisation would therefore be expected to be lower on FR-HP than on FR-LP, but this was not the case. Pigs on FR-LP increased their lipid:protein ratio in the first week of phase 2 more rapidly than the pigs fed FR-HP, but the reverse was true in the second week, resulting in similar rates of lipid deposition in both treatments. These pigs were all at the same protein weight at the end of phase 1; therefore they were not attempting to correct a deficit of protein, but rather a deficit of lipid.

It is interesting to note in Fig. 3.2 that the lipid:protein ratios on all treatments other than LP-LP tended to converge by the end of phase 2, illustrating the desire by the pigs to return to a genetically-determined lipid:protein ratio where this is possible.

3.5 CONCLUSION

Since there were no significant differences in the lipid contents of pigs between initial treatments at the end of phase 1, it would be presumptuous to suggest from these results that the previous state of the animal influences the ability of the pig to utilize dietary protein. However this study does indicate that previously mis-fed animals appear to rectify their lipid:protein ratio when given the opportunity to do so.

The rate of lipid retention was reduced in the previously-fatter pigs when they were placed on a high protein feed, resulting in a lipid:protein ratio consistent with an animal that has not been mis-fed, whereas the restricted pigs attempted to correct their deficit of lipid by increasing their rates of lipid deposition, when restriction was removed.

CHAPTER 4

THE EFFECT OF PROTEIN:ENERGY RATIO ON THE RATE OF LIPID DEPOSITION AND WITHDRAWAL IN GROWING PIGS

4.1 INTRODUCTION

The sex and genotype of an animal primarily determine the 'desired' lipid:protein ratio of an animal. Genetically fat pigs will tend always to be fat within the feasible range of nutritional and environmental variation, and the level of fatness of females and castrated males tend to be higher when compared to intact males (Whittemore, 1993). The short-term strategy to manipulate the fatness of an animal is greatly influenced by the quality and quantity of the food. Feeds that are low in protein encourage the animal to consume more of that feed, and the energy eaten above the requirement leads to additional lipid deposition (Ferguson *et al.*, 1994), whereas an unbalanced feed will result in the animal being either fatter or leaner than it seeks to be. The variation in body composition of growing pigs is greatly influenced by the quantity of feed consumed. As the amount of a balanced feed consumed by the pig increases, initially the daily gains of both lean and lipid respond linearly until lean tissue growth reaches a maximum potential rate. Thereafter, the excess energy consumed will be channelled to lipid deposition (Whittemore, 1993).

Whittemore *et al.* (1988) referred to the target level of fatness as a means of explaining the minimum quantity of lipid relative to protein that a growing pig can deposit. This minimum lipid:lean ratio is a characteristic of sex and breed. Male pigs and pigs of high genetic merit may have higher lean tissue growth rate potentials, lower minimum lipid: protein ratios, or both. Lipid deposition above this minimum can only be achieved when feed supply increases such as to exceed the need for maintenance, maximum potential rate of daily lean tissue growth and minimum level of lipid in normal gain (Whittemore, 1993). The proposition that animals have an intrinsic rate of protein deposition has been accepted by many researchers (Kielanowski, 1969; Whittemore *et al.*, 1988; Moughan, 1999; Schinckel, 2001). In a non-limiting environment, and on a non-limiting food, it has been proposed (Emmans, 1981) that the rate of lipid deposition in an animal will be related to the rate of protein deposition, this being a function of the genotype of the animal. However, the rates of lipid and protein deposition may be totally unrelated in cases where

the environment or the feed are not optimal. Whereas the rate of protein deposition has an upper limit set by the potential of the animal, the rate of lipid growth appears not to have such a limit (Tullis & Whittemore, 1986; Emmans & Kyriazakis, 1999). When modelling the rate of lipid deposition in animals it would be valuable to have an idea of the maximum rate at which lipid is deposited when conditions are such that high lipid deposition rates are encouraged.

The aim of the experiment reported here was to determine to what extent the rate of lipid deposition would exceed the rate of protein deposition when male and female piglets are given unbalanced feeds.

4.2 MATERIALS AND METHOD

4.2.1 Animal Description

Fifty-two crossbred Large White x Landrace pigs (26 females and 26 males), eight weeks of age, were used in the trial. Four pigs (2 males and 2 females) were randomly selected for slaughter at 20kg live weight to determine the chemical composition of the empty body at the start of the experiment. The remaining 48 pigs were fed a commercial pig grower until they reached 20kg live weight, at which time they were randomly assigned to one of four dietary treatments.

4.2.2 Trial Facilities

The trial took place at Ukulinga research farm. The pigs were placed in individual pens. Each pen contained two plastic self-feeding bins (Big Dutchman ®) and a nipple drinker. These facilities allowed for free and continuous access to food and water for all pigs. The pigs were subjected to 16 hours light and 8 hours darkness each 24 hours. The pigs and feeders were weighed weekly. Food weighed in was recorded, and when each pig was removed from its pen for carcass analysis the food remaining in the feeder was weighed.

4.2.3 Feed Ingredients and Composition

The ingredients and chemical composition (g/kg fresh weight) of the high and low protein feeds offered in Phases 1, 2 and 3 are given in Table 4.1 and Table 4.2 presents the analyzed composition of the three blends of high (H) and low (L) protein feeds offered in Phases 1, 2 and 3.

Table 4.1. *The ingredients and chemical composition (g/kg fresh weight) of high (H) and low (L) protein foods*

	Basal feeds	
Ingredient	H	L
Yellow maize	553	687
Maize gluten 60	23.6	12.3
Soya bean meal	115	
Full fat Soya	250	250
Limestone	10.8	10.6
Monocalcium Phosphate	30.0	32.2
Salt	2.50	2.50
Vit and Min Premix	5.00	5.00
dl-Methionine	2.53	
l-Threonine	2.25	
Tryptophan	0.320	
l-Lysine HCl	4.79	0.380
Analyzed Composition:		
DE (MJ/kg)[1]	14.5	14.5
CP (Nx6.25) (g/kg)	197	166
Total lysine (g/kg)	13.55	8.09

[1] Calculated as 3.8 - 0.019 NDF[a] + 0.76 GE[b] (Morgan *et al.*, 1984)

[a] NDF = Neutral detergent fibre

[b] GE = Gross energy

Table 4.2. *Analyzed composition of the three blends of high (H) and low (L) protein feeds offered in Phases 1, 2 and 3.*

Treatment	DE (MJ/kg)[1]	CP (Nx6.25) (g/kg)	Total lysine (g/kg)
50H/50L	14.5	182	10.82
30H/70L	14.5	175	9.73
20H/80L	14.5	172	9.18

[1] Calculated as 3.8 - 0.019 NDF[a] + 0.76 GE[b] (Morgan *et al.*, 1984)

[a] NDF = Neutral detergent fibre

[b] GE = Gross energy

4.2.4 Design of the experiment

Two feeds were formulated to contain similar energy contents but with one having a higher crude protein (CP) concentration than the other (Table 4.1). The high CP diet (H) was formulated to supply excess protein during the period 20 to 45 kg live weight while the low CP (L) was to be deficient in protein. The H and the L diets were blended (Table 4.3) to produce four feeds varying in protein content, these differing between the two sexes used.

Table 4.3. *Blending proportions of high (H) and low (L) protein basal feeds in the four feeding treatments used for male and female pigs.*

	Males		Females	
Treatment	H	L	H	L
1	100	0	100	0
2	0	100	0	100
3	50	50	20	80
4	30	70	30	70

The objective was to create four groups of pigs, within each sex, with a range of body lipid weights. Pigs fed L *ad libitum* were expected to have the highest body lipid contents and

pigs fed H *ad libitum* were expected to have the desired (or normal) lipid contents, indicative of their genetic potential. Estimates of CP requirements were based on the dietary protein concentration (200 g/kg) that produced the optimum response from previous studies conducted with this genotype (Ferguson and Gous, 1997; Ferguson *et al.*, 2000; Ferguson *et al.*, 2001). Dietary amino acids were balanced according to the ideal protein balance, with lysine as the reference amino acid (Wang & Fuller, 1989). All foods were intended to be non-limiting in minerals and vitamins.

At the start of phase 1 of the experiment (when pigs were 20 kg live weight and 56 days old), all pigs were ear-tagged, and then 6 male and 6 female pigs were randomly allocated to each of the four treatments, respectively. The EFG Pig Growth Model was used to predict the fat contents of the pigs on the four feed treatments using genotypes of the following description: mature body protein weight: 39kg for males and 28 kg for females; the rate of maturing: 0.0107/d for males and 0.0120/d for females; and the lipid: protein ratio at maturity (LPRm): 2.6g/g for males and 3.9g/g for females. The Lipid Index, which is the ratio of the observed (expected) and desired lipid contents of the animal, was calculated for each sex and feeding treatment over the period from 56d (20kg) to 100d of age, and these are given in Figures 1 and 2 for males and females, respectively. By sampling pigs from each of these treatments a week apart, i.e. at 63, 70 and 77d of age, and comparing the observed lipid index with the predicted, the accuracy of these predictions could be tested. Two pigs of each sex from each of the feeding treatments were randomly selected for slaughter according to a pre-determined schedule (Figures 4.1 and 4.2).

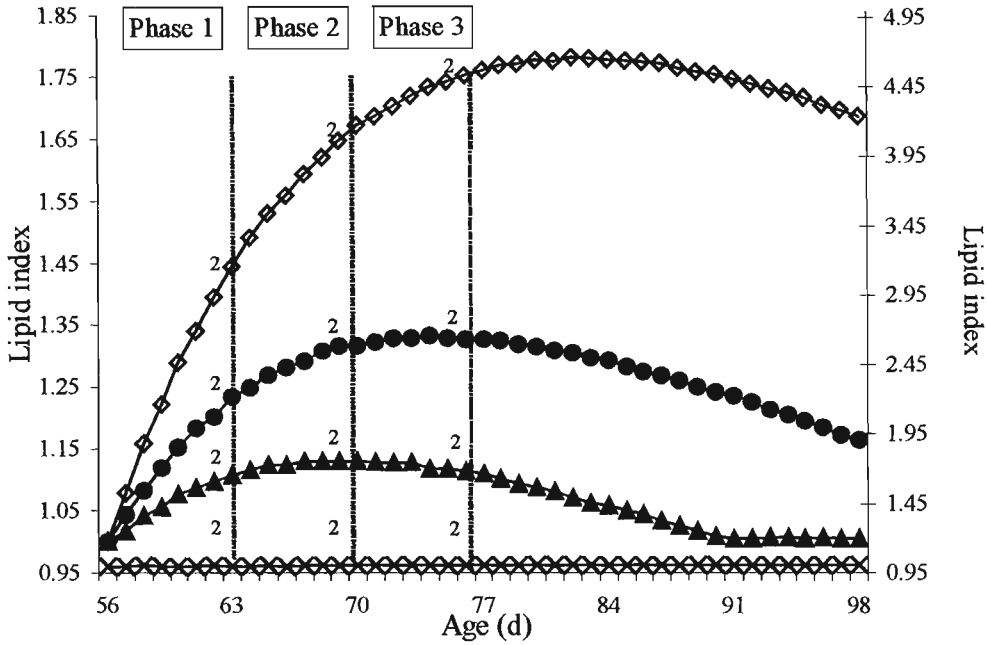

Figure 4.1. *Predicted lipid contents of the male L x LW pigs on the four dietary treatments, L (◊); 70L/30H (●); 50L/50H (▲) and H (x) and the number of pigs slaughtered, for each treatment, after phases 1, 2 and 3. Lipid index is the ratio of actual to the desired lipid content.*

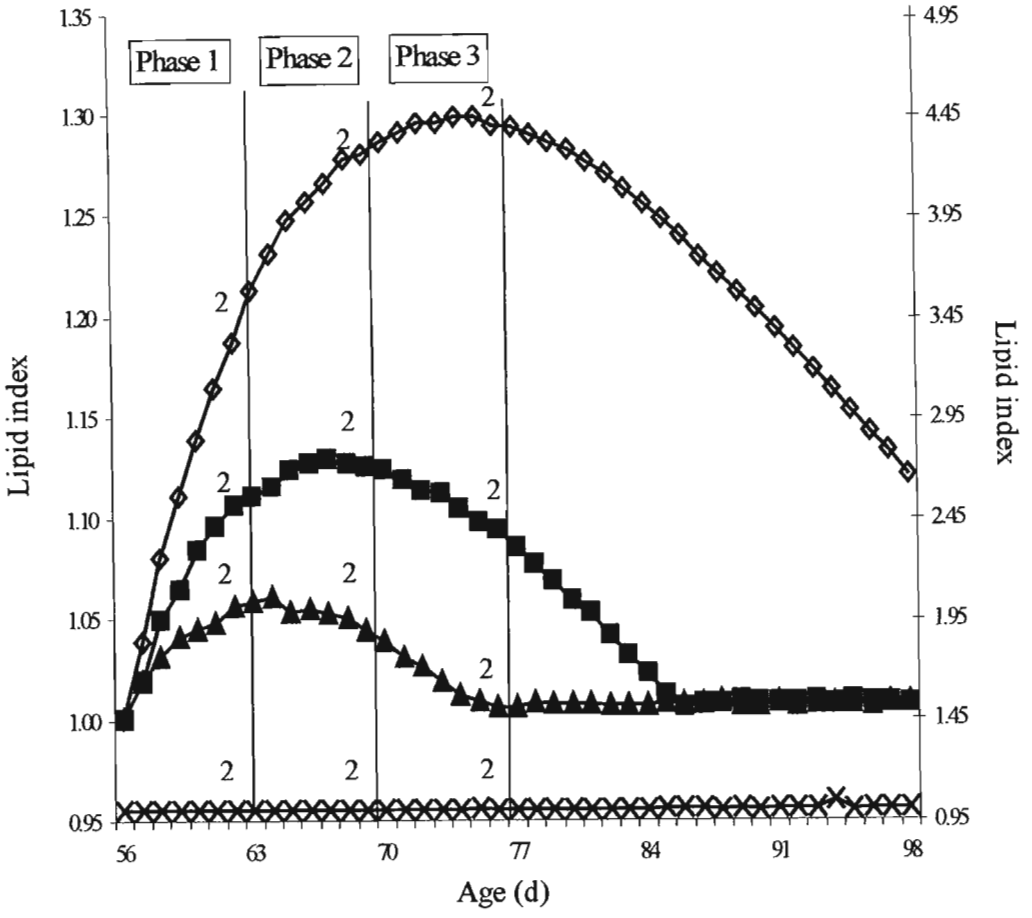

Figure 4.2. *Predicted lipid contents of the female L x LW pigs on the four treatments, L (◊); 80L/20H (■); 70L/30H (▲) and H (x) and the number of pigs slaughtered, for each treatment, after phases 1, 2 and 3. Lipid index is the ratio of actual to the desired lipid content.*

4.2.5 Slaughter Procedure

Four pigs (two males and two females) were killed by injection of sodium pentobarbital once they had reached 20kg live weight, to determine the initial carcass composition of the pigs prior to being placed on the dietary treatments in Phase 1. The carcasses were then placed in a plastic bag and sealed to chill at 0^0C overnight. The stomach and intestines were then removed and weighed full, stripped of their contents and weighed empty. The empty stomach and intestines were added to the carcass weight to provide an estimate of the empty body weight. The viscera and carcass was cut into smaller pieces and placed into

a mincer, homogenized and sub-sampled for chemical analysis. The remaining 48 pigs were killed by exsanguinations at the commercial abattoir when they had attained their respective slaughter live weights. After stunning, the blood from each pig was collected in two-liter plastic buckets. The pigs were eviscerated and the gastrointestinal tract, bladder, heart, liver and lungs were removed. Each empty carcass was then halved along the midline, with the right half of the carcass chosen for further analysis. The half carcass, organs and blood were stored overnight at 0^0C in a sealed plastic bag. The half carcass was then portioned and together with the empty gastrointestinal tract, remaining organs and blood, was stored in a sealed plastic bag and frozen at -20^0C. The combined organs and blood were homogenized and then halved by weight. The frozen carcass portions and half the combined blood and organs were homogenized in a mincer. Two samples were collected (in 500g containers) from each homogenized pig and submitted to the laboratory for proximate analysis according to AOAC (1984) methods, except for lipid, which was calculated from gross energy and crude protein content according to the method described by Ferguson *et al.* (2000) (Equation 3.1).

The duplicated results were combined to provide a single result for each pig. The dry matter content of each sample was determined by freeze-drying the samples for 48 hours. The CP content was calculated as nitrogen x 6.25, where nitrogen content of the dry matter was determined on a LECO nitrogen analyzer (LECO Africa (Pty) Limited, P.O. Box 1439, Kempton Park, South Africa). The rates of retention were determined by subtracting the component weight at 20 kg from the final component weight and divided by the time taken to grow between the two weights. Gross energy of the dry matter was determined by adiabatic bomb calorimetry.

4.2.6 Statistical analysis

During phase 1 the body weights and food intakes of all pigs from each sex and treatment were pooled to determine the mean body weight and food intake for each treatment. The same was done for both phases 2 and 3, with the mean body weights and food intakes of the remaining pigs on trial, for each treatment, being used to calculate the required parameters. Carcass protein and lipid gains were calculated for each treatment and period using the mean carcass composition of all pigs sampled, from the given treatment at the appropriate slaughter periods, and the mean body weights of all pigs on that treatment. The

lipid index was then calculated using the ratio of the lipid contents of the pigs on the lower protein feeds and that on the highest protein content, for both male and female pigs. The values for the lipid index at age 56 days, for both male and female pigs, were taken from the EFG Pig growth Model. All results were then analyzed, to obtain treatment means and standard errors of the means, using the analysis of variance in Genstat (1997) with dietary treatments as factors. The results for male and female pigs were analyzed separately.

Linear and quadratic regressions were done to analyze the responses of protein gain and lipid gain to increases in protein intake. The effect of sex on these responses was measured using the 'group' option in Genstat.

4.3 RESULTS

During phase 1 (56d to 63d), feed intakes for the male ($P<0.01$) and female pigs ($P<0.05$) on L were significantly higher than those on H and the two blends (Table 4.4). The male pigs on L had a higher (1260g/d) feed intake than the female pigs on L (1070g/d), throughout phase 1. There was no significant difference among treatments for any of the production characteristics, chemical components or average daily gain of chemical components, during phase 1 for either male or female pigs.

Throughout phase 2 (63d to 70 d), the male pigs on L had the highest lipid content ($P<0.01$) followed by those on 70L/30H, 50L/50H and H, respectively. The male pigs on L had the highest lipid gains ($P<0.05$), the lowest water gains ($P<0.01$) and the lowest water content ($P<0.05$), during phase 2. The lipid content was the greatest ($P<0.05$) in the female pigs on L followed by those on 80L/20H, 70L/30H and H, respectively. The females pigs on 70L/30H had significantly higher water contents ($P<0.01$) followed by those pigs that were fed H, 80L/20H and L, respectively (Tables 4.5 and 4.6).

The male pigs on L, during phase 3, grew faster ($P<0.05$) and consumed significantly more feed ($P<0.01$) than the pigs fed H, 70L/30H and 50L/50H (Table 4.4). The L fed pigs had significantly higher lipid contents ($P<0.05$) followed, in order, by those fed 70L/30H, 50L/50H and H. Male pigs fed 50L/50H gained the most water ($P<0.01$) and tended to have the greatest water content ($P=0.056$). Female pigs had similar ADG, ADFI and FCE during phase 3 (Table 4.4). However the female pigs on the L diet tended to grow faster

and consumed more feed than the pigs on the 70L/30H, 80L/20H and H diets. Lipid content was the lowest ($P<0.01$) for pigs fed the H diet followed by those fed 70L/30H and 80L/20H, with those fed L having the highest lipid content (Table 4.5). Although there were no significant differences observed for average daily gains of chemical components, during phase 3 for female pigs, the pigs on the L diet did deposit lipid faster than the pigs on the other dietary treatments.

Regression coefficients, during phase 1, showed that dietary protein intake had a linear effect on lipid gain, and that there tended to be a linear difference ($P=0.09$) between sexes with male pigs depositing 46g/d less lipid than female pigs. During phase 2 dietary protein intake had a linear effect on lipid gain and there was a significant ($P<0.001$) linear difference between the sexes. There was a significant ($P<0.001$) linear interaction between protein intake and sex. There were no significant linear or quadratic responses in protein gain to protein intake during phases 1, 2 and 3 (Table 4.7).

During the overall experimental period, there were linear responses in lipid gain to protein intake and there was a significant ($P=0.01$) difference in the amount of lipid deposited between the sexes, with male pigs depositing, on average over all treatments, 71g less lipid per d than the female pigs. A significant linear ($P=0.02$) interaction was observed between protein intake and sex. There was a significant linear ($P<0.01$) and quadratic ($P<0.01$) response in protein gain to protein intake.

Figure 4.3 shows the response of feed intake and body lipid content to increases in dietary protein content (CP). As the CP content increases, the feed intake, for the male pigs, decreases. This is as a result of required quantities of protein being readily available for the animal to utilize. A similar response is observed during phase 1 for the female pigs. However, during phase 2, the female pigs increased their feed intake when the CP content increased from 166g/kg to 172g/kg, thereafter feed intake remained constant. During phase 3, the feed intake decreased from 166 to 172g/kg CP, then increased until 175g/kg CP, thereafter remained constant with increasing CP content. During this phase the female pigs decreased their feed intakes due to adequate supply of CP for utilization.

When analyzing the responses of body lipid content to increases in CP content, it was observed that the lipid contents decrease with increase in CP content, for both male and

female pigs. However, the female pigs appear to have a higher lipid content than the male pigs. The reason being that female pigs have a higher level of fatness than male pigs (Whittemore, 1993). These conclusions coincide with the results obtained in Table 4.8 where male pigs deposit less lipid than female pigs and would therefore be leaner. The male pigs also consume more protein due to their high CP requirements (Table 4.8).

Table 4.4. *Average daily gain (ADG, g/d), average daily feed intake (ADFI, g/d) and feed conversion efficiency (FCE, g gain/kg feed) of male and female LxLW pigs at the end of phases 1 (56d–63d), 2 (63d-70d) and 3 (70d-77d).*

Treatment[a]	Phase 1			Phase 2			Phase 3		
Males	ADG	ADFI	FCE	ADG	ADFI	FCE	ADG	ADFI	FCE
H	590	880	678	644	1.038	622	708	1.22	583
50L/50H	607	970	636	652	1.048	636	699	1.17	597
70L/30H	634	1070	629	674	1.19	602	731	1.27	579
L	649	1260	515	713	1.36	529	783	1.51	518
RMS[b]	1.27[b]	21.1	2.58[b]	0.62[b]	0.0516	1.21[b]	0.0424[b]	0.00293	0.0797[b]
SED[c]	65.1	83.9	92.7	55.6	0.161	77.8	20.6	0.0541	28.2
Females									
H	524	852	612	875	1.24	757	705	1.41	500
70L/30H	546	933	588	778	1.22	718	705	1.37	524
80L/20H	563	1005	561	852	1.23	679	686	1.28	524
L	549	1067	534	385	1.04	292	725	1.46	498
RMS[b]	0.608[b]	13.6	1.006[b]	9.93[b]	0.179	7.67[b]	0.029[b]	0.0157	0.376[b]
SED[c]	45	67.4	57.9	223	0.299	196	17.0	0.125	61.3

H: High protein

L: Low protein

[a] Male pigs were fed high protein (H), 50L/50H, 70L/30H or low protein (L) and female pigs were fed high protein (H), 70L/30H, 80L/20H, or low protein (L), throughout the three phases.

[b] Residual mean square, x 10^4

[c] Standard error of differences of means.

Table 4.5. Chemical composition (g/kg) of male and female LxLW pigs on the four dietary treatments offered during phases 1 (56d-63d), 2 (63d-70d) and 3 (70d-77d).

Treatment[a]	Phase 1				Phase 2				Phase 3			
Males	BW (kg)	Protein	Lipid	Water	BW (kg)	Protein	Lipid	Water	BW (kg)	Protein	Lipid	Water
H	28.4	129	52.5	582	30.6	142	67.5	627	33.1	153	80.9	665
50L/50H	28.5	129	58.1	581	30.7	141	74.1	626	33.1	154	89.4	667
70L/30H	28.9	127	64.5	573	31.3	139	85.5	615	33.7	151	105	656
L	29.2	125	75.6	563	31.5	135	108	600	34.2	145	138	632
RMS[b]	20.6	8.74	119	103	12.5	19.6	27.8	30.5	0.325	42.3	195	84.2
SED[c]	2.62	2.96	10.9	10.1	2.50	4.43	5.28	5.52	0.570	6.51	14.0	9.18
Females												
H	28.3	130	72.5	564	30.5	142	92.6	603	32.8	153	115	639
70L/30H	28.3	130	77.0	565	30.5	142	96.4	605	32.8	154	116	642
80L/20H	28.5	129	80.6	562	30.8	141	103	600	33.1	152	124	636
L	28.6	127	87.8	553	30.9	138	118	587	33.3	148	147	620
RMS[b]	19.4	19.2	175	438	12.4	26.6	24.06	2.032	4.48	44.09	22.03	303
SED[c]	2.54	4.38	13.2	20.9	2.49	5.16	4.91	1.43	2.12	6.64	4.69	17.4

H: High protein

L: Low protein

[a] Male Pigs were fed high protein (H), 50L/50H, 70L/30H, or low protein (L) and female pigs were fed high protein (H), 70L/30H, 80L/20H or low protein (L), throughout the three phases.

[b] Residual mean square

[c] Standard error of differences of means.

Table 4.6. *Average daily gain of chemical components (g/d) of the male and female L x LW pigs at the end of phases 1 (56d-63d), 2 (63d-70d) and 3 (70d-77d).*

Treatment[a]	Phase 1			Phase 2			Phase 3		
Males	Water	Protein	Lipid	Water	Protein	Lipid	Water	Protein	Lipid
H	272	73	50	1335	340	288	1424	370	305
50L/50H	146	47	61	663	209	119	1430	370	342
70L/30H	255	70	95	718	210	194	1430	369	436
L	365	93	148	1245	313	599	1365	350	663
RMS[b]	2.55	0.0826	0.150	0.743	0.473	0.682	2.41	1.17	5.35
SED[c]	160	28.7	38.7	86.2	68.7	82.6	155	108	231
Females									
H	219	59	62.0	1225	324	385	1300	351	480
70L/30H	385	97	95.0	1230	325	380	1300	350	435
80L/20H	299	76	100	1205	325	440	1300	350	465
L	164	46	115	1160	305	570	1255	340	630
RMS[b]	4.404	0.129	0.318	0.0474	0.631	0.566	8.39	1.206	0.608
SED[c]	210	35.9	56.4	21.8	79.4	75.2	290	110	78.1

H: High protein

L: Low protein

[a] Male pigs were fed high protein (H), 50L/50H, 70L/30H, or low protein (L) and female pigs were fed high protein (H), 70L/30H, 80L/20H or low protein (L), throughout the three phases.

[b] Residual mean square, x 10^4

[c] Standard error of differences of means.

Table 4.7. *Coefficients obtained from fitting linear regressions of lipid gain (LG, g / d) and protein gain (PG, g / d) on dietary protein intake (P-intake, g / d), with sex as a group (M-male), during phases 1, 2 and 3 (P1, P2 and P3).*

Source	P1				P2				P3			
	LG		PG		LG		PG		LG		PG	
	Coeff	P value	Coeff	P value	Coeff	P value	Coeff	P value	Coeff	P value	Coeff	P value
Constant	-351	0.05	-1	0.992	1017	0.002	16.6	0.411	19	0.975	379	0.216
P intake	2.61	0.02	0.417	0.586	-2.72	0.05	0.73	0.440	1.97	0.439	-0.13	0.916
Sex M	-46	0.09	-5.9	0.773	-3553	<0.001	-49.2	0.202	-3.91	0.689	15.5	0.741
P intake x Sex M					16.39	<0.001						

Table 4.8. *Coefficients obtained from fitting linear regressions of lipid gain (LG, g / d) and protein gain (PG, g / d) on dietary protein intake (P-intake), with sex as a group (M-male), over the three-week experimental period (P1-3).*

Source	P1-3			
	LG		PG	
	Coefficient	P value	Coefficient	P value
Constant	-401	0.034	-2243	0.001
P intake	3.582	<0.001	20.75	0.002
P intake^2			-0.0411	0.008
Sex M	-863	0.014	-39.3	0.182
P intake x Sex M	3.80	0.022		

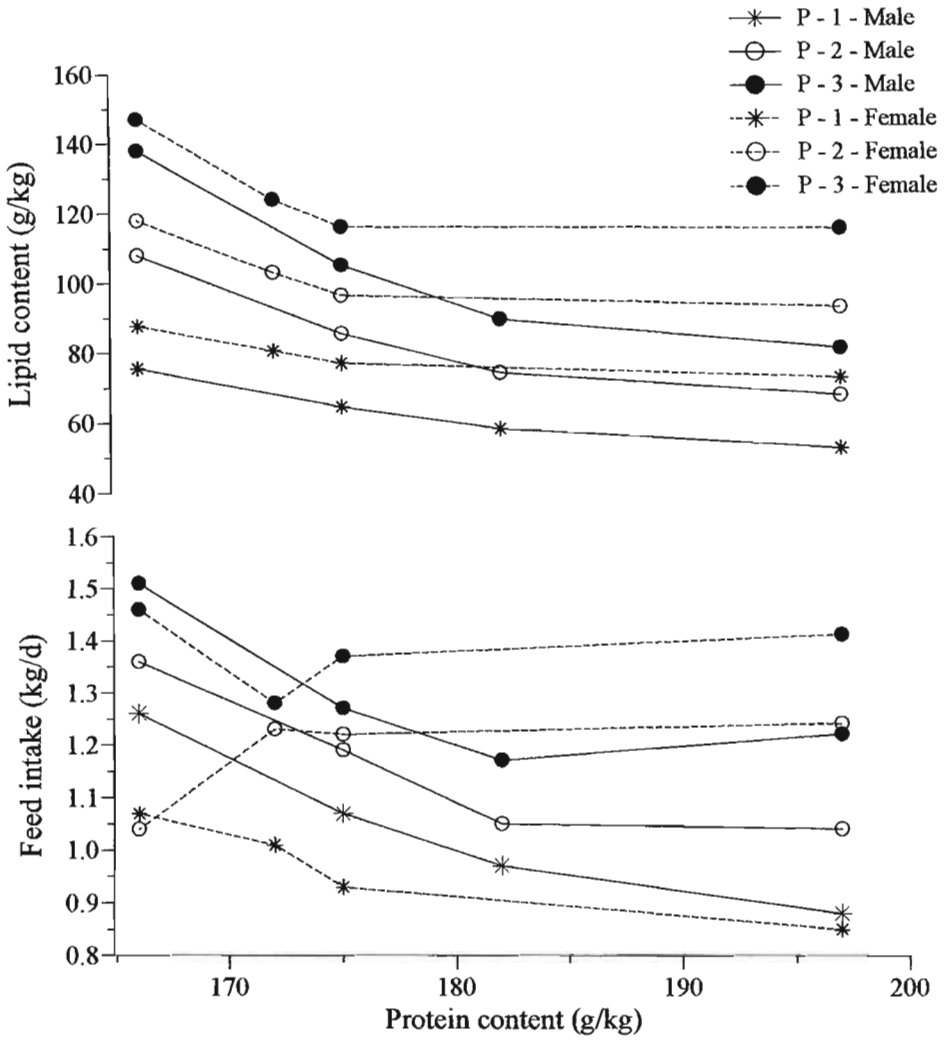

Figure 4.3. *The effect of increasing dietary protein content on feed intake and body lipid content during the three phases (P1, P2 and P3) for both male and female pigs.*

4.4 DISCUSSION

This experiment was conducted to determine the effect of the dietary protein:energy ratio on the rate of lipid deposition. There were two aspects of interest: the difference in the amounts of body protein and lipid deposited by the pigs on the four dietary treatments, and the change in fatness over the three weeks of the trial. It was assumed, based on previous trials, that as the protein content of the feeds was reduced, so the rate of body protein gain would decrease and the rate of body lipid gain would increase, and this was found to be the case. Due to the low CP content of the diet (166 to 172g/kg) these pigs would have to increase their feed intake in order to satisfy their requirements. According to the NRC (1998), the required level of protein for female pigs, between the live weight ranges of 20-50kg, is approximately 210g/kg. What was of particular interest, because this has not been reported previously, was the change in the degree of fatness over the three-week trial period.

The EFG Pig Growth Model, which is based on the theory of food intake regulation proposed by Emmans (1989), predicts that if growing pigs are kept on a feed that is limiting in terms of protein content, the pigs will initially consume excessive amounts of the feed, in an attempt to acquire sufficient of the first-limiting nutrient, and as a result, would become fatter. But as the pigs grow, the feed would become less-limiting, as the requirement for the limiting nutrient, as a concentration in the feed, would diminish, and this would result in less lipid being deposited, until eventually the lipid reserves would be utilized as an energy source, and become depleted. Since the H diet was formulated to meet the requirements of the animal between 20 and 45kg live weight, over-consumption of energy would not have been necessary and hence the rate of lipid deposition would have been close to the desired rate. The graphs shown in Fig.'s 4.4 and 4.5 illustrate this point very effectively, and mirror precisely the predicted contents of body lipid over time.

Of considerable interest is the difference in the maximum lipid index achieved by the two sexes: because males have a higher protein requirement than females, it is expected that they would need to overconsume energy to a greater extent than females when faced with a feed limiting in protein. From Fig.'s 4.1 and 4.2 it can be seen that the maximum predicted lipid index for males on the lowest protein feed was 1.75 and for females, 1.3, i.e. the males were expected to contain 1.75 times the desired amount of lipid in the body prior to

utilizing this lipid as an energy source (when the dietary protein content was no longer limiting). The actual lipid indices measured were exactly as predicted (Fig.'s 4.4 and 4.5) lending credence to the accuracy of the prediction of food intake and lipid gain on these feeds by male and female pigs respectively.

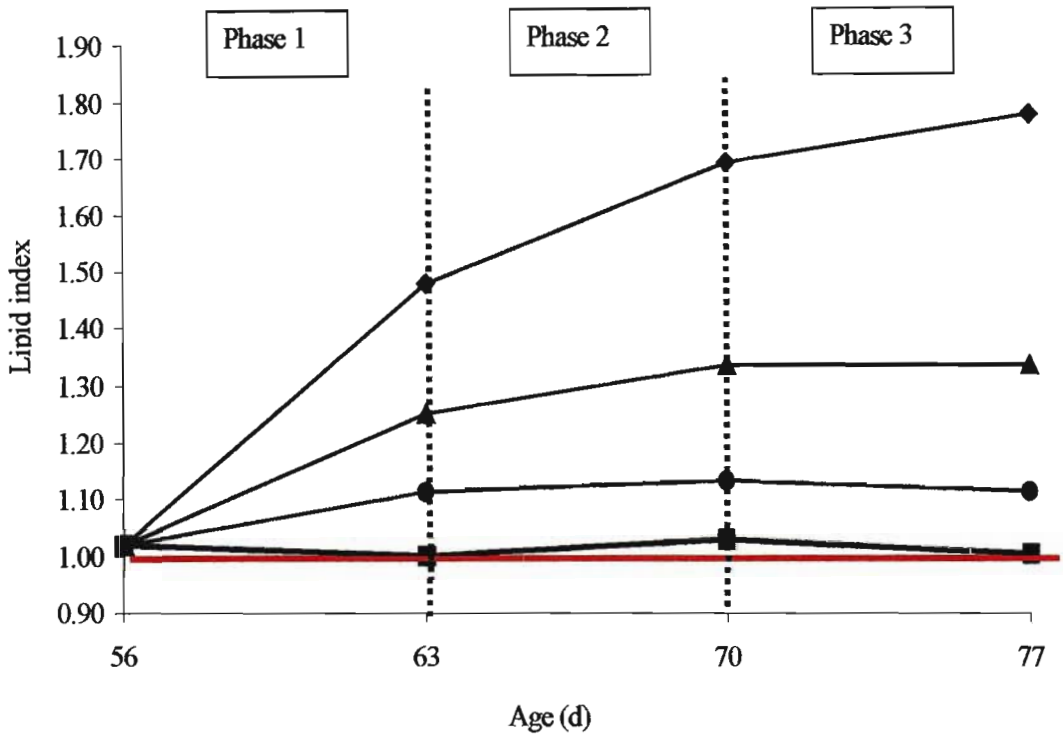

Figure 4.4. *An indication of the quantity of lipid, for male pigs, relative to age, for the low protein (♦), 70L/30H blend (▲), 50L/50H blend (●) and high protein (■) treatments, during phases 1, 2 and 3. The constant line (calculated from the EFG Pig Growth Model) indicates the desired lipid content for male Landrace crossed with Large White (LxLW) pigs.*

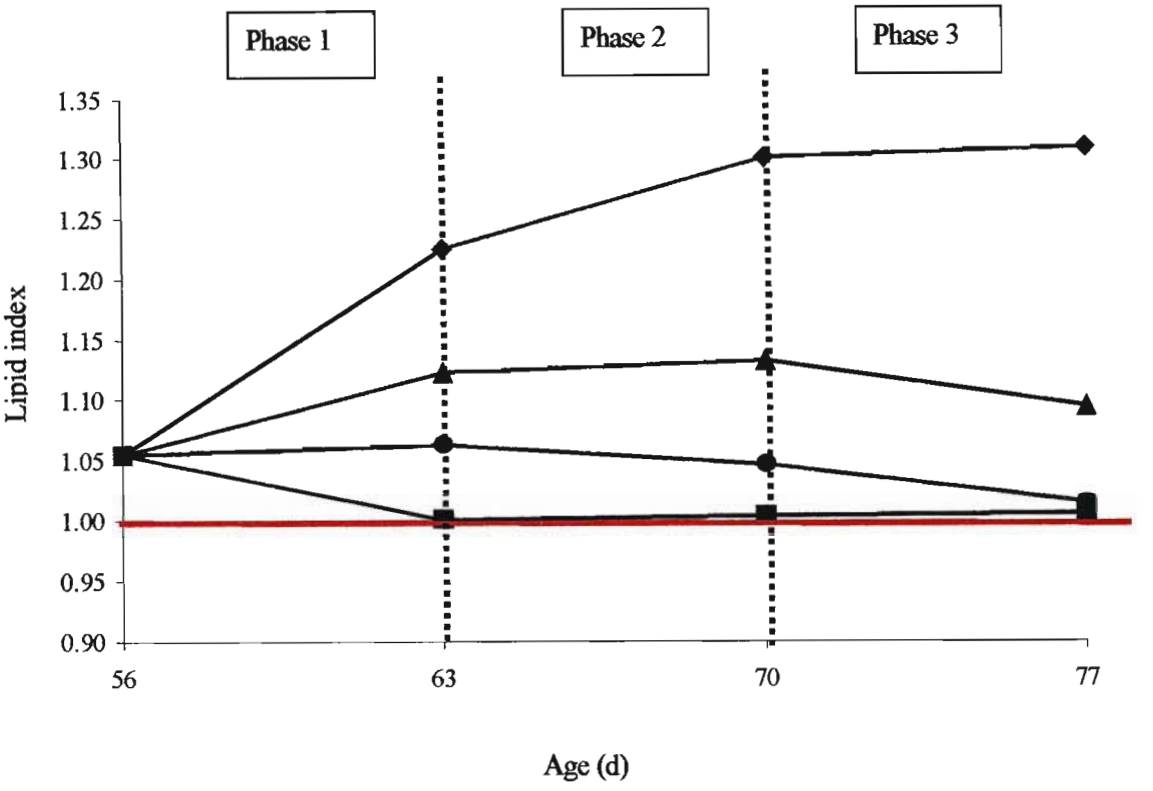

Figure 4.5. *An indication of the quantity of lipid, for female pigs, relative to age, for the low protein (♦), 80L/20H blend (▲), 70L/30H blend (●) and high protein (■) treatments, during phases 1, 2 and 3. The constant line (calculated from the EFG Pig Growth Model) indicates the desired lipid content for female Landrace crossed with Large White (LxLW) pigs.*

4.5 CONCLUSION

This experiment is distinctive in that it monitors the changes in lipid content over time rather than at the end of the trial period. By monitoring the changes in lipid content only at the end of a trial, the researcher is not aware of the changes that have taken place in the body composition during the trial – and if the trial is conducted over an extended period of time, it may well be that very little difference in lipid content is observed at the end of the trial, whereas large differences in lipid content may have taken place during the trial, that went unnoticed. This is one of the many advantages of simulation modelling, as such changes may be predicted for each day of the growing period, thereby improving one's understanding of the theory of food intake regulation in a growing animal.

Lipid will be deposited at various rates depending on the quality of feed being offered to the animal with respect to the dietary protein content, but as the animal grows the requirement for protein decreases and therefore the feed eventually reaches a state where protein is not limiting. As this non-limiting stage is approached, the amount of excess lipid deposited decreases because energy is no longer being overconsumed, and then a point is reached when the excess energy is used as an energy source, reducing the need to consume feed to meet the energy requirement of the pig, and as a result the feed is utilized with great efficiency. In this trial, since the gradual changes in lipid deposition were monitored in the pigs given feeds containing a range of protein contents, these changes in body lipid content were shown to take place precisely as predicted by the EFG Pig Growth Model. This provides strong evidence that pigs overconsume energy when protein is limiting in the feed, and then utilize the body lipid deposited as a result of the excess energy intake, when dietary protein is no longer limiting.

CHAPTER 5

GENERAL CONCLUSIONS

The work presented in this thesis has shown that growing pigs, when offered a feed limiting in an amino acid, will become fatter than their genetically-determined degree of fatness, but once the feed is no longer limiting they will make use of the lipid reserves as an energy source for protein deposition. The initial state of the animal, however, influences the quantity of feed consumed and the efficiency with which it utilizes this feed. Fatter pigs will utilize the feed more efficiently than feed restricted pigs, due to the lipid reserves being utilized as an energy source.

It is evident from these experiments that the desired carcass, with respect to its protein and lipid compositions, can be achieved by manipulating the quantity and quality of feed being offered to the animal. Also, because the state of the animal influences the way in which it responds to a given feed, knowing the state of animals when a new feed is introduced to a group of pigs, would enable a more accurate prediction to be made of the consequences of the newly introduced feeds. A corollary to this is that a feed may be tailored to meet the requirements of a group of pigs more effectively if their present state is known.

That body lipid is available as an energy source, and that it is utilised as such whenever this is feasible to do so, is part of the theory of feed intake regulation that is at the heart of the EFG Pig Growth Model. Greater faith can be placed in this theory given that the rate of lipid deposition on the feeds used here matched so accurately the predicted rates of lipid deposition and withdrawal. Because pigs are graded at the abattoir, and the prices for the carcasses are dependent on, among other traits, the fatness of the animal, the effect on lipid deposition of the feeding programme used during the growing period is more important with pigs than with broilers, where no price differential exists for fat or lean birds. Optimising the feeding programme for pigs is therefore more complex than for broilers, as the final carcass composition influences the revenue obtained for the carcass, and must therefore be considered when designing the feeding programme. The results of these trials indicate that the lipid content of the pig may be manipulated considerably by dietary means, such that the optimum feeding programme is more difficult to calculate without some means of predicting the consequences of feeding.

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