# A DESCRIPTION OF THE GENOTYPE OF PIGS USING SIMULATION MODELLING

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It is the glory of God to conceal a matter,
to search out a matter is the glory of kings.
(Proverbs 25:2)

I HEREBY DECLARE THAT THE RESEARCH IN THIS DISSERTATION IS OF MY OWN INVESTIGATION. WHERE USE WAS MADE OF THE WORK OF OTHERS IT HAS BEEN DULY ACKNOWLEDGED IN THE TEXT.

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# GENERAL INTRODUCTION

Predicting the performance of animals is a general problem in animal production. The solution to this problem lies in the use of simulation models to describe the causal relationship between inputs and the predicted responses. Simulation models require a satisfactory theory to describe the behaviour or responses of the simulated system. For a given system and it's associated problems the responses to be predicted must first be identified. The responses to be predicted in pig nutrition are the growth and carcass characteristics of a group of pigs, in a particular environment, when given a specific feed. To understand or solve this dilemma a theory needs to be developed. If the theory does not provide acceptable answers to the problems then it may be necessary to redefine the system or problems. The process is then repeated until a feasible theory is attained. The components of the system need to be defined and must be consistent with the theory of the system in order to predict the solutions. In this thesis new concepts in modelling pig growth and food intake are discussed based on the approach of Emmans and Oldham (1988) which combines three components *viz.* a description of the genotype, feed and environment, into an integrated system or simulation model.

There is sufficient data to provide an accurate description of the nutritional quality and composition of the feed component (e.g. ARC, 1981; NRC 1988) and therefore there is no need to seperately discuss feed composition. However, there was an inadequate description of the genotype and insufficient knowledge on various components of the environment, particularly the effect of heat production on voluntary food intake in pigs fed protein-deficient diets.

There is no consensus nor any general discussion in the literature on methods of defining genotypes that will allow similarities and differences between animals to be compared, other than the recognition that differences do exist between animals in mature size (Taylor, 1980) and that selection can alter mature size and the scaled growth rate and fatness at a degree of maturity (Emmans, 1988). If it is accepted that an animal needs to be described in order to model its growth and nutrient requirements then the problem becomes one of what inherent parameters should be used to best describe a particular kind of animal. To answer this question, it is first necessary to determine what makes one animal different from another. The work by Emmans (1987) and Emmans (1988) provides a simple and logical method of determining the differences and similarities of different types of animals. According to Emmans (1987) there are two aspects in which genotypes differ. The first is their mature state and the second is how they develop on route to maturity. It is important to elaborate on these two points because this forms the foundation upon which the criteria for evaluating different types of animals is based.

Any description of how an animal grows and develops must encompass both size and form, and the

subsequent rate of state change (Emmans and Fisher, 1986). The mature state can be quantified by measuring the size (e.g. body protein weight) and the form (e.g. the degree of fatness) of the animal. The form or composition can be expressed in a number of ways viz. chemical (protein, lipid, moisture and ash); or physical (muscle, fat and bone); or as anatomical parts of the body (head, ham, loin, ribs, etc.). This means that a Large White sow and a Pietrain sow with the same mature body weight may have different mature body compositions. Using mature size alone will not provide an adequate description of how the animal might develop. Similarly, two different breeds with the same mature size and form may have taken different periods of time to reach maturity. Therefore, it is important to qualify and quantify the rates of change in size and form. An inherent biological parameter or parameters that can define both these rates of change is essential to properly characterizing an animal (Emmans, 1988).

Although the framework described is rather general, it does provide a solution to the current problem in growth simulation models of inadequate and non-standardized animal parameters (Moughan and Verstegen, 1988). Before taking this general framework to its logical conclusion and providing more specific functions and constants, it is necessary to investigate what parameters and what alternatives are currently in use in pig growth models. In this thesis, a comparison and critical analysis is made of different approaches that have been used to describe a genotype for simulation modelling purposes. This is followed by a proposed approach to evaluating genotypes which is simple but effective. To test the theory an experiment was conducted and the relevant animal parameters determined.

There is a further consideration in the process of adequately defining the genotype and that is the variability within the different parameters describing the animal. The problem with most growth simulation models is that only a single response can be predicted and not a range of responses that is necessary for predicting population responses (Brockington, 1979). In an attempt to solve this problem variation in animal growth characteristics need to be introduced. The main problem with introducing stochastic elements into a model is the lack of suitable data from which to determine the nature of the distribution. This then suggests the use of guess work which may or may not be detrimental to the prediction process depending on the supporting theory behind the theoretical values. This thesis investigates using the model to determine the variation in the genetic parameters of individuals within a population followed by a comparison between the response of an average individual and the population mean to dietary lysine content.

The second area where the model identified there being inadequate data was in the environmental component. There is little or no information pertaining to the influence of heat production on voluntary food intake in growing pigs fed protein-deficient diets and in particular, the maximum heat an animal can loss. It is understood that environmental temperature affects food intake, growth and heat production but it is not clear how environmental temperature interacts with protein intake to

affect protein metabolism. The theory of food intake described in this thesis depends on an accurate estimate of the maximum heat an animal can lose to its environment to predict the maximum intake of a given food in a given environment. Without this estimate the prediction of voluntary food intake and subsequent growth is seriously compromised. To determine the maximum heat loss and to test the theory that voluntary food intake is constrained in animals fed protein-deficient by the maximum amount of heat the animal can lose, an experiment was conducted.

# CHAPTER 1

# A THEORY OF GROWTH AND FEED INTAKE IN GROWING PIGS

## 1.1 Introduction

A growth model can be described as a series of mathematical expressions based on biological responses that are used to predict the physiological response of an animal to a range of nutritional and environmental inputs (Crenshaw, Boyd and Orr, 1986). There are many advantages of being able to predict the growth and feed intake of an animal, such as the determination of nutrient requirements for different periods of growth, making more decisive financial and management decisions, improving the accuracy of genetic selection, identifying research needs and many more. Animal simulation models are generally dynamic systems, which purpose to imitate the behaviour of animals to different internal and external stimuli. The continuous nature of such models allows one to mimic changes in the system components over small time increments, which is characteristic of biological processes (France and Thornley, 1984).

The building of models ranges from the use of empirical regressions derived from experimental observations to a deductive approach using a sequence of mathematical equations (Moughan and Verstegen, 1988; Whittemore, 1993). The empirical relationship between responses and their causes provides regression equations that contain biologically-sound constants and parameters but are limited to the bounds of the original trial. Furthermore, they are static and inflexible, contributing little to the understanding of the actual nature of the predicted responses. The use of empirical elements will always be included in simulation models due to the lack of hard facts about the causal forces behind the resultant response. They should, however, be updated or replaced when further knowledge about cause-effect relationships are elucidated (Black, Davies and Flemming, 1993).

The deductive approach or factorial model is more interpretive and flexible and allows prediction beyond the circumstances in which the information was collected. The more deductive the model, the more useful it will be. Due to the current gaps in growth and nutrition theory, the deductive model can contain a large proportion of hypothesis and too few facts. Working information is needed particularly in the areas pertaining to maximum protein growth rate, factors controlling feed intake, compensatory growth and the inter-relationship between lipid and protein deposition (Whittemore, 1993).

The ideal model should be a system based on first principles and quantifying causal forces which turn inputs into responses (Brockington, 1979). This requires an understanding of the mechanisms in which a system operates and a knowledge of the causes of responses so that new responses can be predicted. Due to the hypothetical nature and the current limitations in knowledge, the best

models will incorporate both empirical elements and deductive processes. To quantify these components, a model invariably consists of a large series of sequential calculations or text statements. This predisposes the use of computers to rapidly and accurately calculate, store and present response data to varying inputs Black, Flemming and Davies, 1989).

This chapter examines a theory of animal growth and feed intake, and the concepts and their functional forms which were used to develop the theory. Several other pig simulating models have been developed (Roux, 1976; Whittemore and Fawcett, 1976; Philips and MacHardy, 1983; Bridges, Turner, Smith, Stahly and Louwer, 1986; Black, Campbell, Williams, James and Davies, 1986; Moughan, Smith and Pearson, 1987; Pomar, Harris and Minvielle, 1991). The theories incorporated into these earlier models have, in all likelihood, been modified in the last few years. However, little information of such modifications is available in the literature as models have now become commercially valuable and therefore the intelectual property has an increased value hence is unlikely to be published. Most of the these models are based either on more complicated biochemical or mathematical procedures or on inadequately defined and quantified procedures. The model, which was originally developed in 1989 (Ferguson, 1989), proposed in this thesis is simple in approach yet effective in predicting growth and nutritional requirements. It differs from the other pig models because it incorporates a new approach to modelling feed intake, bioenergetics and the effects of temperature by making use of the effective energy system proposed by Emmans and Fisher (1986) and adopts the systems approach described by Emmans and Oldham (1988).

## 1.2 Systems Description

The methodology of Emmans and Oldham (1988) provides the framework to model the relationship between inputs and the predicted responses and is illustrated in Figure 1.1. From a description of the genotype and current state of the animal, maintenance, growth and fattening requirements can be defined. Given a set of environmental and nutrient resources the desired food intake will be that amount of food that satisfies the animal's requirements. However, the animal may not be able to consume its desired intake because of a number of constraints such as toxins, bulk capacity and the environment may be too hot for the animal to lose the amount of heat produced from consuming the food offered it. The actual food intake and subsequent growth performance will depend on whether the animal is able to eat its desired food intake.

The underlying principle behind the model is that an animal has a innate desire to attain a mature size as fast as it possibly can. According to Emmans and Fisher (1986) amd Webster (1989) it is not unrealistic to assume that an animal has a purpose to achieve its intrinsic potential. It will only achieve this goal if it is given adequate nutrition and a favourable environment. Given an accurate description of the animal (genotype), this potential growth rate can be predicted. The corollary to this

theory is that if the first limiting nutrient and the potential protein growth rate are known or can be predicted, then by making use of the allometric relationships between protein and the other chemical components to determine empty body mass, the required (or desired) feed intake can be determined. This proposition has the advantage of avoiding the complicated biochemical mechanisms associated with describing feed intake at a particular level predicting rather what the actual level will be. When the nutritional and environmental inputs are inadequate the animal will fail to achieve its potential growth, the extent to which it is constrained being predicted according to a set of rules which deal with failure (Emmans, 1988). These rules will be discussed under the relevant sections.

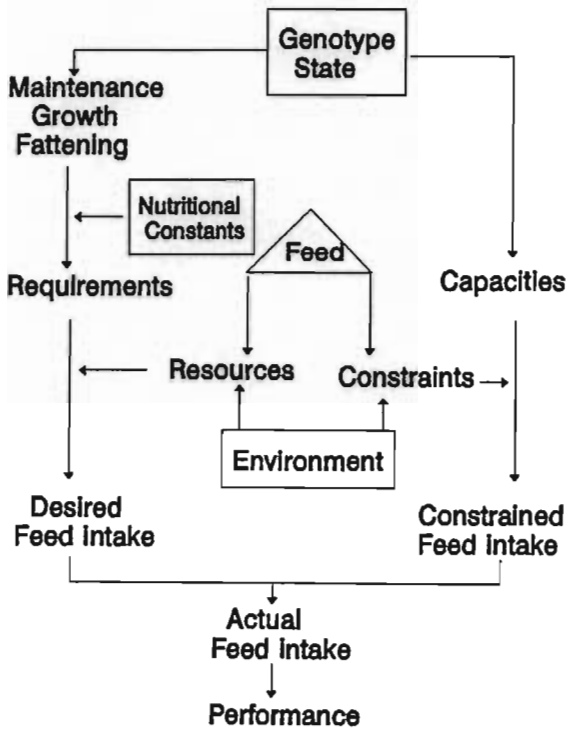


Figure 1.1 A systems approach to predicting growth and feed intake in growing animals (after Emmans and Oldham, 1988).

A central problem to all simulation models is the need to keep the description of the system as simple as possible without limiting its usefulness. Models predicting animal growth can be simplified into three components, namely, an adequate description of the genotype and its current state, the feed and the environment. As there is an abundance of literature on the description of feed this component will not be seperately discussed but included, where necessary , in the discussion onthe theory of food intake. The remaining two components are discussed below in the sections on animal characterization and environmental constraints, respectively.

## 1.3 Animal Characterization

### 1.3.1 Animal growth

The usefulness and accuracy of any theory describing animal growth and development depends on how well the animal is defined. Certain genetic characteristics of the animal need to be quantified in order to know how the animal grows. To determine what intrinsic parameters define an animal, a general discussion is required on animal growth to identify what variables or constants are animal dependent.

To quantify animal growth some measure of the change in body weight over time needs to be recorded. If live weight is then plotted against time the best fitting line will be sigmoidal in shape (Brody, 1945). Parks (1982) states that the sigmoid curve is sufficiently prevalent among fitted curves of animal data to accept this type of curve as a basis for animal growth. The usefulness of the mathematical function describing this curve is that only the parameters change across species and class under various environmental conditions. It follows then that the sigmoidal form represents a common pattern that animal growth will follow from conception to maturity in a non-limiting environment. It can be divided into an exponential growth phase, which continues to a point of inflection, where maximum rate of growth occurs, followed by a decelerating phase until a specific asymptotic mass is reached (AFRC, 1991).

According to Whittemore (1986), the exponential growth phase relates mainly to prenatal growth and that by birth the animal should be following a linear growth pattern. Where curvilinear growth occurs immediately postpartum it is a consequence of the inability to provide a perfect environment for young animals and is not a consequence of any biological time-based component. This is contrary to the more acceptable idea that the rate of growth accelerates from birth to puberty before decelerating (Brody, 1945; Lindsay, 1983), but does stress the relevance of environmental influence on growth. Although controversy over the early stages of growth exists, growth in the last stages proceeds as if the normal condition were the mature size and the rate is proportional to the growth needed to reach mature size (Brody, 1945, AFRC, 1991).

Although the sigmoidal pattern of growth has been well established in the literature, there are several different mathematical expressions that have been used to fit growth data (Parks, 1992). The more common functions are those of Gompertz (1825), Robertson (1908), von Bertalanffy (1938), Brody (1945) and Parks (1970). More recently Taylor (1980) proposed a single standardized growth curve based on genetic size scaling of animal growth. Bridges *et al.*, (1986) forwarded a continuous mathematical function that they claimed was a new approach but was similar in expression to that of Brody's (1945). The equations developed in the earlier

part of the century are generally empirical in nature. This does have the advantage of not being derived on theoretical grounds and having parameters that are biologically meaningful. The main drawback is that they may not be useful for describing all cases of growth. The more recent functions, in particular that of Parks (1970), are mathematically sound and suitable for predicting growth under most environmental conditions but have parameters that are difficult to quantify and have little pragmatic value.

Parks (1970) and Roux (1976) make a valid criticism about the first four functions mentioned above, in that they are limited to describing animal growth as outputs only and exclude the vital input component viz. feed intake. Based on the assumption that the rate of *ad libitum*-feed consumption increases at a diminishing rate over time, Parks (1970) predicted growth as a function of live weight, cumulative feed intake and time. While it is useful to know how *ad libitum* feed intakes change with age, it still does not describe what controls feed intake. As the approach to simulating growth in this dissertation is based on a systems analysis of the factors controlling feed intake, the mathematical expressions of Parks (1970) and Roux (1976) are not suitable.

The term "genetic potential" has often been used to describe the upper limit of growth (Moughan and Verstegen, 1988) and yet it cannot be tested experimentally because, for an animal to express its genetic potential or maximum growth, either the environment has to be non-limiting or there must be no external influence that will prevent the animal from expressing its potential. To determine whether an environment is limiting is practically impossible because the requirements of growing animals are changing constantly. It does, however, propose useful practical applications. The concept can best be described as a genetically-defined limit in the response of an animal to a non-limiting environment. Emmans (1988) explains genetic potential as the animal's potential rate of normal growth at a given time which should be seen in terms of protein growth rate as opposed to an output of body weight.

### 1.3.2 Protein growth

In physical terms growth can be measured as the sum of gut-fill and empty body weight; the latter referring to the protein, lipid, moisture and ash weights, collectively. The carbohydrate component is usually small enough to warrant exclusion without adversely affecting the body composition. The rate of growth would be the changes in these body components with time. The essence of simulating growth in animals is to predict, as accurately as possible, the changes in body composition and size over time. According to Emmans and Fisher (1986) there are three approaches to solving the dilemma of predicting growth rates:

(1) predict the changes in empty body mass as a whole;
(2) predict the growth of the protein, lipid, moisture and ash components separately; or

(3) predict only one component and then quantify the allometric relationship between this base component and the remaining three.

For the purpose of the model developed in this thesis, the third option is used. By making body protein and its derivative, the rate of protein retention, the central building block, the model is simplified without losing any accuracy in predicting changes in body composition. Body protein content is used to define the current state or condition of the animal, which is then used to quantify the remaining body constituents and their respective growth rates (Taylor, 1980). This is achieved by implementing the allometric relationships between protein and lipid, moisture and ash (Moughan *et al.*, 1990). A suitable function describing protein growth must be used. Whittemore, Tullis and Emmans (1988), Kyriazakis and Emmans (1990) and Ferguson and Gous (1993b) found the Gompertz growth function to be a suitable expression for predicting protein growth. Although the Gompertz function of growth is not the only function available for predicting protein growth, it was chosen for the following reasons :

(1) simplicity;
(2) it has mathematical properties that simulate a biological response fairly precisely;
(3) it fits growth data well;
(4) there are only three parameters,and these all have biological meaning; and
(5) it describes protein growth fairly accurately.

The Gompertz equation to describe protein mass is :

$$Pt = Pm \times e^{-e^{(\ln(-\ln(u_o)) - B \times t)}} \quad (kg) \qquad (1.1)$$

where Pt = protein mass at time t (kg)
Pm = mature protein mass (kg)
$u_o$ = degree of maturity at birth
B = rate of decay of relative growth rate ($day^{-1}$)
t = age (day)

The derivative of this equation describes the rate of protein growth as:

$$\frac{dP}{dt} = B \times Pm \times u \times \ln(1/u) \quad (g/day) \qquad (1.2)$$

where ln = natural logarithm
u = degree of maturity, (Pt/Pm)

These two functions allows the potential rate of protein growth of an animal to be predicted from only two inherent characteristics, viz. B and Pm, and its present body state, u. The equations above indicate that the rate at which an animal grows will depend almost entirely on its current state or size (Taylor, 1980). To quantify the rate of maturing or growth constant (B), a modified serial slaughter experiment needs to be done in order to plot the logarithm of body protein against the relative protein growth rate. The mature protein weight can be extrapolated from this function. This technique is described in detail in later chapters.

If each chemical component were independent of all the others then there would be a mature weight and B value for each component. However, it would appear that the components are dependent on each other such that it would not be a gross oversimplification to consider that the same B value applies to potential protein, lipid, moisture and ash content (AFRC, 1991). It is axiomatic that the composition of gain would change systematically as the animal matures. This will allow the use of allometry to predict body lipid, moisture and ash contents from body protein weight.

As the characteristics B and Pm are inherited they will vary both between and within sexes and strains. Examples of estimated constants for different sexes and strains of pigs derived from the literature are shown in Table 1.1. Whittemore (1983) and Whittemore *et al.* (1988) provide additional estimates of mature protein weight.

Table 1.1. Inherent animal growth characteristics for different sexes and strains of pigs obtained from various literature sources.

| Literature source and pig type | B (/day) | Pm (kg) | LPm | pPRmax (g/day) | t* (days) |
|---|---|---|---|---|---|
| Campbell *et al.* (1985a) | | | | | |
| Large White x Landrace commercial male | 0.0125 | 36.0 | 3.50 | 167 | 137 |
| Campbell *et al.* (1985b) | | | | | |
| Large White x Landrace commercial male | 0.0140 | 27.0 | 3.30 | 139 | 105 |
| Campbell and Taverner (1988) | | | | | |
| Large White x Landrace superior male | 0.0118 | 42.0 | 3.00 | 182 | 134 |
| Kyriazkis *et al* (1990) | | | | | |
| Large White x Landrace superior male | 0.0135 | 44.0 | 2.80 | 219 | 122 |
| Gatel *et al.* (1992) | | | | | |
| Large White x Landrace superior female | 0.0135 | 34.0 | 2.30 | 169 | 121 |
| Ferguson and Gous (1993b) | | | | | |
| Large White x Landrace improved male | 0.0107 | 38.7 | 2.60 | 152 | 144 |
| Large White x Landrace improved female | 0.0120 | 28.4 | 3.89 | 125 | 123 |

* Age when PRmax is attained.

The model assumes that protein growth reaches a peak at a live weight of 0.368 of its mature weight and then declines thereafter to zero at maturity, in accordance with the Gompertz growth function. The maximum rate is dependent on both sex and strain. Table 1.1 shows the predicted maximum potential protein growth rates for different combinations of sex and strain. These estimates are higher than those suggested by Whittemore (1983) but similar to those estimated by Campbell and Dunkin (1983) and by Whittemore *et al.* (1988).

The age at which maximum protein deposition is attained is, by the function defining protein growth, proportional to the mature size of the animal and will therefore vary according to genotype. Values shown in Table 1.1 are similar to those reported by the Standing Committee on Agriculture (SCA) (1987).

### 1.3.3 Lipid growth

One of the main problems with modelling growth in an immature animal is that of determining potential lipid growth. The genetic characteristics of lipid growth are easily and readily confounded by the environment and nutrition. Feeding a balanced, ideal protein:energy ration in a thermally neutral environment will result in minimum fat deposition. The theory of the model proposed here is that this minimum lipid gain is described as the desired rate of lipid deposition or the inherent fatness of the animal. The desired amount of fat will be determined by the amount of structural fat, storage fat and the way the animal is fed (de Greef, 1992).

Given an ideal set of growing conditions an immature animal will deposit a predetermined quantity of fat which implies that the animal is attempting to maintain an intrinsic state of being rather than depositing body tissue in a random and disorganised manner or as a consequence of living. Both Parks (1982) and Emmans and Fisher (1986) postulate the theory that animals grow to fulfil their genetic potential and that changes in the composition of growth reflect the animal's attempt to correct any deviations from this intrinsic ideal. Further support for this hypothesis has been forthcoming from the work conducted by Kyriazakis and Emmans (1991) and de Greef (1992).

It is practically impossible to measure the desired fatness of an animal because of the confounding effects of the environment and nutrition on lipid growth and the constantly changing 'ideal' environment and nutritional requirements over time. Nevertheless it would be incorrect to disqualify a theory on the basis of an inadequate technique to quantify the concepts behind the theory. Trying to prove a concept that is almost impossible to measure should not and must not be used as a reason to discredit the concept. However, the theory should be transparent enough to be able to explain observed experimental results. What is therefore required is some indication whether, in practice, there is evidence contrary to the basic philosophy such that one could disprove the theory rather than attempt to prove it.

There is ample experimental evidence to show that previously restricted pigs with lower levels of fat than unrestricted pigs, returned to normal levels of fat, for a given protein weight (Cole, Duckworth, Holmes and Cuthbertson, 1968; Owen, Ridgman and Wyllie, 1971; Stamataris, Kyriazakis and Emmans, 1991). More recently there has been evidence to show that pigs previously made fatter than normal by feeding a food deficient in protein also returned to a normal lipid:protein ratio after subsequent feeding of a higher protein diet (Wahlstrom and Libal, 1983; Kyriazakis, Stamataris, Emmans and Whittemore, 1991; Kyriazakis and Emmans, 1991; de Greef, 1992) .

It may be argued that the restoration of the lipid:protein ratio is a direct consequence of consuming a more 'ideal' ration and has little to do with an inherent characteristic of the animal. This argument presupposes that an animal eats for the sake of eating rather than for the sake of trying to satisfy its goal of attaining a desired mature state. Kyriazakis and Emmans (1991) observed animals that had been made fatter by feeding a low protein diet and were then given a choice between a low and high protein food, ate over twice as much more of the high protein food than those animals that were given the same choice but were not as fat. The results inferred that the fatter animals deliberately chose to eat more of a food that would enable them to deposit less fat and more protein tissue, such that the lipid:protein ratio could be restored to a value which is independent of their nutritional history. Although this is not proof that an animal has an ideal intrinsic body composition, it does provide strong evidence for such a concept.

The use of an inherent level of fatness to describe the potential lipid growth rate presupposes that there is a relationship between lipid and the remaining lipid-free component of the body, such that for any given protein weight the potential lipid weight can be determined. The high correlation coefficients between the desired lipid and non-lipid contents (Doornenbal, 1971,1972; Moughan, Smith and Stevens, 1990) implies that given the ideal conditions an animal will partition energy between protein and lipid deposition according to a predetermined level. The animal will be prevented from achieving this inherent level of fatness by a number of extrinsic factors such as the energy and protein intakes, high ambient temperatures and other environmental factors.

According to de Greef (1992) the current state of the animal has a marked effect on the rate of protein and lipid deposition and yet it has not been included in any pig growth models other than the one proposed here. The theory of a desired level of fatness will solve this problem by determining the rate of fat deposition as that required by the animal to maintain a normal lipid:protein ratio and therefore energy can be partitioned between protein and lipid accordingly.

According to Webster (1989) and Emmans (1989) as an animal strives to achieve an inherent mature size, described by the asymptotic body protein weight on the sigmoidal growth curve, it deposits tissue to attain a desired condition. Included in this body tissue is a certain level of fat which is best described in relation to body protein in the form of a Lipid:protein ratio at maturity (LPm) and an allometric coefficient relating lipid content to protein. The lipid content of an animal growing at its potential can thus be predicted at any time from the current protein weight of the animal. A knowledge of the desired fatness is particularly useful in situations where the animal has deviated from its desired level of fatness (discussed later). Linked to the desired level of fatness is the extent to which the diet being fed is balanced with regard to the first limiting nutrient:ME ratio. A poor quality diet will result in an animal being fatter than its inherent fatness.

Similarly, restricting feed intake will be associated with a leaner animal (Emmans, 1989) (Figure 1.2).

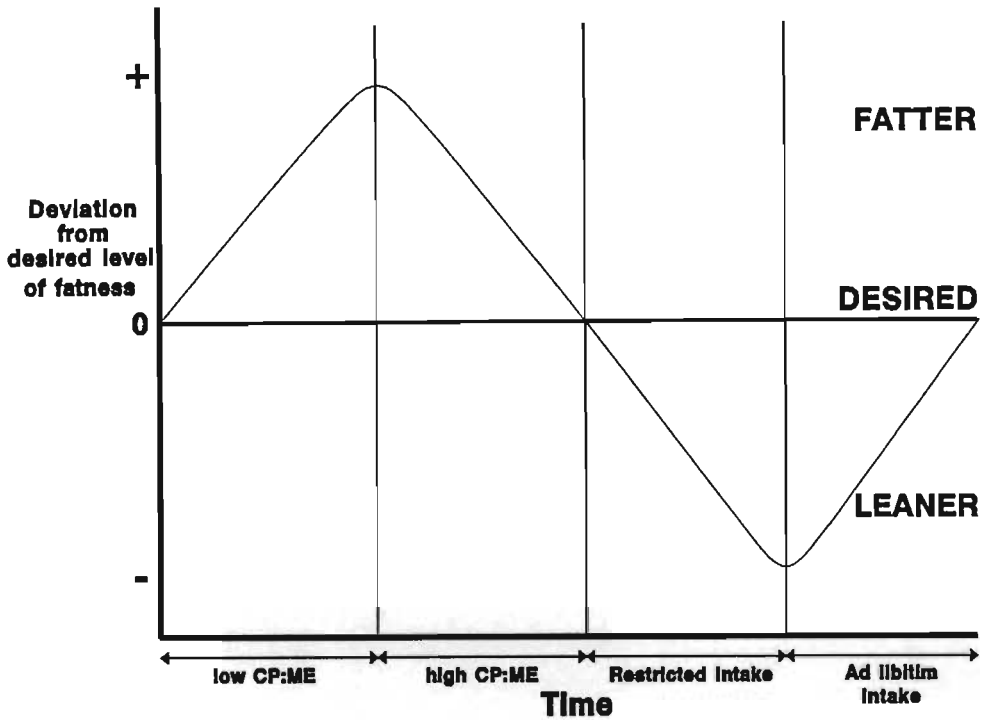


Figure 1.2 Animal responses to different nutritional stimuli.

As few data exist on the mature weight of lipid for different strains of pigs, it is very difficult to obtain LPm values. An additional constraint is that body lipid weight is entirely dependent on the supply of resources. Therefore, the problem with determining the LPm at maturity from experimental data is the large variation in experimental conditions. Unless the pigs are given free and continual access to a non-constraining feed in a non-constraining environment the ratio will vary considerably between experiments (Emmans, 1989). In addition to this, the inherent fatness will vary both between sexes and strains, so different LPm values will be required if the model is to be useful in predicting growth under different conditions. At present only Ferguson and Gous (1993b) have published estimates of LPm for pigs (Table 1.1), although Bridges *et al.*, (1983) and Whittemore *et al.* (1988) have provided realistic estimates of 2.15 and 2.00 respectively for boars and 3.70 and 3.53 respectively for castrates. By making use of the experimental technique described by Ferguson and Gous (1993a) to determine the mature protein and lipid weight, this problem can be solved.

To predict growth and particularly lipid growth in growing pigs it is imperative that recognition be given to the resilient nature of the animal after undergoing a period of nutritional deprivation both in quality and quantity. Compensatory lipid growth has been readily demonstrated in growing

pigs (Tullis and Whittemore, 1986; Tullis *et al.*, 1986 and Kyriazakis *et al.*, 1991; Stamataris *et al.*, 1991). Using the concept of a desired fatness compensatory growth in lipid can be determined by summation of the desired lipid growth (dLr) and the difference between actual body fat and desired body fat content.

$$dLr = pLr + \frac{(DesiredL_t - L_t)}{1000} \qquad (g/day) \qquad (1.3)$$

where pLr = minimum potential lipid deposition (kg)
$DesiredL_t$ = Desired body fat content (kg)
$L_t$ = Actual body fat content (kg)

$DesiredL_t$ is the expected fat content of the body based on the current protein content. If the animal is fatter than desired then the desired Lr on the following day will be less, in order to compensate for the extra fat deposited the previous day (Kyriazakis and Emmans, 1991; Kyriazakis *et al.*, 1991; de Greef, 1992). Provided it is possible the animal will deposit less lipid on the following day. Similarly, if the animal is leaner than expected, for a given protein content, then the desired Lr would be higher than the minimum genetically-determined Lr.

Determining the compensatory responses of an animal based on its body state is preferable to the approach of Black *et al.* (1986) who used a compensatory gain factor to multiply the protein deposition rate, irrespective of the current physiological status of the animal.

### 1.3.4 Moisture and ash growth

For growth in non-limiting conditions the relative proportions of moisture and ash are less likely to vary between sexes and strains than are the proportions of lipid (Moughan and Verstegen, 1988; Moughan *et al.*, 1990; AFRC, 1991). The weights of moisture and ash are likely to be a simple power function of protein weight. This is discussed in greater detail below.

### 1.3.5 Empty body weight

During growth the relationships between the four chemical components change to allow functional and anatomical changes. According to Taylor (1965) the composition of the empty body changes systematically during development with a definite relationship between protein and the non-protein components (C) , such that for any given stage of maturity the proportions of the moisture and ash content relative to protein will remain constant. Hodge (1974), Hakansson, Eriksson and Svensson (1978) and Blaxter, Fowler and Gill (1982) all showed a linear relationship between the logarithm of C (*ln C*) and the logarithm of protein (*ln P*). For growth in

non-limiting conditions the relationship between the weight of protein and lipid, water and ash can therefore be expressed as an allometric function (AFRC, 1991):

$$Ct = a \times Pt^{b} \quad (kg) \tag{1.4}$$

where a = a scalar value
$b = (\ln C_m - \ln C_o) / (\ln P_m - \ln P_o)$
$C_m$ = mature component weight (kg)
$C_o$ = component weight at birth (kg)
$P_m$ = mature protein weight (kg)
$P_o$ = protein weight at birth (kg)

This relationship can be explained mathematically by making a few reasonable assumptions. If it is assumed that the Gompertz function describes protein, lipid, moisture and ash growth and that B is common for all components then Equation 1.1 will hold true for potential lipid, moisture and ash growth. Modifying Equation 1.1 by transferring the mature weight component to the left hand side, makes it possible to predict the degree of maturity achieved for a given component weight.

$$\frac{Ct}{Cm} = e^{-e^{-(\ln(-\ln(u_o)))-B\times t}} \tag{1.5}$$

where Cm = mature component weight (kg)

Relating the degree of component maturity to the degree of protein maturity produces the following expression:

$$\frac{Ct}{Cm} = \left(\frac{Pt}{Pm}\right)^{b_c} \tag{1.6}$$

where $b_c = (\ln(-\ln(u_o))_c - (\ln(-\ln(u_o))_p$
c and p subscripts refer to component and protein respectively

so that:

$$Ct = \left(\frac{Cm}{Pm^{b_c}}\right) \times Pt^{b_c} \quad (kg) \tag{1.7}$$

Since Cm, Pm and $b_c$ are constants for a given genotype equation 1.7 can be simplified as:

$$Ct = a_c \times Pt^{b_c} \quad (kg) \tag{1.8}$$

where $a_c = Cm/Pm^{b}$

Equations 1.4 and 1.8 show the potential weights of lipid, moisture and ash are simple power functions of the weight of protein.

The estimates of *a* and *b* for lipid are extremely variable across genotypes and very difficult to determine, as lipid growth is sensitive to both the environment and the quality of the feed. However, it is expected that *b* or the "rate of fattening" will be greater than 1.0 because fattening

occurs at a faster rate than deposition of proteinaceous tissue (Whittemore, 1993). As previously discussed the lipid weight at maturity also varies between sexes and strains, necessitating a parameter to define the intrinsic fatness of an animal.

The relative proportions of moisture and ash is fairly constant across genotypes, such that allometric functions can be used for most animals (Hodge, 1974; Moughan *et al.*, 1990; de Greef, 1992; Whittemore, 1993; Kyriazakis and Emmans, 1994). The amount of water relative to protein diminishs systematically with an increase in live weight with the result that the moisture *b* value will be less than 1.0. From a number of different sources a value between 0.850 and 0.880 would provide a close approximation for *b* across various genotypes (Whittemore *et al.*, 1988; Moughan *et al.*, 1990; de Greef, 1992; Kyriazakis and Emmans, 1992a,b). The *a* value, varies across genotypes because of its relationship to Pm. If it can be assumed that the mature water:protein ratio is relatively constant for most animals, approximately 3.25, *a* can be calculated for each genotype and therefore need not be another animal parameter.

The growth of ash relative to protein growth is similar such that the ratio of ash to protein remains fairly constant throughout the growth of the pig in the region of 0.19 to 0.23 (Doornenbal, 1975; Whittemore *et al.*, 1988; Kyriazakis and Emmans 1992a,b). The allometric coefficient, *b*, is therefore presumed to be 1.0, and the *a* value, on average, equals 0.21.

To predict the changes in body lipid, moisture and ash over time a similar approach to that of predicting actual weights can be adopted. If the protein growth rate is known or can be determined and there is a relationship between protein and the component in question, then the growth rate of each component (dC/dt) can be predicted. Expressed in an equation form this is :

$$\frac{dC}{dt} = \frac{dP}{dt} \times \frac{dC}{dP} \qquad (g/d) \qquad (1.9)$$

where dC/dt = lipid, moisture or ash growth rate (g/d).
dP/dt = protein growth rate (g/d)
dC/dP = relationship between lipid, moisture or ash and protein.

This function forms the basis for predicting daily empty body weight gains (EBWG), being the sum of the protein, lipid, moisture and ash weight gains. It is therefore necessary to determine the growth rates of the individual component.

Differentiating Equation 1.4 gives:

$$\frac{dC}{dP} = a \times b \times P^{b-1} \qquad (g/g\ protein) \qquad (1.10)$$

The straight line defined has only two parameters, the slope (*b*) and a point on the line. Mature weight is the point most conveniently used. If the slope of the graph *ln C* versus *ln P* is equal to *b* then the slope describing the logarithm of the component:protein ratio (CP) versus the logarithm of the degree of maturity will be *b*-1. Equation (1.10) can now be written as :

$$\frac{dC}{dP} = CPm \times b \times u^{b-1} \qquad (g/g\ protein) \tag{1.11}$$

where CPm = component:protein ratio at maturity

Adding Equation (1.11) and (1.2) into (1.9) gives the change in component weight over time or growth rate, namely:

$$\frac{dC}{dt} = Pt \times B \times \ln(\frac{1}{u}) \times CPm \times b \times u^{b-1} \qquad (g/day) \tag{1.12}$$

From the summation of all four component growth rates the EBMG can be described as:

$$EBWT = (Pt \times B \times \ln(\frac{1}{u})) \times (1 + (LPm \times b_l \times u^{c_l}) + (WPm \times b_w \times u^{c_w}) + (APm \times b_a \times u^{c_a})) \qquad (kg/d) \tag{1.13}$$

where subscripts: c = b-1
l = lipid
w = water
a = ash

The prediction of the potential growth and composition of an animal is therefore dependent on the degree of maturity or state, the component:protein ratio at maturity and the allometric constants and coefficients of the different components, B and Pm. As the b coefficient estimates (except those for lipid) remain constant for most sexes and strains of pigs the genotype of the pig is defined by four animal variables viz. Pm, B, LPm and $b_l$.

As the model is dynamic in nature, the genotype and state of the animal at the beginning of the day will determine the potential rate of growth of protein on that day. The potential growth rate of the other chemical components of the body can be predicted, by allometry, from the protein growth rate. If this potential growth rate is added to the initial condition of the animal, the state of the animal at the end of the day can be predicted. This state becomes the initial state on the following day, and the process is repeated.

Whether the animal is able to achieve its potential growth rate each day is dependent on the feed being offered and on the environment in which it is housed. The constraining effects of the feed and the environment have to be calculated in order to predict the actual growth rate and carcass composition of the animal each day.

### 1.3.6 Maintenance requirements

The ability of the animal to remain in an unchanged state is referred to as maintenance (Brody, 1945). According to the ARC (1981) maintenance requirements for energy is defined as the amount of metabolizable energy (ME) required to obtain zero energy retention. A number of different approaches to measuring maintenance energy requirements ($ME_m$) have been suggested (ARC, 1981; NRC, 1988). The most commonly used method is based on the regression of energy retention on energy intake and the extrapolation of energy intake to zero energy retention to obtain the estimate of $ME_m$. The problem with this approach is that extrapolating to zero energy retention does not necessary mean that protein and fat retention are both equal to zero, which is the true definition of $ME_m$. It may well be that fat is lost whilst protein accretion occurs at zero energy equilibrium (Fuller, Webster, MacPherson and Smith, 1976; Close and Mount, 1978). This situation can be further exacerbated by environmental conditions. It is incorrect to assume that the thermoneutral conditions, in which the animals were kept to obtain estimates of energy retained relative to energy intake, will hold true for extrapolated values at zero energy retention. At very low energy intakes, such as at maintenance, the environmental conditions will need to be significantly warmer to ensure that no extra fat is mistakenly lost to cold thermogenesis. The lower the environmental temperature is compared with the thermoneutral temperature the more fat will be lost in maintaining energy equilibrium. This is also applicable to the method of using fasting heat production to estimate $ME_m$.

Even where $ME_m$ has been determined from multiple regression analyses with fat and protein retention as independent variables there can be a problem of overestimating the true maintenance energy requirements. This is because the amount of heat produced from nitrogen excretion in the urine and the amount of heat produced from defecation have not been considered. With the consumption of any feed there will be some heat produced as a result of defecation and urination. True maintenance energy requirements should therefore be dependent on the food given and the environmental conditions. Generally across all live weights the recommendations of $ME_m$ by ARC (1981) and NRC (1988) will be higher than the true maintenance requirements. A further problem with maintenance functions that use live weight as the independent variable is that water and fat contents will be large components of the requirement for maintenance when, in fact, most maintenance is associated with proteinaceous tissue (Blaxter *et al* , 1982).

For maintenance, energy, protein and other nutrients are required to supply the mechanisms and functions that maintain the animal in its current state. The problem is to quantify the rate these nutrients need to be supplied for different genotypes at different stages of maturity. According to Emmans (1990) the problems of expressing maintenance requirements can be

solved by scaling between genotypes at maturity and between degrees of maturity for a given genotype. With this approach it would be possible to determine both the energy and protein requirements for maintenance.

Taylor (1970) recommended a general size scaling rule for maintenance based on the findings that maintenance at maturity is directly proportional to mature weight, and for immature animals maintenance is a function of weight. The maintenance rule states that the supply of nutrients for maintenance is a function of the present state of the animal and its genotype. Since most maintenance activity occurs in the intestines, liver and muscle tissue, it is reasonable to assume that maintenance is a function of protein weight rather than live weight (Metz and Dekker, 1981; Whittemore, 1983). This was found to be the case in sheep (Blaxter et al., 1982), cattle (Taylor and Young, 1968) and in chickens (Hakansson et al., 1978). The advantage of using protein weight is that the degree of fatness of the animal and how it achieved this level of fatness does not have to be taken into consideration. Emmans and Fisher (1986) propose a version of Taylor's (1970) rule such that :

$$MN = m \times Pm^{0.73} \times u \qquad (MJ/d\ ;\ g/d) \tag{1.14}$$

or,

$$MN = m \times Pm^{-0.27} \times P \qquad (MJ/d\ ;\ g/d) \tag{1.15}$$

where m = nutrient requirement per maintenance unit (g/kg or MJ/kg)

The estimated values of m for energy is 1.63 MJ/($P_m^{0.73}$) and for protein it is 8 g/($P_m^{0.73}$) (Emmans, 1988a).

### 1.3.7 Growth and Fattening requirements

The previous sections have shown that from a description of the genotype and the state of the animal, the rate of growth and fattening can be predicted. From Figure 1 it is apparent that the next problem is to calculate the energy and protein requirements of the animal in terms that are similar to those used to describe the feed, in order to predict the desired food intake. To solve the energy problem an energy scale needs to be defined by using nutritional constants to transform the rates of growth and fattening into rates of energy and protein supply. This will allow both requirements and feed resources to be measured on the same scale (Oldham and Emmans, 1990). Table 1.2 contains the values of all the coefficients used in the following statements. For more details on the energy scale described in the next few equations refer to the work by Emmans (1994).

The ME of a diet is described as the energy available for metabolism after faecal and urinary energy losses have been accounted for. Based on the law of energy conservation the definition is :

$$ME = ER + H \qquad (MJ/day) \tag{1.16}$$

where ER = energy retained (MJ/day)
H = total heat loss or produced (MJ/day)

Expanding the components of this formula gives :

$$ER = h_p \times PR + h_l \times LR \qquad (kJ/day) \tag{1.17}$$

where PR = protein retained (g/day)
LR = lipid retained (g/day)
$h_p$ = heat of combustion of protein (kJ/g)
$h_l$ = heat of combustion of lipid (kJ/g)

and,

$$H = FHP + HI \qquad (kJ/day) \tag{1.18}$$

where FHP = fasting heat production (kJ/day)
HI = heat increment (kJ/day)

Substituting Equations (1.17) and (1.18) into (1.16) allows ME to be defined as :

$$ME = FHP + h_p \times PR + h_l \times LR + HI \qquad (kJ/day) \tag{1.19}$$

Included in the FHP is an amount of energy that would be lost through the work done on excreting fasting urinary nitrogen (FUN). This means that maintenance heat (MH) can be described as :

$$MH = FHP - w_u \times FUN \qquad (kJ/day) \tag{1.20}$$

where $w_u$ = work done in excreting urinary nitrogen (kJ/g)
FUN = fasting urinary nitrogen (g/day)

With all the parameters in Equation (1.19) being qualified the problem arises of how to predict the HI for different animals and diets. Oldham and Emmans (1990) and Emmans (9194) discuss this problem and propose that, apart from maintenance, work is required only for five functions: excretion, fermentation, defecation, growth and fattening. The amount of heat produced by each function is assumed to be constant across genotypes and diets. In the case of the pig, fermentation can be assumed to be negligible and is therefore ignored. Heat increment is therefore defined as the increment in the work done as a consequence of a feed increment. This can be stated as the following :

$$HI = w_u \times (UN - FUN) + w_d \times FOM + w_p \times PR + w_l \times LR \qquad (kJ/day) \tag{1.21}$$

where $w_d$ = work done in defecation (kJ/g)
$w_p$ = work done in protein deposition (kJ/g)
$w_l$ = work done in fat deposition (kJ/g)
FOM = faecal (undigested) organic matter (g/day)
UN = urinary nitrogen (g/day)

Where UN = 0.16 . (DCP - PR) substituting Equations (1.20) and (1.21) into (1.19) and rearranging leads to :

$$ME = w_d \times FOM + w_u \times 0.16 \times DCP + MH + PR \times (h_p + w_p - 0.16 \times w_u) + LR \times (h_l + w_l) \quad (kJ/day) \qquad (1.22)$$

where DCP = digestible crude protein (g/day)

As it is a common practice in feeding pigs, to include a certain amount of fat in the diet, allowance has to be made for dietary fat being used for lipid deposition. Fat is deposited more efficiently if the source of energy is from dietary fat rather than protein or carbohydrate sources. A proportion (k) of the dietary fat (DFAT) is retained with the remaining lipid retention (LR - k.DFAT) arising from other sources. The total heat production of lipid deposition is thus :

$$H(LR) = w_l \times LR - k \times DFAT \times (w_f - w_l) \quad (kJ/g) \qquad (1.23)$$

where k = proportion of dietary fat retained as body fat
DFAT = dietary fat (g/kg)
$w_l$ = work done in retaining fat from dietary protein and carbohydrate sources (kJ/g)
$w_f$ = work done in retaining fat from dietary fat (kJ/g)

This means that more energy is available for other processes and as such the ME value of the feed will increase proportionately to the amount of dietary fat by a value of k.DFAT. ($w_l - w_f$).

A further correction to Equation (1.22) is needed before a final estimate of the available energy content can be determined. There is a problem with the amount of ME yielded by digestible protein. A proportion of digestible protein is catabolized emitting less energy than that obtained from bomb calorimetry results. As the nitrogen from the catabolized protein is excreted in the urine some nitrogen correction factor is required. The method in this model is based on the procedure suggested by Emmans and Fisher (1986) that the urinary energy, assuming all of the digested protein had been catabolized, should be deducted from both the diet and the protein retained. The ME value becomes,

$$ME_n = ME - a \times DCP \quad (kJ/g) \qquad (1.24)$$

where $ME_n$ = ME corrected for zero nitrogen retention (kJ/g)
a = heat of combustion of urine (kJ/g)

The amount of dietary energy that is effectively available for maintenance, growth and fattening can be determined by transferring the first two terms of Equation (1.22) to the left hand side and incorporating Equation (1.24) to give,

$$EEC = ME_n - w_d \times FOM - w_u \times 0.16 \times DCP + k \times DFAT \times (w_f - w_l) \quad (kJ/g) \qquad (1.25)$$

Table 1.2 Estimated values of the coefficients used in the model (after Emmans, 1994).

| Description | Value | Unit |
|---|---|---|
| $w_u$ | 29.20 | kJ/(g 0.16*DCP) |
| $w_d$ | 3.80 | kJ/g FOM |
| $w_f$ | 4.40 | kJ/g lipid deposited |
| $w_l$ | 16.40 | kJ/g lipid deposited |
| $w_p$ | 36.50 | kJ/g protein deposited |
| $h_p$ | 23.80 | kJ/g protein retained |
| $h_l$ | 39.60 | kJ/g lipid retained |
| a | 34.4 | kJ/g nitrogen |
| k | 0.30 | - |

Substituting values from Table 1.2 gives,

$$EEC = ME_n - 3.80 \times FOM - 4.67 \times DCP + 12 \times k \times DFAT \quad (kJ/g) \tag{1.26}$$

The variable k, varies between zero, when there is no lipid deposition, to one when all dietary fat is deposited as body fat. The value will vary according to the diet composition and the state of the animal. It is estimated that k will be close to 0.3 (Emmans, 1988).

The effective energy scale considers the energy lost due to an increased heat increment following dietary protein utilization. Consequently for a given ME supply there will be less energy available for growth as dietary protein supply is increased. The extra heat loss affects the partitioning of energy with less available for fat deposition (Noblet, Henry and Du bois, 1987).

The same energy scale used to determine the energy content of the feed is also used to measure the energy requirements of a growing animal in a given state and living in a non-limiting environment. The function describing the requirements consists of those variables in Equation (1.22) that are not included in Equation (1.25) to give :

$$EER = MH + PR \times ( (h_p - 0.16 \times a) + (w_p - 0.16 \times w_u) ) + LR \times (h_l + w_l) \quad (kJ/day) \tag{1.27}$$

Applying values from Table 1.2 gives :

$$EER = MH + 50.3 \times PR + 56.0 \times LR \quad (kJ/day) \tag{1.28}$$

The concept of an ideal protein allows the protein value of the diet and the amino acid requirements of the animal to be expressed in a single common quantity (Fuller and Wang, 1990). Using the prediction of the potential rate of protein growth and the maintenance needs

for a particular animal, the quantities of amino acids to satisfy these functions can be determined. The factorial approach in this model is analogous to that defined by the AFRC (1991) and Edwards and Campbell (1991). The required amino acid intake (AAR) is defined in terms of a response function relating intake of the first limiting amino acid to the potential level of production and maintenance of the animal (Fuller, McWilliam, Wang and Giles, 1989). However, instead of the response being described in terms of live mass, protein growth rate and maintenance protein are used. This will give :

$$AAR = \frac{(a_i \times PR)}{e_p} + \frac{(b_i \times MP)}{e_m} \qquad (g/day) \qquad (1.29)$$

where $a_i$ = coefficient of first limiting amino acid for growth (mg/g protein)
$b_i$ = coefficient of first limiting amino acid for maintenance (mg/g protein)
PR = dP/dt (g/day)
$MP = 0.008 \times P_m^{-0.27} \times P$ (g/day)
$e_p$ = efficiency of utilization of first limiting amino acid for growth
$e_m$ = efficiency of utilization of first limiting amino acid for maintenance

To determine the availability of amino acids the digestibility of each amino acid is required. As the digestibility depends on the source of dietary protein and not the quantity of protein, it is considered a decision variable that is entered by the user. A certain amount of inefficiency does exist when dietary available amino acids are converted into actual tissue, with the result that ideal protein requirements need to be adjusted before being stated as actual requirements. In this regard an important assumption in the model is that the coefficients of utilization of the essential amino acids for growth (*a*) and for maintenance (*b*) are constant across sexes, strains and genotypes of pigs. From this assumption the ideal amino acid balance for growth will be similar to that found in the protein tissue. Whittemore (1983) suggests a coefficient of net utilisation of amino acids for growth of between 0.85 and 0.95, whilst Fisher (1988) predicts a lower value of 0.75. In this model allowance is made for the possible differences in net efficiency between amino acids for growth and maintenance by allowing these values to be changed by the user. The default efficiency values are 0.75 for growth and 1.00 for maintenance (ARC, 1981).

## 1.4 The theory controlling food intake and the subsequent growth responses

Having scaled the requirements of the animal and the yield of the food resources in similar terms, the rules controlling food intake can be discussed. However, in order to comprehend fully the changes in body state with time, feed intakes need to be considered, because body changes are the responses, or outputs, to inputs of nutrients (Parks, 1982; Henry, 1985; Pekas, 1985; Kemm, Siebrits, Ras and Badenhorst, 1991). Quantitative descriptions and hypotheses of the controlling forces behind the growth response to feed consumption are thus necessary. Allowance for feed intake must

include not only the quantity but the quality of the feed available to the animal, because these two components will both contribute to the changes that occur in carcass composition as the animal grows (Kyriazakis and Emmans, 1992a,b).

According to Whittemore (1986) growth responses should be considered in terms of feed intake and not of time. This approach assumes an initial linear phase, as feed supply increases, up to a plateau representing the maximum potential protein growth. Once this maximum has been attained, all the extra food consumed is diverted to fat. The problem with this approach is that the potential protein growth rate is assumed to be dependent on appetite and independent of the state of the animal. This is contrary to what Taylor (1980) suggested when describing the usefulness of the "degree of maturity" in predicting growth of different species and genotypes (degree of maturity being measured as the proportion of body protein to mature body protein weight). Furthermore, Emmans and Fisher (1986) reason that Whittemore's model is not appropriate as the potential protein growth rate, as defined by the Gompertz equation, is a function of state or stage of maturity rather than food intake. The maximum rate of protein deposition at a particular time is determined by the protein content of the body at that time. Whether the intrinsic limit is attainable will depend on extrinsic factors such as energy and protein intake. The preferred theory, and the one used in this thesis, is that animals will attempt to eat an amount of food sufficient to reach their potential growth rate and desired body composition.

The theory involved in predicting feed intake is based on that proposed by Emmans (1981), Emmans and Fisher (1986) and Emmans and Oldham (1988). The theory has shown a degree of pragmatic value with realistic results for broilers (Emmans, 1987; R.M. Gous, 1992 unpublished), turkeys (Emmans, 1989) and growing pigs (Ferguson and Gous, 1993b). This present model demonstrates the feasibility of this theory for predicting the voluntary feed intake of growing pigs and is a more logical and appealing approach to animal growth than that of Black *et al.* (1986) and Pomar *et al.* (1991) because of its simplicity, accuracy and general application.

The theory is based on the premise that an animal will attempt to consume an amount of feed that will satisfy its requirements for potential growth and maintenance. The animal will succeed if it is able to eat the amount of food which just allows it to achieve its desired purpose. The idea of attributing some objective to the animal has also been implied in other theories of voluntary food intake (Booth, 1978; Forbes, 1980). In a thermal neutral environment, the constraining factor is likely to be the first limiting nutrient.

The desired feed intake (DFI) will therefore be the quantity of the diet needed to satisfy the requirement (RQ) for the most limiting nutrient, whether it be energy, an amino acid or some micro-nutrient and is defined as:

$$DFI = \frac{RQ}{FCON} \quad (g/day) \tag{1.30}$$

where RQ = animal requirement for first limiting nutrient (g/d)
FCON = concentration of first limiting nutrient in the diet (g/g)

If energy is the most limiting nutrient then substituting equations (26) and (28) into equation (30) the desired feed intake in a thermoneutral environment will be that required to satisfy energy ($DFI_e$):

$$DFI_e = \frac{EER}{EEC} \quad (g/day) \tag{1.31}$$

If on the other hand an amino acid is the first limiting nutrient then the desired feed intake ($DFI_p$) will be based on the available amino acid requirement and the concentration of dietary available amino acid (Batterham, Giles and Dettman, 1985; Kyriazakis and Emmans, 1990; Henry and Seve, 1993). To determine the availability of the limiting amino acid in the diet, the quality of the protein has to be considered (ARC, 1981; Whittemore, 1983; Moughan *et al.*, 1987). The quality of protein supplied is quantified by the relative biological value (BV). The BV represents the proportion of the first limiting amino acid in the feed relative to the ideal protein balance. The $DFI_p$ to satisfy potential protein growth (pPr) from the first limiting amino acid is:

$$DFI_p = \frac{(\frac{pPR}{e_p} + \frac{MP}{e_m})}{dCP \times BV} \quad (g/day) \tag{1.32}$$

Where pPR = potential protein growth rate (g/d)
$e_p$ = efficiency of protein utilization for growth
$e_m$ = efficiency of protein utilization for maintenance
MP = Maintenance protein (g/day)
dCP = digestible crude protein (g/kg)
BV = biological value of diet

The efficiency of protein utilization for growth ($e_p$) and maintenance ($e_m$) is affected by a number of different dietary factors including the availability of amino acids after processing and the amount of energy supplied (ARC, 1981). The effect of amino acid availability is very difficult to incorporate into a model when the composition of the diet is an input variable because it is dependent on the composition and treatment of dietary protein. For this reason protein and amino acid digestibilities have been included in the model as input variables.

To facilitate the effect of energy intake on the retention of protein, the model uses the paradigm proposed by Kyriazakis and Emmans (1992a,b), where $e_p$ is defined as a function of the energy:protein ratio (ME:dCP) in the feed. The relationship between $e_p$ and ME:dCP is best described by a linear-plateau model with a maximum $e_p$ value of 0.81. As ME:dCP decreases beyond the critical value, $e_p$ declines with a concomitant decrease in protein deposition and an increase in lipid deposition. Similarly, as the amount of energy in the diet, relative to protein, increases there is an increase in $e_p$ until a point is reached beyond which no further improvements in $e_p$ occur. This critical

point according to Kyriazakis and Emmans (1992a,b) occurs when the ratio of ME:dCP equals 72.55 MJ ME/g dCP. Beyond 72.55 the extra energy, after satisfying protein growth and maintenance requirements, will be deposited as fat and therefore has no further effect on the efficiency with which protein is retained. Above this critical point the actual amount of protein retained will depend on the intake of protein and will be independent of energy intake. If the ratio of ME:dCP drops below 72.55 then there will be insufficient energy to utilise all the protein supplied with the result that the excess protein that is not retained will be catabolized. The net result will be a reduction in $e_p$. Therefore, with a low ME:dCP ratio protein retention will be dependent on energy intake such that with an increase in the rate of supply of energy there will be a concomitant increase in protein deposition.

This theory of considering simultaneously the effect of energy and protein intake on $e_p$ is supportive of the recognized linear/plateau relationship between protein intake and retention (Campbell *et al.*, 1985; Dunkin and Black, 1987; Edwards and Campbell, 1991). However, it is contrary to the idea that maximum protein deposition is solely a function of energy or protein intake as proposed by ARC (1981), Emmans (1981) and Emmans and Fisher (1986). The model will therefore allow for the prediction of protein and lipid growth rates as a response to a given diet. The net efficiency of ideal protein utilization is described as:

$$e_p = 0.0112 \times \left(\frac{ME}{dCP}\right) \qquad (1.33)$$

with maximum $e_p = 0.81$

The effect of sex and genotype on $e_p$ is inconsistent and inconclusive with ARC (1981), Ellis, Smith, Henderson, Whittemore, Laird and Phillips (1983), Campbell and Taverner (1988) and Kyriazakis, Dotas and Emmans (1994) proposing the more popular choice that sex and genotype of the animal does have an effect on the $e_p$ value. On the other hand Campbell, Taverner and Curic (1983), Dunkin and Black (1987), and more recently Kyriazakis and Emmans (1992b) observed results that did not support this theory. The apparent contradictions may have to do with the differences in the experimental design and implementation, the stage of maturity of the experimental animals as well as the level of protein intake. The proponents of sex and genotype having an affect on $e_p$ base their argument predominately on the results of Campbell and Taverner (1988), which may or may not be defensible, depending on the experimental procedure. The results of this experiment,however, reveal very low ash:protein ratios for all strains (0.14 - 0.15) relative to the the normal ratio of between 0.19 and 0.23 (Moughan *et al.*, 1990). This would suggest that there may have been a deficiency in one of the micro-nutrients. This in itself may not be a problem except that the experimental design is based on the assumption that energy is the most limiting nutrient. If, as suggested, energy had not been the first limiting nutrient then the observed growth response to increased levels of food (energy) intake were not due to energy but to the limiting micro-nutrient. This would then cast doubt on the inferences drawn from the observed results.

The results of a recent experiment by Kyriazakis *et al.* (1994) showed that there were no differences in $e_p$ between two very different genotypes, the Large White x Landrace cross and the Chinese Mieshan respectively.

Kyriazakis and Emmans (1992b) found no differences in $e_p$ between young male and female pigs up to 40 kg live weight. Similarly Duncan and Black (1987) observed very little and inconsistent changes in the slope of nitrogen retention on energy intake after 47 kg live weight.

If the $e_p$ value is dependent on the sex and genotype of the animal then the implications for modelling animal growth are disastrous because for every breed, strain, sex and level of feeding a different $e_p$ value would be required. To measure $e_p$ for all possible combinations of animals would require sophisticated experimentation which is not only costly and time-consuming but is also contrary to the basic philosophy of modelling of having as few decision variables as possible which are readily available and easy to measure. It may be argued that simplicity should not be maintained at the expense of accuracy. This may be true for situations where critical decisions within the model are required. However, in this case, it is questionable how much accuracy would actually be lost by opting for the simpler approach of assuming a constant $e_p$ value across different animals.

Where there are no physical constraints on food intake the actual feed intake (AFI) of the pig in a thermal neutral environment would be the larger of $DFI_e$ and $DFI_p$.

$$if \quad DFI_e > DFI_p \quad then \quad AFI = DFI_e \qquad (g/day) \tag{1.34}$$

or

$$if \quad DFI_p > DFI_e \quad then \quad AFI = DFI_p \qquad (g/day) \tag{1.35}$$

For a perfectly balanced feed:

$$AFI = DFI_e = DFI_p \tag{1.36}$$

Taking this approach one step further one is faced with the problems of what happens when DFI is not attainable, what rules are their to partition scarce resources and what will AFI be in such a case? From Figure 1.1 it can be seen that there are three possible reasons (two extrinsic and one intrinsic) why DFI might not be attained. The two possible extrinsic constraints are the environment and the feeding of an imbalanced or bulky feed. These two factors are interactive such that feeding an imbalanced feed can cause the animal to eat more and produce more heat than it can lose in its present environment. As these relationships are central to this theory of food intake they will be investigated and discussed in a latter chapter. The third source of prevention is the physical limitation of the gut capacity of the animal which is a function of both diet and genotype.

The pig would fail to eat its DFI if the density or bulkiness of the diet were such that gut capacity became a limiting factor or when the environment imposed certain constraints (Cole and Chadd, 1989; AFRC, 1991). The concept of a bulk constraint is a more rational approach to determining dietary constraints than that of imposing fixed maximum feed intakes irrespective of the actual dietary constituents (Whittemore,1993; Kyriazakis and Emmans, 1995). At present only the work by Kyriazakis and Emmans (1995) on the effect that feed bulk has on voluntary food intake, has the relationship between nutrient density of a diet (using water-holding capacity) and gut capacity been properly quantified. The model attempts to implement a bulk constraint by using the function proposed by Emmans (1981) namely:

$$BULKDN = 0.1 \times digOM + (1 - water - ash - digOM) \times (5 + fform) \quad (1.37)$$

where digOM = digestible Organic Matter of the diet
ash = ash content as a proportion of the diet
water = moisture content as a proportion of the diet
fform = physical form of the feed

The constrained feed intake determined by the bulk density (CFI) would be as follows:

$$CFI = \frac{90 \times Pt^{1.0}}{BULKDN} \quad (g/day) \quad (1.38)$$

Although the functional coefficients may not be absolutely correct because of inadequate data, the concept is preferable to any proposed in other models.

Predicting AFI of growing pigs is made difficult because of the constantly changing environmental and nutritional conditions and animal requirements with time. The model predicts feed intake as a function of sex, strain, physiological state of the animal and the quality of the diet. The latter factor needs to be expounded as it contributes significantly to the rates and composition of growth and to the daily requirements for energy and protein.

The quality of a diet is inextricably linked to the desire of the animal to deposit fat according to its physiological state (Kyriazakis and Emmans, 1991). The current state of the animal would reflect the response of the animal to its thermal environment as well as its nutritional history. An important corollary to the concept of maintaining a desired level of fatness is that at all times the animal can utilise body fat reserves, to a greater or lesser extent, to supplement dietary ME, when the need arises (Fowler, Fuller, Close and Whittemore, 1980; Metz and Dekker, 1981). The maximum amount of body fat available for utilisation on any one day is assumed to be half of the total body fat. The use of body fat reserves is limited to periods when the desired LR is less than or equal to 0. It is therefore possible to obtain significant protein growth rates at the expense of fat gains, which would not be possible if a minimum lipid to protein ratio were used, as proposed by many other models (Whittemore and Fawcett, 1976; Moughan *et al.*, 1987; Pomar *et al.*, 1991).

The recent work by Kyriazakis and Emmans (1991), Kyriazakis *et al* (1991) and de Greef (1992) provides substantial experimental support for the above mentioned theories. Kyriazakis and Emmans (1991) found that young pigs that were made fat by eating a poor quality diet (low CP:ME ratio) deposited fat at a much slower rate than pigs that were leaner when both were placed on a high protein diet. Similar results were observed by de Greef (1992) in older animals. What this implies is that the pig will attempt to return to a level of fatness associated with its current protein weight by restoring its inherent lipid to protein ratio (Figure 1.2).

If the pig is fatter than its inherent fatness then it will deposit less fat as soon as the constraint causing it to deviate from its desired fatness is removed. Similarly if it is very lean and it is given the chance to fatten, the pig will deposit fat at a faster rate than a pig that is at its desired degree of fatness (Stamataris *et al.*, 1991). Therefore, the efficiency with which the energy is utilised will vary according to the state of the animal and its inherent level of fatness (Kyriazakis *et al.*, 1991). Fatter animals will utilize a high quality diet more efficiently than will leaner animals because they will make available more energy from mobilizing fat reserves, for potential growth. This will result in less dietary energy being required. In this way the pig can achieve its potential protein growth whilst reducing its excess body fat. The effect will be to reduce feed intake, provided an amino acid or some other nutrient does not become limiting, until such time as the animal reaches its desired fatness. This has clearly been demonstrated by Kyriazakis and Emmans (1991) and de Greef (1992).

Assuming that the environment is not a constraining factor, there are three possible paths that could be followed by the animal. Associated with these paths are certain rules that control the partitioning of energy and protein resources into protein and lipid tissue.

### 1.4.1 Food Intake = $DFI_e$

This is the simplest of cases where the animal consumes enough protein to satisfy potential protein growth, and energy to provide for a certain amount of lipid growth that is associated with "normal" growth. Any excess protein is deaminated which incurs an energy cost, thereby reducing the amount of ME available for growth. The net result will be that feed intake will have to be increased to overcome the lower effective available ME and to provide sufficient energy for growth and maintenance. The potential rate of protein retention, as defined by its current state, and the minimum desired lipid deposition would be realised.

### 1.4.2 Food Intake = $DFI_p$

In this situation there is sufficient energy, but protein, or more specifically an amino acid is first limiting. There is considerable evidence indicating that pigs have the ability to regulate food intake according to their protein requirements (Batterham, Giles and Detterman, 1985; Henry,

1985; Cole and Chadd, 1989; Kyriazakis *et al* ., 1991; Henry and Seve, 1993). However, the response to a marginal deficiency in the first limiting amino acid appears to be contradictory with both increases and decreases in food intake being reported (Henry, 1985; Stamataris, Emmans, Hillyer and Whittemore, 1986; Kyriazakis and Emmans, 1990; Henry, Colleaux and Seve, 1992; Henry, Seve, Colleaux, Ganier, Saligaut and Jego, 1992; Henry and Seve, 1993). The extent of the contradiction is mainly a consequence of experimental procedure, the concentration of the deficient amino acid, and the environmental conditions in which the animals have been kept. Cooler conditions are more conducive to compensatory increases in food intake than warm environments. As the response to a limiting amino acid is fundamental to the food intake theory described in this thesis, it is necessary to investigate these responses further. This is covered in chapter 6. At this point it will suffice to say that the model adopts a general approach for all amino acids that an animal will attempt to satisfy its requirements for the most limiting amino acid by increasing food intake. This response is only possible if the environment is sufficiently cool to allow excess heat production to be dissipated.

The response to very high and very low dietary concentration of the limiting amino acid will be a reduction in voluntary food intake (Henry and Seve, 1993). The energy above that used for maximum protein retention and maintenance will be deposited as fat (Campbell *et al.*, 1984, 1985). The additional fat deposited will result in the pig being fatter than its inherent fatness. On the following day the animal would attempt to deposit less fat in order to return to its desired state (*c.f.* equation 1.3). It could only achieve this if the constraining factor, which had caused it to deposit more fat, were removed. In this case, it would mean increasing the concentration of the limiting amino acid.

Associated with the increase in fat deposition is the amount of heat produced by the animal. If the heat produced is greater than that which could be lost to the environment then additional constraints are placed on growth rate and feed intake. This will be discussed in more detail in the environmental section below. The amount of protein and lipid deposited will depend on the environment as well as the level of amino acid deficiency. It is possible for the potential protein deposition rate to be achieved if the environment is cool enough to be able to allow the animal to dissipate the extra heat generated from consuming an imbalanced feed. Lipid deposition will also increase to accommodate the extra energy consumed.

### 1.4.3 Food Intake = CFI

When the bulkiness of the food prevents the animal from meeting its potential growth rate, then a further factor has to be considered viz. what is the next most-limiting nutrient in the feed. This is an important consideration as it determines whether the animal can reach its potential protein

growth rate or not. It may be possible for the animal to consume sufficient protein to enable it to reach its potential but be restricted in energy intake. This would be the case if energy were the next most limiting factor after bulk. The model is designed first to allocate energy for maintenance. Secondly, energy will be allocated to maintain potential protein growth (pPr). If there is insufficient energy for pPr then Pr will be lower than pPr. In addition to this, the efficiency with which protein is deposited will be adversely affected. The change in efficiency is dependent on energy intake (Campbell and Taverner, 1988) or more specifically the energy:protein ratio, as demonstrated by Kyriazakis and Emmans (1992a,b).

Finally, any remaining energy will be deposited as fat. This amount will be less than desired resulting in a reduction from the animal's desired level of body fatness (*c.f.* Figure 1.2).

$$Lr = \frac{(AFI \times EEC) - (50.3 \times PR)}{56.3} \quad (g/day) \qquad (1.39)$$

The other alternative to energy being limiting, as a result of a bulk constraint, is if protein is limiting. The limited amount of amino acid is used firstly to satisfy maintenance and the remainder is used for growth. The limited amount available for growth will mean that Pr is less than pPR and the energy that would have been used for potential protein growth (pPr-Pr) is deposited as fat, which will increase above that desired. The consequence of this will be that the following day the pig will attempt to use the excess fat that has been deposited to return to its desired fat level or, if possible, it will deposit less fat. If this is not possible then further accumulation of fat will occur.

### 1.4.4 Restricted or Controlled food intake

Restricted food intake (RFI) or controlled food intake is the amount of food fed to the animal that is less than *ad libitum* food intake. The approach adopted in this model is to assume that the same initial rules apply that are applicable to *ad libitum* food intake except that daily food intake is constrained by some predefined limit. If in spite of the restriction imposed, there are sufficient quantities of the most limiting nutrient, be it an amino acid or energy, for potential growth to occur then potential protein growth will be attained. This will have consequential effects on energy partitioning with fat deposition being restricted to the remaining energy after requirements for maintenance and protein growth have been met..

There is no minimum lipid:protein ratio required, as adopted by most other models (Whittemore and Fawcett, 1976; Moughan *et al.*, 1987; Pomar *et al.*, 1991) to define the partitioning of energy when energy is limiting. Recently Whittemore (1993) has questioned whether a minimum lipid:protein ratio is really applicable to modern genotypes with a very high predisposition for lean

tissue. There is enough evidence to show that pigs do deposit protein at rates which far exceed that expected from a minimum lipid:protein ratio, and in some cases there have been positive protein gains at the expense of fat catabolism (Close, Mount and Brown, 1978; Metz and Dekker, 1981; Campbell and Taverner, 1988b; Kyriazakis and Emmans 1991). However, it is unlikely and improbable that any animal irrespective of its predisposition for lean tissue, will continue to deposit protein at its maximum potential when there is insufficient fat reserves available to supplement the dietary energy inadequacy. There is therefore a need to ensure that body fat reserves are not depleted beyond some realistic value. The model assumes a minimum body fat reserve of 0.1 of body protein. This will allow for the prediction of positive protein gains with negative fat gains as observed by feeding according to maintenance requirements (Close *et al.*, 1978).

### 1.5 Environmental constraints

Up till this point the model has assumed that the non-nutritional environment has had no constraint on feed intake and growth. The climatic environment does, however, have a considerable effect on voluntary food intake (Bruce and Clarke, 1979; Mount, 1975; Verstegen, 1987). It is necessary to establish the extent of the interaction of the environment with the animal and with the diet before the voluntary food intake of the animal, and hence its actual growth rate, can be assessed. The environment can both increase and decrease the amount of dietary energy required by the animal, and it can have a constraining effect on the voluntary food intake of the animal.

To remain in thermal balance the amount of heat that a pig produces, through various functions, such as maintenance, growth, food intake, digestion, excretion, etc., must equal the amount of heat lost to the environment, as heat storage in the pig is minimal. More heat can be lost in cool than in hot environments.

At high temperatures more heat is lost by evaporative means than by sensible heat loss. The pig will therefore attempt to increase the amount of heat that needs to be lost through evaporation, but because of the absence of sweat glands a point is reached when feed intake will have to be reduced (Mount, 1975; Steinbach, 1987). This will result in a reduced growth rate. On the other hand, when heat production is insufficient to match the demand of the environment then the pig must increase heat production and less energy will be available for productive purposes (Bruce and Clarke, 1979). The pig will compensate by increasing feed intake to satisfy both its growth requirements and the increased environmental heat demand.

It is difficult to determine whether the environment for immature pigs is effectively cold or hot, as growth rate, body composition and feed intake are constantly changing with time (Campbell and

Tavernier, 1988b; Rinaldo and Le Dividich, 1991). Nevertheless, an environment can be defined as cold if the amount of heat produced by the pig in a thermoneutral environment is insufficient to meet the heat demand from the environment (Steinbach, 1987). A hot environment is one in which the animal is prevented from consuming its desired feed intake because the amount of heat produced would be greater than what could be lost.

Many approaches to modelling heat production have been attempted, ranging from a simple approach of calculating the difference between ME intake and the amount retained (Whittemore, 1983), to the sophisticated physical type model (Bruce and Clarke, 1979). In the present model an intermediate approach is adopted with a set of rules governing the rate of heat production and the subsequent effects on voluntary food intake and protein and lipid growth. These rules are tested in Chapter 6. Heat storage is assumed to be zero such that heat production is determined as the sum of the components of evaporative (latent) and non-evaporative (sensible) heat loss (Figure 1.3).

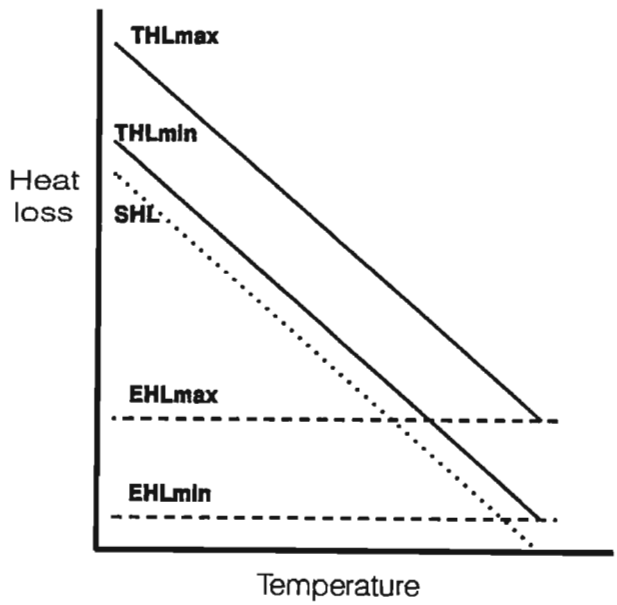


Figure 1.3 Components of total heat loss (THL) (after Emmans, 1989). Thl (—); EHL (–); SHL (···).

Sensible heat loss (SHL) constitutes the radiative, convective and conductive components and is dominant under cold conditions. SHL is assumed to diminish at a constant rate with increasing temperature, which is not unreasonable given the functional form of SHL described by Bruce and Clarke (1979). The rate at which SHL decreases ($SHL_{slope}$) depends on factors such as the wind speed, the type of floor material, the insulation of the house, the stocking density and the thickness of the subcutaneous fat layer, with a range of between 30.0 and 50.0 (Curtis, 1983). This deductive approach is more sensible than the "effective temperature" concept recommended by the NRC (1987) because it places more emphasis on the source of heat loss rather than a generalized adjustment of the air temperature.

SHL is predicted as follows:

$$SHL = SHL_{slope} \times (38\text{-}T) \times EBWT^{0.67} \quad (kJ/day) \qquad (1.40)$$

where $SHL_{slope}$ = rate of heat loss (kJ/°C)
EBWT = empty body weight (kg)
T = temperature (°C)

At a temperature of approximately 38 °C, SHL will be zero.

The SHL component contributes very little towards heat production at high temperatures, because sensible heat loss depends on the difference in temperature between the environment and the surface of the pig, and the subsequent exchange of heat will depend on the temperature gradient (Mount, 1975). As the temperature increases so the gradient diminishes, with less heat lost through non evaporative means. In effect, heat can be transferred to the body, as opposed to leaving the body, if the air temperature is very high. Such a condition will show SHL to have a negative value.

Evaporative heat loss is the amount of heat given off through evaporation from skin and respiratory surfaces (Figure 1.3). At low temperatures the heat loss due to evaporation is minimal (EHLmin) and is constant for a particular live weight (Verstegen, Close, Start and Mount, 1973, Close and Mount, 1978). The minimum evaporative rate is estimated to be 20% of the total heat loss under thermoneutral conditions. Thermoneutral heat production (TNH) is defined as the rate of heat produced by the pig growing at its genetic potential in a thermally neutral environment when fed a balanced feed, with 13.5 MJ/kg of ME. The TNH is dependent on ME intake and the energy retained but is independent of the thermal environment (AFRC, 1991) and calculated as:

$$TNH = (DFI_e \times ME) - (50.3 \times pPR) - (56.0 \times LR) \quad (kJ/day) \qquad (1.41)$$

The EHLmin is determined as:

$$EHLmin = 0.2 \times TNH \quad (kJ/d) \qquad (1.42)$$

Maximum evaporative heat loss (EHLmax) is assumed to be constant across all temperatures and is several times greater than EHLmin (Emmans, 1989). The exact difference will depend, in part, on the absolute water capacity of the air (AH) and the air temperature. EHLmax is calculated as:

$$EHLmax = AH \times EHLmin \quad (kJ/day) \qquad (1.43)$$

Where

$$AH = RH \times ( 3.73+(0.34928 \times T)+(0.0004886 \times T^3) ) \quad (no\ unit) \qquad (1.44)$$

where RH = Relative humidity
T = air temperature (°C)

In hot conditions it is assumed that the behavioural response of a pig will be to reduce the environmental heat demand by wetting the skin surface, with a maximum of 20% of the surface area

being wet at one time (Bruce, 1981; Black *et al.*, 1986). This will allow the animal to lose more heat (Rinaldo and Le Dividich, 1991).

The maximum total heat loss (THLmax) can be defined as:

$$THLmax = SHL + EHLmax \qquad (kJ/day) \tag{1.45}$$

As the derivation of EHLmax involves a fair amount of guess work and is very difficult to measure in practice, it would be better to measure THLmax directly. This approach is discussed in more detail in Chapter 6.

The minimum amount of heat that is lost is:

$$THLmin = SHL + EHLmin \qquad (kJ/day) \tag{1.46}$$

From Figure 1.3 it can be observed that heat loss is affected by ambient temperature and that, for a given temperature there is a range of heat losses within which the animal can remain comfortable. The range of heat outputs is bounded by a THLmin and a THLmax within which the animal must remain.

Having reviewed the factors defining the environment, the problem is to define the response of the animal to environments which inhibit maximum expression of growth. The environment will become inhibiting if

a) temperatures are excessively low or high, or
b) if a diet is very imbalanced or of a poor quality.

The amount of heat the animal produces is defined as the difference between energy intake and that retained:

$$HEAT = AFI \times ME_n - (23.8-5.6) \times PR - 39.6 \times Lr \qquad (kJ/day) \tag{1.47}$$

The heat of combustion for protein tissue is reduced from 23.8 kJ/g to 18.2 kJ/g because of the nitrogen correction to ME.

The response of the pig to a cold environment is to increase heat production, or cold thermogenesis, by increasing feed consumption (Verstegen, 1987) . The extra feed required will depend on the energy content of the diet and the additional environmental heat demand. The only constraint on the amount of food required in cold conditions is the bulk constraint, CFI. Provided gut capacity does not

limit the animal from consuming the amount of feed required to maintain body temperature and growth, the pig will consume more food.

In warm conditions if the potential amount of heat produced exceeds the maximum amount of heat that can be lost, then feed intake will fall in order to prevent a hyperthermic rise in body temperature (Steinbach, 1987). Less energy will, therefore, be available for the productive processes of protein and lipid accretion. The amounts of protein and lipid deposited will depend on the intake of energy and amino acids, with preference afforded to maintenance functions.

The potential amount of heat produced by fast-growing genotypes during growth is more likely to be greater than the maximum heat the animal can lose in hot environments. This is particularly so when poor quality diets or diets high in protein are fed (Kyriazakis *et al.*, 1991). Consequently it is unlikely that potentially fast-growing animals would be able to reach their potential when kept at high temperatures. The initial response of the animal will be to attempt to alleviate the heat stress by consuming less food , moving away from the heat source, and or reducing activity to a minimum (Emmans, 1989).

The reduced feed intake will have specific effects on the composition of body growth. Less of the most limiting nutrient will be consumed, and if this is an amino acid then Pr will decline. Fat deposition may increase or decrease depending on the severity of the heat stress. It is more likely to decline than to increase (Close, 1989). The amount by which LR will increase or decrease depends on the amount of extra energy made available from a reduction in protein retention.

If energy is first limiting then it is necessary to determine to what extent the animal could transfer more energy directly from the food into fat without causing a reduction in feed intake and thereby reducing the heat stress. This option is limited by the extent to which the animal can deposit fat in a hot environment (Close, 1989). If this response fails to reduce the heat stress then both AFI and LR will decline. However, a check is necessary to see whether the new AFI will satisfy the new requirement for the first limiting amino acid. If it does not then PR and AFI will be simultaneously determined to ensure that enough of the limiting amino acid is consumed without increasing heat production. Further adjustments will also be made to LR, to ensure that the heat production does not increase. The relationship between food intake, protein and lipid retention and total heat loss in pigs fed a protein-deficient feed is investigated further in Chapter 6.

## 1.6 Conclusions

The problem of predicting the growth rate, body composition and feed intake of an animal is that it involves many interactive causal forces which combine to produce a response to specific conditions. A modelling approach is the only defensible means of quantifying these forces.

The major advances that this model has achieved are:

(a) the prediction of the voluntary food intake. This is unique to this model as all other models expect intake to be a decision variable.

(b) In order to predict voluntary food intake use is made of an innovative theory describing how the animal interacts with its food and environment. This interaction requires nutritional constants to convert animal requirements into feed requirements, using common units. The effective energy system is an advance over other systems of predicting heat increment, leading to increased accuracy in predicting food intake. In addition to this, the theory considers the response of the animal to the first limiting nutrient, a concept that is not commonly recognized.

(c) With knowledge of the interaction of an animal with its food and environment it is possible to calculate changes in body composition in a more dynamic way, rather than invoking empirical formulae, minimum lipid:protein growth etc.

Changes in body composition are based on nutrient and environmental interactions as well as the current physiological state of the animal, as measured by the protein content. The logical conclusion of trying to maintain a desired body state is that the animal will always attempt to return to this inherent state, if it has deviated from it. The constraining factors will be the environment and the first limiting nutrient. A consequence of the above conclusion is that feed efficiency is automatically taken into account by the changing rates of lipid and protein deposition, as the body composition returns to its desired physiological state.

Protein growth is simulated using the Gompertz function of time as opposed to measuring biochemical protein turnover rates. The effective energy system (Emmans, 1989) is used to predict food intake and is regarded as being an innovative approach to answering the question of how an animal satisfies its nutrient requirements most efficiently.

The two areas of weakness identified in the model were firstly, the inadequate description of the type of animal to be modelled and secondly, how to accurately predict THLmax. These two aspects of the proposed model need to be addressed to improve the accuracy of predicting voluntary food intake and subsequent growth. However, before discussing these issues it is important to have an insight into what parameters other pig models require to describe the genotype to be modelled.

CHAPTER 2

# PARAMETERS USED IN CURRENT PIG SIMULATION MODELS TO DESCRIBE THE GENOTYPE OF THE ANIMAL

## 2.1 Introduction

Numerous approaches have been made recently to model the growth of pigs (Roux, 1976; Parks, 1982; Whittemore, 1983; Black, Campbell, Williams, James and Davies, 1986; Moughan, Smith and Pearson, 1987; Pomar, Harris and Minvielle, 1991). A summary of the similarities and differences of pig growth models is outlined by Moughan and Verstegen (1988). These differences in approach have resulted in different methods of defining the type of animal that is to be modelled. Most of these models have, to a greater or lesser extent relied on the approach first adopted by Whittemore (1983), who defines the animal in terms of mature protein size and a minimum lipid:protein ratio.

The approach of Roux (1976) and Parks (1982) differs from other models in that growth is described as a function of feed intake, as opposed to time. Roux (1976) developed an allometric-autoregressive model, with autoregression being used to define cumulative feed intake over time. The main disadvantage of using feed intake as an independent variable is the quantification and/or estimation of the amount of feed consumed. It would be extremely expensive, time-consuming and impractical to try to estimate feed intake for different environmental and nutritional conditions as well as for different types of animals. In addition to this problem both these models predict body protein, lipid, moisture and ash after estimating body weight. A better approach is to predict body weight as the sum of the chemical components. Most of the existing models adopt this bottom-up approach.

The theories behind most of the pig growth simulation models are complex and involve a sequential flow of complicated predictive equations. As this thesis is primarily concerned with parameterization of animal characteristics, the description of current simulation models will be limited to the factors related to defining the animal genotype.

## 2.2 Current Growth Simulation Models

### 2.2.1 Roux (1976)

The model of Roux (1976) is described as an allometric-autoregression model, as the theory of the model is based on an allometric function and an autoregressive time component. The animal is considered as an input-output device with the description of growth being in terms of body weight (output) and feed intake (input). This model stresses the requirement for an accurate description and evaluation of an animal and how it grows. It has had limited success as a predictive model in pig nutritional studies (Roux and Kemm, 1981).

The important parameters required to describe the animal are cumulative feed intake, the allometric constant (*a*) and coefficient (*b*) values, and the slope of the autoregressive relationship between time and cumulative feed intake (Roux, 1976). To calculate the cumulative feed intake, estimates of the feed intake at conception and at infinity are required. Both these, measurements are almost impossible to obtain directly by experimentation and therefore can only be estimated.

The problems associated with this model are:

(I) Practical application and usage are limited to those circumstances where feed intake is known.

(ii) It does not provide any insight to the mechanisms which govern feed intake.

(iii) Initial cumulative feed intake at conception is a calculated guess.

(iv) The heritable parameters *a, b* and the slope of the autoregressive relationship have little biological meaning in themselves but are proportional to feed efficiency.

(v) The parameters are dependent on the quality of the feed given and of the environment in which the animals are kept. Therefore, the values of these parameters will have little general application.

(vi) Chemical composition of the empty body weight is determined from linear regression analyses of live weight, and as such the level of accuracy of predicting protein and lipid contents is questionable.

### *2.2.2* Whittemore and Fawcett (1976)

The model developed by Whittemore and Fawcett (1976) was a major breakthrough in that it moved away from a strictly factorial approach toward a flexible, mechanistic model. Four important concepts in modelling animal growth were introduced for the first time in this model viz.

(I) Protein growth was regarded as a function of body protein weight.

(ii) Growth was a net response to environmental and nutritional stimuli. The effect of the environmental heat demand was determined by considering factors such as temperature, ventilation, floor type and bedding.

(iii) Maximum or potential protein growth rate was considered.

(iv) Allowance was made for differences in protein and lipid growth between breeds and, more importantly, between different strains within a breed.

The structure of this model has formed the bases of most subsequent pig growth models, such as those developed by Moughan *et al.* (1987) and Pomar *et al.* (1991). The model has since been adjusted and improved as discussed by Whittemore (1983).

The model details growth in pigs as a partitioning of nutrients into body tissue. The partitioning process is regulated by biochemical and physiological control points (Moughan and Verstegen, 1988). The general structure of the model can be summarized as follows:

(I) Determine body composition at the start of growth.

(ii) Nutrient intake is defined by the user or estimated as a function of metabolic weight or time or body weight.

(iii) Protein deposition is calculated taking into account the utilization of available amino acids, maintenance of proteinaceous tissue, a maximum limit to protein retention and the interaction between energy intake and protein accretion.

(iv) Determination of energy requirements for cold thermogenesis.

(v) Lipid accretion is considered as the energy remaining after maintenance requirements, protein accretion and cold thermogenesis have been met.

(vi) The model works on a day-to-day basis with the body composition at the end of one day being the initial state for the next. Therefore, it is possible to estimate the body composition of an animal at a given slaughter weight and use this to obtain a monetary value of the carcass.

The required inherent characteristics of the animal are limited to a sex and strain-dependent maximum protein retention value (PRmax) and a minimum lipid:protein ratio (LPmin). Although the minimum lipid:protein ratio is rather inflexible it does attempt to explain the physiological response observed in the animal to degrade protein, or to deposit less protein in order to supply energy for lipid synthesis, if residual energy is not sufficient to meet this minimum lipid deposition requirement (Emmans, 1981; Moughan and Verstegen, 1988).

The main shortcomings of the model are:

(I) The inflexibility of the two animal parameters, PRmax and LPmin. In practical terms a large number of these parameters would be necessary to define all the current genotypes.

(ii) The minimum lipid rule should be expressed in terms of body lipid content rather than daily lipid gains because body lipid catabolism is a function of lipid content rather than of the rate of lipid accretion (Whittemore and Gibson, 1983).

(iii) There are too few animal parameters to adequately define different genotypes. Factors such as the mature size and form of the animal, and the rate of development are not considered.

(iv) The approach to feed intake is based upon a user-input value or an empirical approach. The maximum limit to the amount of feed consumed is a function of body weight which does not consider the bulk density or nutrient content of the feed consumed.

(v) There is only a limited description of the potential growth and composition of the animal.

### 2.2.3 Emmans (1981)

The theory behind this approach to modelling animal growth is well documented in a series of papers by Emmans (1981,1987,1988), Emmans and Fisher (1986) and Emmans and Oldham (1988). The model predicts feed intake and body composition changes over time on the basis of the inherent potential protein growth rate of pigs varying in genotype. By making body protein and its derivative, the rate of protein retention, the central building block, the model is simplified without losing any accuracy in predicting changes in body composition. The body protein content is used to define the current state of the animal, which is then used to quantify the remaining body constituents and their respective growth rates (Taylor, 1980). This is achieved by implementing the allometric relationships between protein and lipid, moisture and ash in an animal growing at its genetic potential.

Protein growth is simulated using the Gompertz function of time as opposed to measuring biochemical protein turnover rates. The simplicity and usefulness of this approach is that only three inherent animal characteristics viz. a growth parameter (B), the mature protein weight (Pm) and the Lipid:protein ratio at maturity (LPRm), need be defined before the potential growth and feed intake can be predicted. The rate at which the animal will grow will depend almost entirely on its current state or size, a concept well described by Taylor (1980).

The uniqueness of this theory is highlighted by the following inclusions:

(I) The animal has an inherent level of fatness which it attempts to maintain. This inherent-fatness concept is particularly useful in simulation modelling and, is best described in relation to body protein, as the lipid-to-protein ratio at maturity (LPRm). The reason for its usefulness, is that the desired body fat content can be predicted at any time from the current state of the animal as well as determining possible compensatory fat gains (Emmans, 1988). However, the actual body fatness is likely to be different from what the animal would like to be, as a number of external factors, such as dietary energy and amino acid intakes, and temperature, will prevent the animal achieving its inherent desire.

(ii) This modelling approach answers the question of how an animal satisfies its nutrient requirements most efficiently by using an "effective energy" system (Emmans, 1981). In general, the effective energy system can be described as the metabolizable energy (ME) of a diet less the heat production due to defecation and potential excretion resulting from the food being eaten. The fermentation heat increment is excluded for pigs as it is assumed to be negligible. The advantage of this energy system is that it can calculate the desired feed intake, which can be defined as the amount of feed an animal needs to consume to satisfy its potential requirement for the first limiting nutrient (Emmans and Oldham, 1988).

If there were no constraints on the animal then the desired intake would be attained and the animal would achieve its potential rate of protein growth. The amount of fat deposited would depend on which nutrient was first limiting. If it were energy then it would achieve its desired fatness. If, however, protein was first limiting then the excess energy consumed would be deposited as excess fat. The rate and composition of growth will, therefore, be dependent on the amount of food actually eaten.

There are two kinds of constraints that may limit the animal achieving its desired food intake (Emmans and Oldham, 1988). Firstly, there is the bulk or density of the feed. In conjunction with the gut capacity of the animal, the bulkiness of a diet may limit the daily food intake. There is a finite amount of food that can be stored and transported through the intestinal tract of an animal over any time period. Therefore, for any given length of time, the bulkier the diet the less the amount of food consumed. The second constraint is the environment and in particular, the hotness of the environment (Emmans, 1981). The maximum amount of heat an animal can lose and therefore can produce, is a function of the environmental conditions and the intake of a given feed (Holmes and Close, 1977; Stahly and Cromwell, 1979). Therefore, the environmental temperature will impose an upper limit to the rate of intake of a given food.

The improvement of this model over current pig growth models lies, firstly, in its ability to predict accurately changes in body composition with time using fewer variables than those used in other models. Secondly, because of the structured relationship between the environment and the animal, the predicted responses for temperatures outside of the thermal comfort zone will resemble real-life more closely than models that have a more informal or indirect relationship between environment and animal. Thirdly, changes in body composition are based on nutrient and environmental interactions as well as the current physiological state of the animal, as measured by body protein.

The limitations of the model are:

(I) Certain key components, such as B, Pm have, as yet, not been quantified for most pig breeds.

(ii) The poorly understood relationship between the environment and its effect on changes in body composition especially at high temperatures, makes it difficult to incorporate accurate functions and constants within the model. The model attempts to solve this problem from first principles by comparing the difference between the heat produced by the animal and the environmental heat demand.

### 2.2.4 Parks (1982)

The model of Parks (1982) is similar to that of Roux (1976), in that the animal is described as an input-output box, with growth being the response to how the animal has been fed. The model uses a sigmoid curve as a basis for animal growth. It defines the biological factors that control growth as body weight and feed intake. The rate of growth is a function of feed intake and feed efficiency which increases at a diminishing rate over time until a mature or asymptotic value is obtained.

The theory behind the model is based on a number of differential equations and assumptions, which for the purpose of this discussion are not necessary to discuss in detail. A brief summary of the model is given by Whitehead and Parks (1988). The relevant parameters which distinguish one animal from another are mature body weight (A), mature feed intake (C), a growth efficiency factor (AB) and an appetite factor ($t^*$). The weight at maturity and C are self explanatory, although it is difficult to determine a mature feed intake *a priori* without some knowledge of the environmental and nutritional constraints. This can only be achieved if one assumes a potential mature feed intake in a non-limiting environment and fed a non-limiting diet. The AB value defines the cumulative feed intake required to reach a given body weight. To estimate AB for different breeds and strains of pigs would involve the accumulation of live weight and feed intake measurements over a long period of time and a number of different nutritional and environmental conditions. The impracticality of obtaining such information limits the general use of this model. The appetite factor represents the resistance an animal has to increasing its appetite and is defined in terms of a time delay constant. The lower the value of $t^*$, the more rapidly feed intake will increase and less time will be required for the animal to reach C (Whitehead and Parks, 1988). Similarly to AB, $t^*$ is an impractical measurement.

The main limitation of the model are:

(I) The complexity of defining the animal characteristics renders the model impractical for general nutritional usage. Whitehead and Parks (1988) were able to obtain a certain level of accuracy in predicting results from different experiments but this was as a result of modifying certain equations within the theory.

(ii) To estimate the input parameters requires long-term experiments.

(iii) The model does not solve the problem of predicting the physiological causes governing the feed intake response and the change in body form.

(iv) The model determines the current state of the animal from body weight, which as discussed is not the most accurate means of predicting the development of an animal. This problem could be overcome by extending the growth equations to allow prediction of protein and fat gains for pigs (Moughan and Verstegen, 1988).

### 2.2.5 Black *et al.* (1986)

The simulation model described by Black *et al.* (1986) differs from most other models in that it is a complete management package covering both the growing and reproductive stages. It considers the effects of environmental conditions on growth and covers the interactions between animal type, diet, and body condition in a more comprehensive way than all the previous models, except that of Emmans (1981). Additional features include compensatory growth, social factors and a more complete description and cause and effect relationship between growth and environmental factors.

The model attempts to predict the *ad libitum* feed intake of the pig as a function of potential growth. The results of the prediction are fairly accurate but a scaling factor is included in the model to adjust predicted intakes to that of observed values. From a modelling point of view this is unacceptable and reflects either a problem in the theory behind predicting feed intakes or incorrect constant values used in the equations.

The model is based on protein and energy interrelationships, with daily protein accretion being a function of metabolizable energy (ME) intake, maximum protein accretion, sex and genotype. The empirically derived relationship between protein gain and ME intake is different for different live weights when energy intake limits potential protein deposition. The slope of the protein deposition and energy intake function varies according to the genotype. However, Kyriazakis and Emmans (1992; 1994) observed that there were no such differences between sex or genotype.

The potential rate of protein and energy retention are predicted for different sexes and genotypes, with the assumption that there is an upper limit to daily protein accretion. There is no direct estimate of potential lipid accretion. Instead, this is calculated as the deposition of excess energy after the requirement for maintenance and for protein deposition have been met.

The animal characteristics required to determine different genotypes are defined by numerous constants. These include, the maximum daily rates of energy and nitrogen gains, the mature body energy and nitrogen contents, and an energy and protein exponential constant. The practical implication of requiring a large number of parameters to describe the genotype of the animal is the need for very detailed and complicated experiments to be conducted in order to obtain estimates of these parameters. The use of large numbers of parameters to describe a genotype should be avoided if the model is to have universal acceptance, unless these parameters are absolutely essential in segregating one strain or breed from another.

The limitations of the model are:

(I) Food intake is emperically derived;

(II) The scaling of feed intake to ensure a better fit with observed data.

(iii) A compensatory growth factor is used to adjust the protein deposition rate irrespective of the current physiological status of the animal.

(iv) Some of the empirical formula are specific to Australian conditions. However, this problem could be overcome with minimal adjustments.

(v) Too many animal characteristics are required, and complicated experiments are required to obtain these parameters.

(vi) Too much emphasis is placed on the maximum rates of energy and protein retention to determine daily growth rates, without considering the current state of the animal.

### *2.2.6* Moughan *et al.* (1987)

The model described by Moughan *et al.* (1987) is similar to that of Whittemore and Fawcett (1976). The main difference is the description of amino acid absorption and utilisation. The model is very simplistic and is limited to predicting daily protein and lipid deposition. Important factors such as environmental interactions and nutritional constraints are not considered.

Protein accretion is assumed constant for the entire simulation period (20 - 90 kg), the only differences being between sex and strain. Feed intake is an input variable, from which lipid accretion is calculated, after the total energy cost of protein deposition has been met. Protein deposition is constrained by the ratio between body lipid and body protein. If total body lipid is less than total body protein then protein accretion must be adjusted to ensure that protein accretion is equal to or less than lipid accretion. The interaction between lipid and protein retention is a function of whole-body lipid and protein rather than of the rates of retention.

The only input parameters that are animal-related are sex and strain, both of which are qualitative rather than quantitative parameters. All the quantitative parameters associated with these two animal characteristics are considered as fixed values.

The limitations of this model are as follows:

(I) *Ad libitum* feed intake is not predicted within the model but is an input variable.

(ii) Too many important variables are assumed constant, particularly those associated with the environment.

(iii) The model is limited to simulating growth between 20 and 90 kg live weight.

(iv) Daily protein retention and the minimum lipid:protein ratio are constant values for the whole simulation period. Protein values are genotype- dependent but the lipid:protein ratio is not.

(v) Poor simulation results are obtained at low energy intakes.

(vi) The use of the model is limited to situations where a cereal-based diet is fed and the feed intake is known.

### 2.2.7 Pomar *et al.* (1991)

Pomar *et al.* (1991) make use of body DNA and protein content at maturity to define the genetic growth capacity of the animal. The authors maintain that total body DNA content and the rate of DNA change provide a better understanding of protein accretion and degradation than does total body protein because the level of DNA is the intrinsic limitation to protein synthesis. This is true, provided that there is enough accurate information available to quantify the initial and mature DNA content. However, Pomar *et al.* (1991) realise that few data are currently available to define pigs in terms of their total DNA content. To overcome this problem a protein precursor weight is used to approximate the total DNA content.

Potential daily protein deposition is the difference between synthesis and degradation. Protein synthesis is a function of a protein precursor weight and two other non-biological constants. The change in the precursor weight is in turn a function of the mature precursor weight and the precursor weight at a given time. Feed intake is the main determinant of lipid growth rate, if the minimum lipid:protein relationship is satisfied. To define a genotype in this model requires estimates of six non-biological parameters and the protein precursor weight at maturity. In addition a minimum lipid:protein ratio is required to regulate protein and lipid growth rates.

This problem emphasises the danger, in nutritional modelling, of constructing models at a level of understanding lower than the physiological and production level, as defined by France and Thomley (1984). The model of Pomar *et al.* (1991) has been constructed at the metabolic level, where there is almost no information available. This makes it more difficult to determine values for the meaningful biological parameters that can define what makes one pig different from another, and hence, which are virtually impossible to test.

The main limitations of this model are:

(i) Feed intake is empirically derived from the exponential relationship between digestible energy intake and live weight.

(ii) There are no environmental interactions.

(iii) The model assumes that the diet is well balance with regard to the ideal protein balance. The result is that lysine is always considered the most limiting amino acid, which may not always be the case. The quality of the dietary protein is therefore not considered.

## 2.3 Comparison of Animal Genotype Descriptions

A summary of the differences and similarities pertaining to the type of animal described in the current simulation models, is shown in Table 2.1.

Table 2.1. A summary of the important animal characteristics required by current pig simulation models.

| Models | Form | | | Potential growth | Animal Parameters |
|---|---|---|---|---|---|
| | Mature State | Protein | Lipid | | |
| Roux (1976) | - | (body weight) | Excess energy | No | Cumulative feed intake<br>Allometric constant and coefficient |
| Whittemore and Fawcett (1976) | - | (maintenance,<br>feed intake,<br>protein quality) | Excess energy,<br>Min. lipid:protein | Limited | Max. protein gains,<br>Min. lipid:protein |
| Emmans (1981) | Body protein<br>Lipid:protein | (rate constant,<br>mature protein weight,<br>degree of maturity) | (lipid:protein,<br>protein weight,<br>degree of maturity | Yes | Growth rate constant<br>Mature protein weight<br>Lipid:protein at maturity |
| Parks (1982) | Body weight | (body weight) | Excess energy | Yes | Mature body weight<br>Mature feed intake<br>Growth efficiency factor<br>Appetite factor |
| Black et al (1986) | Body Nitrogen<br>Body Energy | (body weight,<br>max. protein gains,<br>degree of maturity) | Excess energy | Yes | Max. N deposition rate<br>Max. energy deposition rate<br>Mature body N content<br>Mature body energy content<br>N exponential constant<br>Energy exponential constant |
| Moughan et al (1987) | - | Constant | Excess energy<br>Min. lipid:protein | No | None |
| Pomar et al (1991) | DNA<br>Body protein | Protein synthesis - degradation | Excess energy<br>Min. lipid:protein | Yes | Mature protein weight<br>Protein precursor<br>Protein synthesis constants<br>Min lipid:protein |

Body protein is the driving variable in most of the models (Emmans, 1981; Whittemore, 1983; Black *et al.*, 1986; Moughan *et al.*, 1987; Pomar *et al.*, 1991), with moisture and ash contents, and rates of growth, determined by their allometric relationships with protein. In all the models, with the exception of that of Emmans (1981), the rate of lipid retention is a function of the energy surplus consumed by the animal. These methods assume a knowledge of feed intake which is calculated using some function of body weight, of which body lipid is a component. Therefore a potential feedback effect exists which will affect the estimation of lipid growth. The approach of Emmans (1981) overcomes this problem by predicting a desired rate of lipid deposition as a function of the current state of the animal and a lipid to protein ratio at maturity. With this approach it is possible for the animal to lose lipid under certain conditions. Feed intake can then be predicted without any feedback effect.

The models of Parks (1982) and Roux (1976) are structured around feed intake. The predicted growth of the animal is the response to the way it has been fed. The body weight and rate of change of body weight is predicted from what the animal has been fed, from which the growth of the chemical body components are determined. The driving variable in the other current pig models is body protein. However, each of the models differ in the way in which the protein content is estimated (Moughan and Verstegen, 1988). Whittemore (1983) calculates protein retention as a function of maintenance requirement, feed intake and the quality of the dietary protein;

Black *et al.* (1986) predict potential protein deposition as a function of body weight, maximum protein retention and the current degree of maturity of the animal; Pomar *et al.* (1991) determine protein retention as the difference between total protein synthesis and total protein degradation.

The most sensible approach to modelling growth would be to describe the potential growth rate of the animal before the effects of nutrition and the environment can be simulated (Emmans and Fisher, 1986). Whittemore (1983), Moughan *et al.* (1987) and Pomar *et al.* (1991) simultaneously determine body components, particulary lipid, with dietary constraints, instead of determining the potential growth first and then modifying the potential growth rate according to the dietary and environmental constraints.

Protein content is not the only important mature state parameter. The inherent mature fatness is also an important characteristic specific to each animal (Emmans, 1987). The relationship between protein and lipid is a heritable characteristic specific to the genotype of pig. The mature fat level is best described in relation to body protein in the form of lipid:protein ratio. The reason being, that the potential body fat content can be predicted at any time from the current state of the animal. This, however, has not been considered in any of the pig models, which have calculated fat as the excess energy available after maintenance and protein deposition have been met. The closest most models have come to differentiating between different sexes and strains with regards to fatness is to place

a lower limit on the amount of lipid, relative to body protein content, that is expected with normal animal growth (Whittemore, 1983). Both Moughan *et al.* (1987) and Pomar *et al.* (1991) attempt to define the fatness of the animal by this same method. This ratio does not quantify the intrinsic desired level of fatness and will, therefore, not predict potential fat growth under *ad libitum* feeding conditions. Moughan *et al.* (1987) found that using this ratio resulted in a poor predictive growth response for low feeding levels.

Emmans and Fisher (1986) and Emmans (1988) have shown that a few, simple, assumptions can lead to a description of an animal that is sufficient for predicting its performance in non-limiting conditions and for calculating what these are. It seems sensible to be able to predict performance in non-limiting conditions before the more difficult question is tackled, of defining growth in limiting conditions. This approach to modelling the growth of animals is accepted as being both simple and accurate in predicting potential growth rate. Having observed the differences in approach to describing the genotype of an animal, it is therefore necessary to provide a simple, standardized method of quantifying the inherent animal parameters.

CHAPTER 3

# THEORETICAL ASPECTS OF MEASURING ANIMAL PARAMETERS

## 3.1 Introduction

In the previous Chapter, a description is given of the numerous approaches that have recently been made to simulate the growth of pigs (Roux, 1976; Parks, 1982; Whittemore, 1983; Black *et al*, 1986; Moughan *et al* 1987; Pomar *et al* 1991). There is no consensus nor any general discussion in the literature on methods of defining genotypes that would allow similarities and differences between animals to be compared, other than that proposed by Emmans (1988). There is agreement that differences do exist between animals in mature size (Taylor, 1980) and that selection can alter mature size and the scaled growth rate and fatness at a degree of maturity (Emmans, 1988). There is also consensus amongst simulation modellers that a standard set of parameters to describe an animal are needed, that these should be easy to estimate and that they should accurately characterize differences between breeds and strains.

## 3.2 A Theory to Standardize Animal Growth Parameters

Any biological growth model must be defined by a system which describes the growth of the animal being modelled (Emmans and Fisher, 1986). Most of the theory used in this chapter is based on the concepts, functions and constants proposed by Emmans (1988). The reason is that the theory satisfies the general criteria for simulation models of being simple; few parameters are required; it is constructed at the animal level and, when implemented into a working model (Ferguson, 1989), produces very accurate results. The method of evaluating genotypes proposed by Emmans (1988) uses the Gompertz growth function to describe the potential growth rate which an animal desires to achieve. There are good reasons for selecting this growth function, for example, the values of only three parameters need be known, all of which have biological meaning; the function fits data as well as other more complex growth functions that do not have the above properties; and allometric relationships between the chemical and physical components of the body can be defined in terms of the growth rate parameter in this function.

Two assumptions are made in defining the chemical composition of the genotype, the first being that body protein, water, lipid and ash each have potential growth rates which are Gompertz functions of time, and the second being that each of these body components have the same growth rate parameter for a given genotype. There is evidence to suggest that these two assumptions are valid (Doornenbal, 1971; 1972; 1975, and Whittemore, Tullis and Emmans, 1988).

Instead of predicting growth from the empty body as a whole, body protein is predicted and used as the base component to predict the remaining three components. This is done by making use of the allometric relationships that exist between protein and moisture, ash and lipid . Body protein (Pt) is used to describe the current state of the pig and the subsequent growth rates of the remaining body components viz. body moisture, ash and lipid (Emmans and Fisher, 1986; Stranks, Cooke, Fairbairn, Fowler, Kirby, McCracken, Morgan, Palmer and Peers, 1988). The Gompertz function used is as follows:

$$Pt = Pmat \times e^{-e^{\ln(-\ln U_o) - (B \times t)}} \qquad (kg) \qquad (3.1)$$

Pm = Mature body protein weight (kg)
$U_o$ = (Body protein weight at birth) / Pm
B = Rate of maturing ($day^{-1}$)
t = Age (days)

The information required to describe a pig consists therefore of three parameters in the Gompertz function, namely, the initial and the mature body protein weight and a rate of maturing. In addition to these inherent growth parameters, the allometric relationships between body protein and the other chemical components of the body need to be defined if these components are to be estimated from the protein weight. Moisture and ash are relatively constant relationships for most genotypes (Emmans, 1988; de Greef, 1992). There is some evidence to suggest that, for the moisture allometric function, significant variability between different strains may exist (Stranks *et al.* 1988). The proportion of potential lipid to protein between and within breeds is not fixed and therefore needs to be specifically defined.

The relationship between protein and lipid is a heritable characteristic specific to the genotype of pig. To quantify this inherent fatness an additional parameter is required viz. the lipid-to-protein ratio at maturity (LPRm). This ratio defines the inherent amount of lipid at maturity relative to protein, being specific to a given genotype. For example, the LPRm of fat strains of pigs is in excess of five, whereas very lean male strains can have an LPRm of as little as one (Whittemore *et al.* 1988; de Greef, 1992).

The Gompertz growth function describes a sigmoidal curve (Figure 3.1a) from which the rate of growth of the animal can be determined (Figure 3.1b), using the derivative of body protein over time (Equation 3.2). The maximum growth rate occurs at 1/e.

$$\frac{dPt}{dt} = Pt \times B \times \log_e \left(\frac{Pmat}{Pt}\right) \qquad (g/day) \qquad (3.2)$$

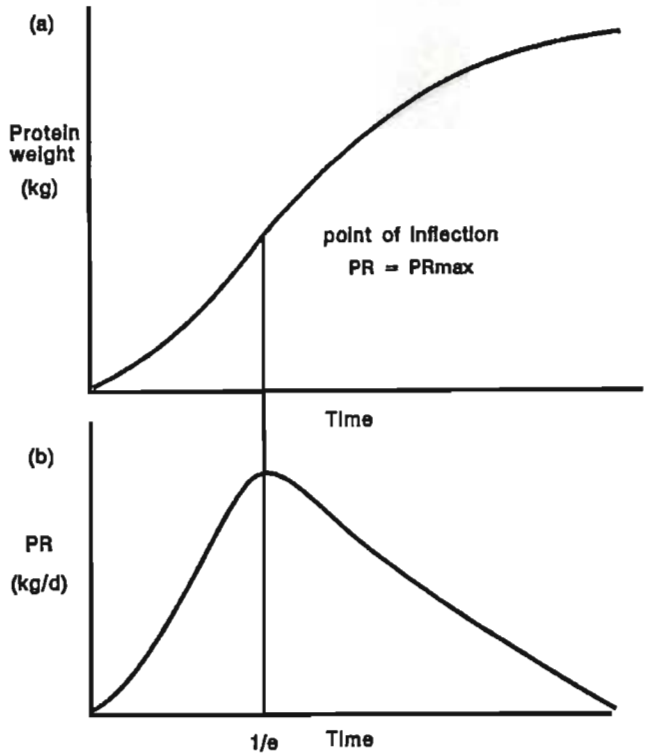


Figure 3.1 (a) The Gompertz growth function over time and (b) the rate of growth as applied to protein growth.

The relative growth rate of an animal can be defined as :

$$Relative\ growth\ rate = (\frac{dPt}{dt}) \ / \ Pt \qquad (3.3)$$

From Fig. 3.1b it can be observed that there is an initial period of rapid protein growth which peaks at 0.368 (1/e) of mature size. This is followed by a declining rate of growth until maturity is attained whereafter no further protein growth occurs. It is therefore reasonable to assume that the relative growth rate as a function of body protein weight follows an exponential declining curve (Figure 3.2).

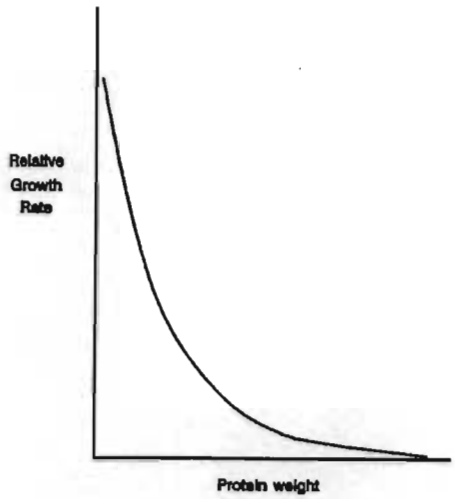


Figure 3.2 Relative protein growth as a function of protein weight.

At low protein weights the rate of protein retention relative to protein weight is considerably greater than at high body protein weights (Whittemore *et al.*, 1988). The implication of a diminishing rate of protein deposition is that as an animal approaches maturity so the protein deposition rate above maintenance will cease.

If these relationships between relative growth and animal size are true then by transforming body protein weight to its natural logarithmic the function would be defined as:

$$\frac{(\frac{dP}{dt})}{Pt} = a - B \times \log_e \times Pt \qquad (3.4)$$

where a = y-intercept
B = slope of the line

Plotting relative growth rate against the log of protein would give a linear response as shown in Figure 3.3.

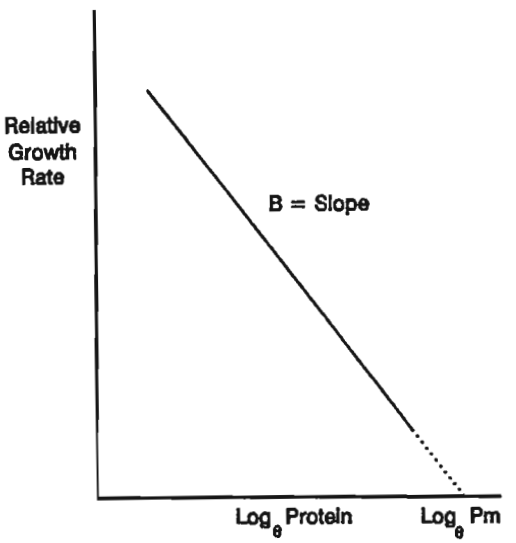


Figure 3.3 Relative protein growth rate as a function of the natural logarithm of protein weight.

The slope of the line is defined as the relative growth rate of the animal (B). This value is an indication of the potential rate of decay in growth. For example, fast growing animals (intact male pigs) will have a lower B value than will slower growing animals (females). Whittemore *et al.* (1988) suggested rates of maturing (B values) of 0.010 /d and 0.011 /d for entire males and females respectively whilst Kyriazakis and Emmans (1992) estimated a combined male and female value of 0.0133 /d.

### 3.3 Experimental Techniques Required to Estimate Growth Parameters

To estimate the growth parameters at least two points will need to be defined to determine the slope of the graph of relative growth against natural logarithm of protein weight. A minimum of two test period is therefore required. The further apart the two points are the more accurate the slope of the line will be. However, it is not necessary to grow the animals to maturity because the scale of the x-axis is logarithmic. The second point need only be measured at, for example, a third of mature size, and still be close to the natural logarithm of mature size. These periods should not encompass the times when management and environmental influences will impede the potential growth, such as weaning, and should be sufficiently far apart, such as after the fourth week of weaning and sometime after the period of maximum growth, to obtain the most accurate estimates of the animal parameters. The effects of weaning will reduce the body lipid content and reduce the rate of protein and lipid deposition as the intake of dry food is insufficient to maintain potential growth. The inclusion of the weaning and immediate post-weaning period must be avoided to reduce the risk of including inappropriate body composition measurements.

#### 3.3.1 Method one - growth rate at two weights.

The method outlined here to describe the potential growth rate of an animal requires a measure of protein and lipid growth, and produces estimates of mature protein size and the rate of maturing. Four points are determined and used to fit the line describing the relationship between relative growth and body size. Two test periods are required, one at an early stage of development, such as prior to weaning; the other, at a later stage of development, starting preferably at about 70 to 80 kg body weight so as to ensure that the two points required to determine B are sufficiently far apart. There should be no dietary or environmental constraints to prevent any deviation from potential growth. The exact number of animals used will depend on the variability in the chemical composition of the animals. A minimum of three animals per sex should be used for each slaughter period in order to measure the variability in chemical composition of the slaughter animals. If the variability within a sex is likely to be high then more animals should be used in order to obtain a more accurate estimate of the mean protein and lipid weight. In the later stage where differences between animals of the same age are most likely to be different, the animals are slaughtered at a given live weight. Slaughtering animals at the same weight should reduce the variation between animals of the same sex from similar parent stock.

3.3.1.1 *Early Period*

A minimum of 12 piglets within a day or two after birth should be used, half of them being entire males, the other half, females. Two males and two females should be killed at the start of the trial for carcass analyses. Chemical analyses of protein, lipid, water and ash should be done on each of these piglets, i.e. the samples should not be pooled. The four males and four females which are left with the sow, should be weighed after ten days when a further two female and two male piglets should be killed for chemical analysis. The remaining two male and female pigs are slaughtered after an additional 10 days. An option here is to use live weight instead of age as a means of determining when to slaughter the pigs. If live weight is used then the piglets are killed after they have gained sufficient weight so as to ensure differences in protein and lipid growth rates, such as at 2 kg, 5 kg and 8 kg live weight. The sow should be producing sufficient milk to allow the remaining four piglets to consume more milk and grow at their potential protein rate. However, the gains in lipid will be greater than desired due to the increased milk intake and the relative over-abundance of energy relative to protein in the milk of the sow.

It is not necessary to measure protein intake during the test period as protein retention is determined by the difference in body protein contents over the experimental period.

3.3.1.2 *Later Period*

Pigs of the same parent stock (or genotype) as used in the early period must be used at a later stage in their development to measure their maximum protein gain relative to body size. The exact slaughter weights used in the later period are not critical provided that the following criteria are met:

(i) the animals are sufficiently heavier than the early period so as to obtain a second point on the logarithmic scale that is closer to mature size; and

(ii) the slaughtering of the second and third group in this period must occur within a short period of time, for example 7 to 10 days, to ensure an accurate estimate of the rate of protein and lipid growth between the two live weights. The longer the period between the two weights the less accurate will be the component growth rate for a given component weight.

At a starting weight of, for example 80 kg, a minimum of 12 pigs should be chosen for the test, with six pigs of each sex being used. Two males and two females should be killed for carcass analyses, and the remaining pigs should be fed *ad libitum* on a high quality feed with an abundant supply of an ideally-balanced protein (at least 18 percent crude protein and 10 g lysine/kg feed), energy (a minimum of 13 MJ DE/kg) and macro and micro nutrients. The pigs

should be weighed weekly, and at 90 kg body weight two pigs of each sex should be killed for carcass analyses. The reason for killing pigs at 90 kg body weight is to obtain estimates of the rate of protein growth over two short time intervals (80-90 kg and 90-100 kg) as opposed to a single rate over a longer time period (80-100kg). This will provide additional data for analysis, as well as providing a more accurate estimate of the protein growth rate because of the shorter time interval. The remaining four pigs are kept on the same feed, weighed weekly and killed when they reach 100 kg body weight.

It is important to note the time taken to reach the respective weights in this part of the experiment so as to have an accurate estimate of the rate of protein retention. Accurate estimates must be obtained of body protein, lipid, water and ash in the carcasses.

The amounts of lipid, water and ash in the carcasses of the animals at the two periods of measurement can be of some value in describing the genotypes of the animal, but it would be unlikely that the animals would have remained in non-limiting conditions throughout the growing period. A non-limiting environment is a pre-requisite for measuring the relative proportions of these components. To ensure that the animal does not become fatter than is dictated by the inherent lipid:protein ratio at maturity, and thereby overestimate the mature lipid size, it is necessary to feed the animal a high protein feed prior to the start of the later period. This will afford those pigs that are fatter than they should be, the opportunity to lose excess fat. This process will not reduce the fat content below the desired level of those pigs that are predisposed to being fat (Kyriazakis *et al.* 1988). Alternately, they should be kept on a relatively high protein diet throughout the growth period.

### 3.3.2 Method two - serial slaughter

Another method of evaluating a genotype, which is similar in technique but which is more costly and requires very good facilities and husbandry, requires a larger number of animals (a minimum of 48 pigs) and an environment that would allow the animals to grow at their potential, without being constrained by heat, humidity, ventilation, underfeeding etc. It is important to bear in mind that fast growing animals generate a great deal of heat that they need to be able to dissipate (Emmans, 1990). A cooler environment would be preferred.

A minimum of 24 males and 24 female pigs are required in such an experiment, to allow for four of each sex to be killed at birth and at five predetermined intervals thereafter. However, a larger number of animals would be preferred because any number of pigs greater than 48 would not be slaughtered but used to increase the number of points to define B by estimating their chemical composition from slaughtered animals of similar live weight. Animals are serially slaughtered on a weight rather than on a time basis (e.g. at 5, 10, 20, 50 and 100 kg live weight).

When the animals reach their predetermined slaughter weight they are killed, whilst the live weight of the remaining animals is recorded. This allows carcass analyses to be performed on animals at the same physiological size or stage of maturity rather than at a chronological age. The protein contents of animals with similar body weights and kept in the same conditions are likely to be more nearly similar than are those of the same age. The reason for the larger number of pigs being killed and the larger number of killing periods is that carcass analyses of the these animals may be used to estimate the protein, lipid, water and ash content of the live animals. A larger number is required in order to have a more accurate estimate of the carcass composition. In addition to this, any animals that do not grow at their maximum rate could afford to be discarded from the analysis. It is difficult to estimate what proportion would fall into this category, but it is assumed to be fairly high.

The additional information that this second method will provide includes good estimates of the relative proportions of each of the components of the body at different stages of growth, and secondly, additional points on the growth curve allow estimates of error in measuring the genotype.

### 3.3.3 Method three - modified serial slaughter

A third method is proposed that requires very accurate estimations of the gross energy and lipid content of the body, and the live weight. A large number of animals is used, with only a few animals being slaughtered and analyzed at various weights. From the chemical analyses of the few slaughtered animals, the composition of the live animals can be determined. Body protein content is estimated from the method used by Kyriazakis and Emmans (1991), as the difference between the gross energy content of the body and the energy deposited as fat. The advantage of this method is that fewer animals need to be slaughtered and analyzed.

## 3.4 Estimation of parameters

To quantify the genetic parameters required, the relative protein growth rate (y axis) is plotted against the natural logarithm ($\log_e$) of body protein weight (x axis). As previously discussed a linear negative slope is expected which is the estimate of the rate of maturing, or B. The slope will intercept the x axis at ($\log_e$) mature protein weight. Mature protein weight (Pm) is calculated as follows:

$$Pmat = e^{\left(\frac{a}{B}\right)} \quad (kg) \qquad (3.5)$$

$$\text{where} \quad a = \frac{(dPt/dt)}{Pt} + B \times \ln(Pt)$$

The rate of protein growth is obtained from the difference in protein contents of the animal between the start and end of each period. Body protein weight is determined by multiplying the protein content of the killed animals, of the same stage of maturity, by the weight of the live animal. It is for this reason that estimates of individuals must be used rather than pooling all the animals together.

A simple linear regression analysis may be used to obtain estimates of these values as well as the statistical accuracy of the parameter estimates.

To obtain an estimate of the LPRm the mature lipid weight must be determined by the same method proposed for protein, which is then divided by the mature protein weight. The accuracy of the estimate of LPRm will be related to the degree to which the animal deviated from its potential rate of growth as a result of environmental and nutritional constraints.

It may be argued that four points on this graph are too few, but because the scale of the x axis is logarithmic the second point chosen is already close to the mature size of the animal, so the accuracy would not be markedly improved by introducing further points on the line. Accuracy can be improved by measuring the growth rate of more animals rather than at different periods of growth.

If the maximum rate of protein deposition ($PR_{max}$) and mature protein weight for a genotype is known then B can be calculated as:

$$B = PR_{max} \times \frac{e}{Pmat} \qquad (day^{-1}) \qquad (3.6)$$

### 3.5 Prevention of Limitations to Potential Growth

It is important that the environment is such that the animals are allowed to grow to their potential (Emmans, 1981). If any environmental condition occurs that will result in the pig not growing to its intrinsic upper limit, the estimation of the genetic parameters will be incorrect. Similarly, the diet must not limit protein growth nor allow excess fat deposition to occur. Imbalanced diets may result in excess deposition of lipid (Kyriazakis *et al.*, 1991; Kyriazakis and Emmans, 1991; de Greef, 1992), which in turn cause an overestimation of the mature lipid : protein ratio and result in an inaccurate description of the inherent fatness of the genotype. These conditions may be satisfied by considering a choice feeding system or providing a high protein diet prior to slaughtering, or providing special environmental facilities.

### 3.5.1 Choice feeding

By providing a choice between a well balanced high protein feed and a well balanced low protein feed the pig is able to consume the amount of protein relative to energy, at different stages of growth, that would allow it to grow at its potential, without overconsuming energy. Both feeds must have equal energy concentrations and an abundant supply of vitamins and minerals. This principle is well established in growing pigs (Kyriazakis, Emmans and Whittemore, 1988,1990; Bradford and Gous, 1991 a,b; Kyriazakis and Emmans, 1991).

Choice feeding would eliminate the possibility of the pig consuming excess energy and therefore depositing excess fat. There is also the possibility that at high temperatures the pig will be able to meet its requirement for both protein and energy without increasing the heat stress.

### 3.5.2 Special environmental facilities

A "lamina flow"- type environment could be provided, in which one end of the room is kept warm, whist the other is kept cool. A temperature gradient (Figure 3.4) is maintained between the two extremes which would allow the animals to choose the temperature at which they feel most comfortable. This comfort temperature would depend on the growth rate of the animal (females would therefore favour a higher temperature than males) and on the feed being consumed.

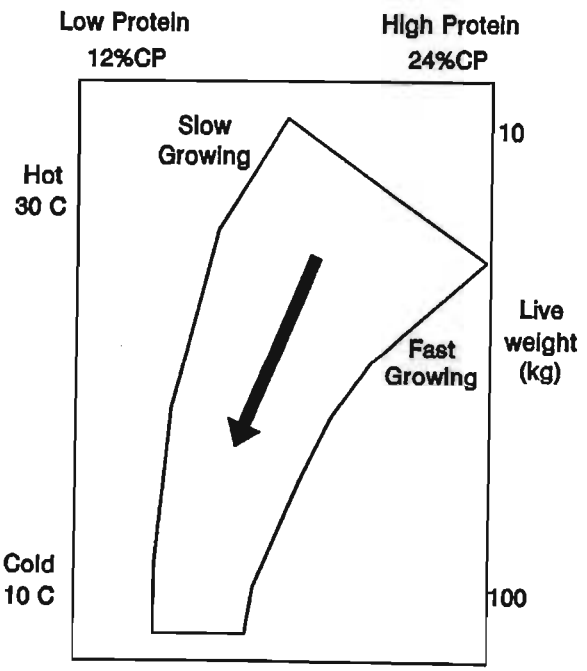


Figure 3.4 A theoretical example of a laminar-flow type environment and the response of different types of animals. The arrow (→) represents the direction in which the pigs will move with an increase in live weight.

By offering the pigs a choice between a high and a low protein feed and by providing them also with a range of temperatures within the building, it is more likely that the potential growth rate of the pigs will be measured, at the level of fatness inherent in that animal. Young lean pigs would be expected initially to select more of the high protein diet and remain in the warmer part of the house. As their growth rate increases they would be expected to move toward the cooler region and to consume a higher proportion of the low protein diet. This is illustrated in Figure 3.4 as the fast growing line. Slower growing pigs of a fatter genotype would consume less of the high protein diet and more of the low protein diet to meet their requirements for protein growth and, when young, would inhabit the warmer area of the room.

### 3.5.3 Provision of a high protein diet prior to slaughter

If a choice feeding system or a high nutrient density diet is not used then a high protein diet should be provided for a period prior to slaughtering the pigs for carcass analysis. This has the effect of reducing the body fat content of those pigs that have become fatter than dictated by their genetic potential (Figure 3.5).

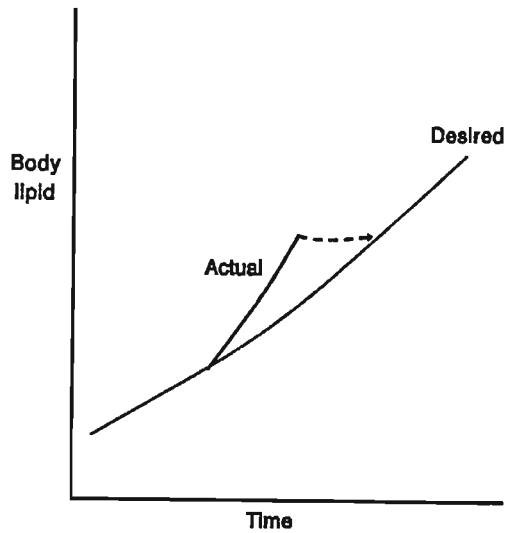


Figure 3.5 The response in body lipid content in overfat pigs when fed a high protein diet.

This assumes that a pig has an inherent level of fatness which it strives to achieve, and there is evidence to support such a theory (Kyriazakis *et al.* 1991). If the pig is fatter or leaner than it desires to be, it will, if given the correct circumstances, attempt to return to its desired fat level by reducing the rate of lipid retention. If the pig is fatter than its inherent degree of fatness at a predetermined slaughter weight the lipid-to-protein ratio at maturity would be over-estimated. By reducing the rate of lipid retention a few weeks prior to slaughtering, a more accurate estimate of the inherent fat level of the pig can be obtained.

The duration of the period of feeding a nutrient density diet depends on body weight, the extent to which the animal is fatter than it would like to be and the energy and protein content of the diet. From the work of Kyriazakis *et al.* (1991) and Kyriazakis and Emmans (1991) it would appear that animals between 20 and 33 kg live weight which previously had been fed a diet deficient in protein would require close on 14 days for their body far levels to return to the levels of those animals fed a well balanced, high protein diet (27.8% crude protein and 17 MJ DE/kg). At heavier weights (65 to 105 kg), de Greef (1992) found that pigs previously fed a very low protein diet (7.2% crude protein and 14.1 MJ DE/kg) from 30 kg to 60 kg live weight had significantly lower fat gains during the rehabilitation period. Although these animals were still 5% fatter after three weeks of being fed a high protein diet (25.3% crude protein and 15.8 MJ DE/kg) the difference in fat content between treatments was reduced from 13.7% at 65 kg to 5.4% at 105 kg. It is likely that had the low protein treatment not been as severe there would have been no differences in fat content after four weeks. It can therefore be deduced that at low body weights a two week period of feeding a high protein, high energy diet will enable those animals that are fatter than their inherent desire an opportunity to reduce body fat levels. At heavier body weights (< 65 kg) a longer feeding period of four weeks may be necessary to achieve the same results.

It is important to note that this method of compensating for over-fatness will not result in genetically fat pigs depositing less fat but rather allows lean pigs an opportunity of expressing their desired state of being.

## 3.6 Experimental Evidence to Test The Accuracy of the Proposed Theory

To test how accurate this technique is in predicting the value of genetic parameters, data from two experiments were used to obtain estimates of these parameters. Estimates of the genotypes of the pigs used in these two experiments were then used in the simulation model described by Ferguson (1989), which relies on these estimates to predict the potential and actual growth rates of the pigs, given information on the feeds supplied and the environment in which the animals were housed. The results of these simulations were then compared with the actual experimental results. Where data required to determine the genetic parameters were not reported for these two experiments, average values were used. The two experiments used to illustrate the method of evaluating a genotype are from Campbell and Taverner (1988) and Whittemore *et al.* (1988).

### 3.6.1 Campbell and Taverner (1988).

As there were only two growth periods used, viz. 20 - 45 kg and 45 - 90 kg, only two points could be calculated and used to estimate the genetic parameters by the regression of relative protein

growth on the natural logarithm of protein weight. Mature protein weight was derived from Equation 3.3. The maximum protein growth rate (PRmax) was derived from the equation:

$$PRmax = \frac{B \times Pm}{e} \qquad (g/day) \qquad (3.7)$$

The values used and the results are shown in Table 3.1.

Table 3.1. Estimation of the B value from data obtained from Campbell and Taverner (1988).

| Time Difference | Initial Protein Weight (kg) | Final Protein Weight (kg) | Mean Protein weight (kg) | $Log_e$ Mean | Protein growth rate (kg/d) | Relative growth Rate | B (/d) | Pm (kg) | PR max (kg/d) |
|---|---|---|---|---|---|---|---|---|---|
| 27.5 | 3.01 | 6.76 | 4.89 | 1.586 | 0.137 | 0.02800 | 0.0126 | 45.0 | 0.208 |
| 32.5 | 6.76 | 12.89 | 9.83 | 2.285 | 0.189 | 0.01922 | | | |

The final protein content for the first period was the same as the initial protein content in the second period, namely, for a pig of 45 kg live weight (40.7 kg empty body weight). As there was no initial protein content specified for the first period an average of 170 g protein / kg empty body weight was used. Since it is unlikely that the animals were grown under ideal conditions the assumption that the rate of fat deposition was not linear between 45 and 90 kg body weight but rather exponential is not unreasonable and therefore, in determining the mean lipid weight between 45 kg and 90 kg, a logarithmic mean is more appropriate than the arithmetic mean lipid weight. Using equation 5 and the calculated B value (0.0126) the rate of lipid growth given in the experiment, viz 351 g/d and the logarithmic mean body lipid weight of 12.03 kg, LPRm was estimated to be 2.80.

The actual results for the pigs fed a restricted intake until 45 kg and those fed *ad libitum* between 45 kg and 90 kg can be compared with those predicted by means of the model in Tables 3.2 and 3.3. There is good agreement between the observed and predicted results.

Table 3.2. Comparison of actual pig performance results from Campbell and Taverner (1988) and those predicted by the model of Ferguson (1989).

| Weight Range (kg) | | Actual | Predicted |
|---|---|---|---|
| 20 - 45 | ADG (g/d) | 809 | 771 |
| | Feed Intake (kg/d) | 1.50 | 1.41 |
| | FCE | 1.84 | 1.83 |
| 45 - 90 | ADG (g/d) | 1224 | 1202 |
| | Feed Intake (kg/d) | 2.80 | 2.75 |
| | FCE | 2.29 | 2.29 |

Table 3.3. Comparison of actual body composition and performance in pigs at 45 and 95 kg live weight from Campbell and Taverner (1988) and those predicted by the model of Ferguson (1989).

| Weight (kg) | | Actual | Predicted |
|---|---|---|---|
| 45 | Body Protein (%) | 16.6 | 16.1 |
| | Body Fat (%) | 17.2 | 17.5 |
| | Body Water (%) | 63.6 | 63.1 |
| | Body Ash (%) | 2.5 | 3.4 |
| 90 | PR (g/d) | 189 | 180 |
| | LR (g/d) | 351 | 364 |
| | Body Protein (%) | 16.2 | 16.0 |
| | Body Fat (%) | 26.0 | 24.2 |
| | Body Water (%) | 56.3 | 56.4 |
| | Body Ash (%) | 2.5 | 3.1 |

### 3.6.2 Whittemore, Tullis and Emmans (1988).

In this experiment, pigs were grown until they were close to their mature size. They were serially slaughtered at different ages and the subsequent carcass analyses were recorded. An estimate of the LPRm was obtained from the data at maturity by dividing lipid content (61.1 kg) by the protein content (29.8 kg) to give a value of 2.1. This value was used in preference to that of 2.75 obtained by using mature lipid value, obtained from the X-intercept of the graph of relative lipid growth versus body lipid. The reasons for not using 2.75 are, firstly, the $R^2$ value from the regression analysis was only 0.33, suggesting that the estimate of mature body lipid content is inaccurate. The second reason became evident when running the simulation model, in that the predicted body lipid content was always overestimated. Table 3.4 provides a summary of the data used.

Table 3.4. Estimation of the genetic parameters to be used in the simulation model of Ferguson (1989) using data from Whittemore et al. (1988).

| Time Difference | Initial Protein Weight (kg) | Final Protein Weight (kg) | Mean Protein Weight (kg) | $\log_e$ Protein Mean | Protein growth rate (kg/d) | Relative growth rate |
|---|---|---|---|---|---|---|
| 39 | 3.38 | 7.69 | 5.53 | 1.711 | 0.110 | 0.0199 |
| 32 | 7.69 | 11.24 | 9.46 | 2.247 | 0.111 | 0.0117 |
| 42 | 11.24 | 16.19 | 13.71 | 2.618 | 0.118 | 0.0086 |
| 54 | 24.09 | 27.44 | 25.77 | 3.249 | 0.062 | 0.0024 |

Linear regression analysis was used to estimate the rate of maturing and the mature size of the pigs used in the second experiment (data from Table 3.4) and the results of this analysis are in Table 3.5.

Table 3.5. Estimated genetic parameters using linear regression.

| B (/day) | s.e | $R^2$ | Pm (kg) | PRmax (kg/d) |
|---|---|---|---|---|
| 0.01118 | 0.00108 | 0.981 | 31.0 | 0.128 |

Estimates of these growth parameters (Table 3.5) were used in the simulation model described by Ferguson (1989), to predict the growth rate. The results are shown in Table 3.6. There is considerable similarity between the observed and predicted results for the weights of each of the chemical components indicating, again, that good estimates of the potential growth of an animal can be obtained with a knowledge of relatively few genetic parameters.

Where differences exist between actual and predicted values, these are likely to result from biological variation associated with different animals having different concentrations of protein, lipid, water and ash at a given age. An example of such differences in chemical composition can be observed in Table 3.6 where,at empty body weights of 142.94 and 155.6 kg, the actual protein content is 26.46 kg and 24.90 kg respectively.

Table 3.6. Comparison of actual body composition for different empty body weights obtained from Whittemore et al. (1988) with those predicted using the growth parameters in Table 3.5.

| Empty Body Weight (kg) | | Body Protein (kg) | | Body Lipid (kg) | | Body Moisture (kg) | | Body Ash (kg) | |
|---|---|---|---|---|---|---|---|---|---|
| Actual | Predicted | Actual | Predicted | Actual | Predicted | Actual | Predicted | Actual | Predicted |
| 20.81 | 20.99 | 3.38 | 3.45 | 2.56 | 2.78 | 13.13 | 13.96 | 0.70 | 0.79 |
| 41.55 | 41.66 | 7.69 | 7.02 | 5.31 | 7.35 | 25.74 | 25.68 | 1.60 | 1.61 |
| 70.97 | 70.81 | 11.24 | 11.87 | 16.24 | 15.88 | 32.16 | 40.34 | 2.49 | 2.73 |
| 91.55 | 91.74 | 16.19 | 15.25 | 18.22 | 22.94 | 51.51 | 50.04 | 3.11 | 3.51 |
| 142.94 | 142.94 | 26.46 | 23.22 | 30.02 | 42.53 | 75.00 | 71.84 | 5.30 | 5.34 |
| 155.60 | 155.40 | 24.90 | 25.11 | 46.41 | 47.69 | 72.10 | 76.82 | 5.77 | 5.27 |

It is statistically more sound to make use of as many data points as possible, to reduce the error in estimating the regression coefficient (in this case, the rate of maturing). However, when only two points are to be used to determine the growth potential, the question then arises as to which two points should be used? This is illustrated by making use of the data from the second experiment. Four time periods were reported in this experiment (Table 3.4), and therefore, six different combinations of paired data are possible. The results of using all the combinations are six different slopes with large variations in the estimate of the B value, ranging from 0.0085 to 0.0153 (Table 3.7).

Table 3.7. Different B values ($day^{-1}$) associated with different starting and finishing relative growth rates.

| | End Point | | | | | |
|---|---|---|---|---|---|---|
| Start Point | 2 | 3 | 4 | SE | Mean B (/day) | SE mean |
| 1 | 0.0153 | 0.0125 | 0.0114 | 0.0025 | 0.01113 | 0.00102 |
| 2 | | 0.0085 | 0.0093 | | | |
| 3 | | | 0.0098 | | | |

The minimum requirements for an accurate estimation of the regression of relative growth rate on (ln protein weight) is two growth periods, each of short duration, spaced relatively far apart such that the estimates of relative growth rate at each point are accurately determined, and that the two points are sufficiently far apart to allow accurate estimates of the slope of the regression between them. It is not necessary to grow the animals to maturity because the logarithm of body protein weight at 90 kg live weight is not substantially different from that at maturity, whereas that at 20 kg live weight is far from the ln of mature body weight. The most suitable periods are those before and after the periods of maximum growth, i.e. within the first three weeks after weaning and between 75 - 100 kg body weight. The larger the number of pigs killed over each time period the more accurately will the relative growth rates be estimated. This in turn will increase the accuracy of the evaluation.

### 3.7 Conclusion

As the B value is sensitive to changes in relative growth, the margin for error is small. This may appear to be a limitation to the effective evaluation of an animal or genotype, but with accurate measurements and the correct environment the error margin should be low.

It is important to note that the estimates of growth parameters obtained with the technique described above are not likely to represent the growth potential of the animals, but rather a potential under the constraints pertaining to the feed and the environment. To ensure that animals grow to their potential the feed and the environment must be non-limiting, conditions that can be provided by making use of the techniques described above.

A minimum of two growth periods is required to estimate the B value, the mature protein weight and the lipid weights. These periods should be sufficiently far apart, such as after the fourth week of weaning and sometime after the period of maximum growth, to obtain the most accurate estimates of the animal parameters.

The technique proposed in this chapter provides a solution to the problem found in most animal growth models (Moughan and Verstegen, 1988), of estimating the potential rate of protein and lipid growth and their respective mature sizes. The method is simple with relatively few data being needed and only three biological parameters being required to define the genotype of an animal. These advantages provide breeders with an effective means of selecting animals based on their inherent fatness and body protein content. Therefore, selection for commercially important characteristics, such as the amount of lean meat and backfat thickness, is made considerably easier and quicker. The technique is sufficiently flexible to determine estimates of the genetic growth parameters of

different genotypes of pigs from past experiments, but it still needed to be tested as a specific experiment.

# CHAPTER 4

# AN EXPERIMENT TO TEST THE TECHNIQUE OF EVALUATING GENOTYPES

## 4.1 Introduction

Associated with any theory that is to be used in practice, is the ability to test the theory in terms of its accuracy and its ease of practical application. An experiment was designed to quantify specific genetic parameters which will describe the growth potential of a pig. The experiment was conducted in two stages, as described in the previous chapter. Linear regression analyses were performed on body protein and lipid weights of boars and gilts, to determine the relative growth parameter (B), the mature body protein weight (Pm) and the lipid:protein ratio at maturity (LPRm).

## 4.2 Materials and methods

The experiment was divided into two periods, an early period and a later period, as described in the previous chapter.

### 4.2.1 Early period

Twelve pigs were obtained from a litter of improved Large White x Landrace pigs; six were female and six were entire males. Two female and two male pigs were killed at two days of age. This was repeated on days 13 and 23. The lightest and heaviest female and male pigs (two pigs of each sex) were selected to be killed at the given time periods. The animals were fasted for 12 hours prior to slaughter and then killed by an overdose of an inorganic anaesthetic (Pentobarbitone sodium) so as not to interfere with the carcass analysis. One male pig died prior to the specified time period and was therefore not included in the analyses. The piglets remained in the farrowing house after birth, with continual heating above their sleeping area, so as to provide an environment conducive to maximum growth. As all these pigs were slaughtered by twenty-three days of age no creep feed was provided. They were kept with the sow until they were killed, whereafter they were frozen in plastic bags until chemical analyses were performed on the carcasses. The frozen carcasses were ground up whole, and three sub-samples were taken at random for chemical analysis. No emptying of the gastrointestinal tracts were performed as it was assumed that, having been fasted for 12 hours prior to slaughter, the intestinal contents of these young piglets would contribute very little to the overall composition of the carcasses.

### 4.2.2 Later period

Eighteen pigs, nine females and nine entire males, were obtained from two litters of unimproved Large White x Landrace pigs. These pigs were reared to 80 kg, when a third of them were slaughtered to obtain initial conditions for the growth period under consideration. Three male and three females were killed when they reached 90 kg, and the remainder were killed at 100 kg. The pigs were randomly assigned a slaughter weight before the experiment began. Of the 18 pigs, one male died and one female was discarded due to ill health. Both these pigs were from the 80 kg slaughter period. All animals were weighed weekly until they were close to their slaughter weight after which they were weighed daily.

The animals were reared in conditions intended to be the best possible. They were given a weaner feed (Table 4.1) from 21 d of age whilst in the farrowing house. They were moved to a weaning house after 28 d (49 d of age) but were kept on the weaner diet. At 10 weeks of age they were moved to a growing house and at this stage the feed was changed to a grower diet (Table 4.1). It was changed once again, when the pigs reached an average of 50 kg live weight, to a finisher diet (Table 4.1). They remained on this diet until they were slaughtered.

Table 4.1. Composition (g/kg) and analysis of the diets.

| | Weaner | Grower | Finisher |
|---|---|---|---|
| Yellow maize meal | 468.0 | 482.0 | 529.0 |
| Sunflower oilcake meal | 216.0 | 184.0 | 124.0 |
| Soyabean oilcake meal | 100.0 | 200.0 | 150.0 |
| Fish meal | 148.0 | 74.0 | |
| Wheat bran | | | 110.0 |
| Oil | 50.0 | 30.0 | |
| Brewers grain | | | 50.0 |
| Monocalcium phosphate | 14.6 | 23.0 | 19.5 |
| Limestone powder | | 4.0 | 10.0 |
| Salt | | 1.0 | 2.8 |
| Vitamin premix | 3.0 | 2.0 | 2.0 |
| Lysine.HCl | | | 2.4 |
| Antibiotic[¶] | 0.4 | | |
| Analysis(determined) | | | |
| Protein (g N x 6.25) | 261.3 | 242.6 | 194.5 |
| DE (MJ/kg) | 15.5 | 15.1 | 13.3 |
| Lysine (g/kg) | 16.7 | 12.6 | 10.5 |

[¶] A commercial feed additive (Emtryl +) was included in the weaner diet only. The active ingredients are Dimetridazole (22.5%), Furazolidone (30.0%) and Sulphadimidine (10.0%).

The pigs were killed by exsanguination, after being stunned, which resulted in some loss of blood. The pigs were dissected and the gastrointestinal tract, bladder, heart, liver and lungs were removed and weighed full. The stomach, intestines and bladder were then emptied and weighed. Only half of the carcass was used for further analysis because of its size. The empty carcasses were halved along the midline, with the right half of the carcass being chosen for further analyses. The dissected organs were also halved, recombined with the half carcass and then minced together with the remaining blood. Three sub-samples were obtained for each carcass and individually analyzed for protein, fat, moisture and ash. Moisture content was determined by freeze drying for three days. The dry matter was analyzed for protein (nitrogen x 6.25) by an auto analyzer; lipid by Soxhlet extraction with petroleum ether at 40-60°C for eight hours; ash by burning in a muffle furnace at 550°C for three hours. After being analyzed individually, the three sample results were pooled to provide a single result per pig.

### 4.3 Results and Discussion

The results of the chemical compositions of each of the animals in the early period are shown in Table 4.2, with those in the later period being shown in Table 4.3.

Protein retention rates (PR) for given body protein contents were determined for the different sexes (Table 4.4) from the individual data for specific slaughter weights (Table 4.2 and 4.3). Similarly, lipid retention rates (LR) were calculated from data in Tables 4.2 and 4.3 and these are shown in Table 4.5. From this information a description of the genotype can be determined.

Table 4.2. Body weights at slaughter and chemical composition of the whole body in the early period.

| Sex | Age at slaughter (days) | Live weight at slaughter (kg) | Protein (kg) | Fat (kg) | Water (kg) | Ash (kg) |
|---|---|---|---|---|---|---|
| B | 2 | 1.8 | 0.30 | 0.16 | 1.27 | 0.06 |
| B | 2 | 1.5 | 0.25 | 0.14 | 1.04 | 0.06 |
| G | 2 | 1.9 | 0.27 | 0.16 | 1.34 | 0.07 |
| G | 2 | 1.7 | 0.24 | 0.14 | 1.23 | 0.06 |
| B | 13 | 3.7 | 0.50 | 0.33 | 2.68 | 0.09 |
| B | 13 | 3.0 | 0.47 | 0.31 | 2.11 | 0.09 |
| G | 13 | 3.8 | 0.50 | 0.40 | 2.68 | 0.10 |
| G | 13 | 2.8 | 0.44 | 0.26 | 1.96 | 0.09 |
| B[¶] | 23 | 5.2 | 0.75 | 0.56 | 3.70 | 0.14 |
| G | 23 | 5.8 | 0.77 | 0.56 | 4.25 | 0.12 |
| G | 23 | 5.0 | 0.73 | 0.60 | 3.48 | 0.09 |

[¶]Data for one male only as the other died prior to its predetermined slaughter age.

Table 4.3. Body weights at slaughter and chemical composition of the empty body in the later period.

| Sex[¶] | Age at slaughter (days) | Live weight at slaughter (kg) | Empty body weight at slaughter (kg) | Protein (kg) | Fat (kg) | Water (kg) | Ash (kg) |
|---|---|---|---|---|---|---|---|
| B | 135 | 80.5 | 75.7 | 11.65 | 19.24 | 41.69 | 1.79 |
| B | 131 | 79.0 | 74.6 | 11.86 | 19.21 | 40.57 | 1.56 |
| G | 125 | 80.0 | 76.2 | 11.29 | 19.52 | 42.09 | 2.94 |
| G | 141 | 82.0 | 75.4 | 10.20 | 18.65 | 41.92 | 2.00 |
| B | 135 | 90.5 | 85.9 | 13.49 | 24.74 | 42.72 | 1.96 |
| B | 158 | 90.0 | 84.6 | 13.58 | 21.57 | 45.22 | 2.79 |
| B | 141 | 90.5 | 84.0 | 13.12 | 21.19 | 45.72 | 2.55 |
| G | 142 | 92.0 | 85.1 | 11.28 | 25.66 | 44.56 | 2.32 |
| G | 141 | 93.0 | 84.0 | 12.57 | 19.69 | 47.19 | 2.59 |
| G | 156 | 89.0 | 82.0 | 11.79 | 22.66 | 43.84 | 1.83 |
| B | 141 | 102.0 | 96.9 | 14.64 | 22.00 | 52.67 | 3.36 |
| B | 158 | 103.0 | 95.8 | 14.37 | 23.35 | 52.67 | 3.19 |
| B | 164 | 99.4 | 93.4 | 13.74 | 29.04 | 44.11 | 3.32 |
| G | 158 | 100.0 | 94.0 | 12.90 | 27.50 | 49.08 | 2.88 |
| G | 155 | 98.5 | 89.6 | 12.38 | 26.49 | 46.71 | 3.01 |
| G | 159 | 99.0 | 91.0 | 13.69 | 24.02 | 47.05 | 2.72 |

[¶] Data for only two male and two female pigs at live weight of 80 kg as one male died and the female was discarded because of illness.

Simple linear regression analyses were performed separately on the data in Tables 4.4 and 4.5 to obtain the B value, Pm and LPRm, and a summary of the results is given in Table 4.6.

Table 4.4. Rates of protein retention for given body protein weights.

| | Period | Average body protein weight (kg) | Protein retention (g/d) | Relative growth rate |
|---|---|---|---|---|
| Boars : | | | | |
| | 2 - 13 days | 0.38 | 19.4 | 0.0511 |
| | 13 - 23 days | 0.62 | 26.2 | 0.0424 |
| | 80 - 90 kg | 12.57 | 164.3 | 0.0131 |
| | 90 - 100 kg | 13.82 | 142.3 | 0.0103 |
| Gilts : | | | | |
| | 2 -13 days | 0.36 | 19.4 | 0.0532 |
| | 13 - 23 days | 0.61 | 27.5 | 0.0452 |
| | 80 - 90 kg | 11.31 | 113.3 | 0.0100 |
| | 90 - 100 kg | 12.43 | 137.9 | 0.0111 |

Table 4.5. Rates of lipid retention for given body lipid weights.

| | Period | Average body lipid weight (kg) | Lipid retention (g/d) | Relative growth rates |
|---|---|---|---|---|
| Boars : | | | | |
| | 2 - 13 days | 0.24 | 15.4 | 0.0657 |
| | 13 - 23 days | 0.44 | 24.0 | 0.0545 |
| | 80 - 90 kg | 20.86 | 327.4 | 0.0157 |
| | 90 - 100 kg | 23.65 | 382.6 | 0.0162 |
| Gilts : | | | | |
| | 2 -13 days | 0.24 | 16.4 | 0.0682 |
| | 13 - 23 days | 0.45 | 25.2 | 0.0554 |
| | 80 - 90 kg | 20.88 | 358.8 | 0.0172 |
| | 90 - 100 kg | 24.34 | 416.0 | 0.0171 |

Figures 4.1 and 4.2 illustrate the effectiveness of using four points to obtain estimates of the growth parameters for both sexes.

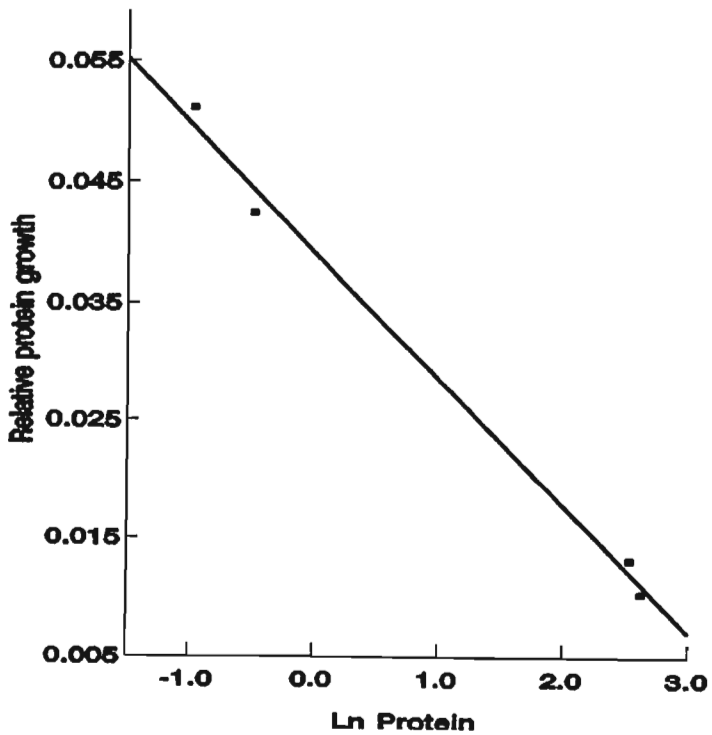


Figure 4.1 Relative protein growth of male pigs. (■) Actual values; (—) Predicted values from the regression equation y = 0.0391 - 0.01071 x LogX.

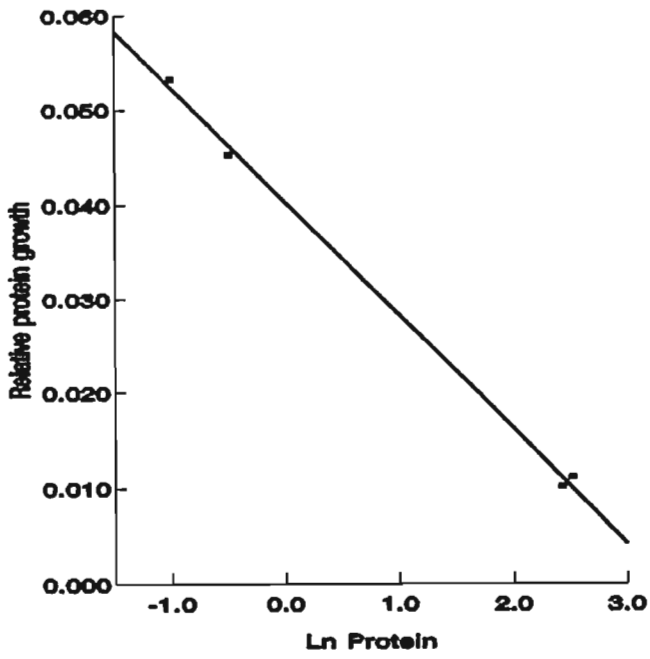


Figure 4.2 Relative protein growth of female pigs. (■) Actual values; (—) Predicted values from the regression equation y = 0.0402 - 0.0120 x Log X.

The estimated B values obtained from lipid analysis ( 0.01043 and 0.01065 $day^{-1}$ for boars and gilts respectively) were slightly lower than from the protein analysis (0.01071 and 0.01201 $day^{-1}$, boars and gilts respectively).

Table 4.6. Genetic parameters of unimproved male and female pigs.

| Parameters | Boars | Gilts |
|---|---|---|
| Protein analysis: | | |
| B ($day^{-1}$) | 0.0107 | 0.0120 |
| s.e. | 0.00060 | 0.00044 |
| $R^2$ | 0.994 | 0.997 |
| Lipid analysis: | | |
| B ($day^{-1}$) | 0.01043 | 0.01065 |
| s.e. | 0.00064 | 0.00074 |
| $R^2$ | 0.993 | 0.991 |
| Pm (kg) | 38.73 | 28.41 |
| PRmax (g/day) | 164 | 138 |
| Lm (kg) | 100.7 | 110.5 |
| LPRm | 2.60 | 3.89 |

Protein growth is less likely to be adversely affected by conditions that are not perfect for the realisation of potential growth than is lipid growth, which is dependent on prevailing nutritional and environmental conditions (Kyriazakis, Stamataris, Emmans and Whittemore, 1991). The difference

in the estimate of the B value therefore probably suggests that some nutritional or environmental conditions were not ideal to allow protein and lipid growth to proceed at their potential during the test period (Kyriazakis *et al.*, 1991). From the regression analyses for gilts, the standard error of B, using body lipid, was 0.00074 whilst the estimate from protein analysis was 0.00028. This indicates a greater variability in the amount of fat retained for a given body fat content. As protein growth is much less variable, the B value from the analysis of protein has been used in further analyses and discussion. The estimates of B for boars, from the protein and lipid regression analyses, were very similar with standard error values of 0.00060 and 0.00064 respectively.

The rates of maturing (B) of boars and gilts (0.0107 and 0.0120 $day^{-1}$, respectively) are similar to those estimated by Whittemore, Tullis and Emmans (1988) of 0.010 and 0.011 $day^{-1}$ respectively for unimproved Large White x Landrace pigs. Whereas Whittemore *et al.* (1988) estimated these values by application of the Gompertz function to live-weight change, the results in this experiment confirm the closeness of their estimates when using protein weight instead of live-weight. With the results obtained in Table 4.6, the estimated protein growth of the type and sex of the animal can be predicted by the Gompertz growth function.

Siebrits, Kemm, Ras and Barnes (1986) obtained maximum PR values of 156 g/day and 120 g/day for boars and gilts respectively. Similar results were obtained in a different experiment by Kemm, Siebrits, Ras and Badenhorst (1991). The pigs used in their experiments were of a similar genotype to those used in this experiment. The estimated maximum PR values in this experiment of 164 g/day and 138 g/day for boars and gilts respectively supports the accuracy of the proposed analytical procedure in predicting pig genotypes. Unfortunately, in both previously mentioned experiments the animals were slaughtered prior to maturity and therefore no estimates were obtained of mature protein size nor of LPRm. However, with a high degree of accuracy in predicting maximum PR it is possible to estimate the remaining genetic characteristics from these values.

Emmans and Fisher (1986) and Emmans (1988) introduce a scaled growth rate parameter ($B^*$). Adapting Taylor's (1980) scaling rule, B is related to Pm, across genotypes, such that:

$$B^* = B \times Pmat^{0.27} \qquad (4.1)$$

This means that $B^*$ is independent of Pm and can be used as a means of observing differences between genotypes at different time periods, which is a very useful tool for studies in genetic selection. Emmans (1988) estimates $B^*$ for current pig genotypes as 0.04. From the results obtained in this experiment $B^*$ for both boars and gilts is 0.03.

The maximum PR values predicted by Whittemore *et al.* (1988) were lower for boars (130 g/day) than

in the present experiment but fairly similar for gilts (120 g/day). The differences may be associated with the use, by Whittemore *et al.* (1988) of live-weight rather than protein weight.

### 4.4 Conclusion

The application of simulation models in practice is constrained by an inadequate description of the type of animal that is to be simulated and, where animals are well defined, by no simple, routine method to estimate the parameters. The analytical procedure given here provides a solution to the these limitations, firstly, by describing the animal using a small set of variables and, secondly, by providing a procedure to estimate these genetic variables. Pig breeders, therefore, have at their disposal a technique which can be used to sufficiently describe the type of animal they are producing. The accuracy of genetic selection can be improved by comparing the animal parameters between individuals within a population and between different populations and by measuring the rate at which these parameters change over time.

Although no mention has been made of the relationships between B, Pm and LPRm, in this chapter, there are certain assumptions that can be made which will assist the breeder in the selection process. There is likely to be no correlation between Pm and LPRm. Pigs with a low protein weight at maturity are not necessarily fat and, similarly, pigs with a high mature protein weight may have either a high or low fat content. Similarly, there is likely to be no relationship between $B^*$ and LPRm. According to Emmans (1988), B and Pm are inversely correlated, whereas there is little correlation between $B^*$ and Pm. From these relationships, a pig geneticist could select for a high Pm or $B^*$ value, and/or a low LPRm value. Selecting for a high protein weight at maturity or a high scaled growth rate will not necessary result in a leaner animal, but will result in a faster growing animal with a larger mature size.

Where premium prices are paid for heavier carcass weights and there is less emphasis on fat content, the breeders should select for higher Pm or $B^*$ values. Animals, selected for a high Pm or $B^*$ value will reach these heavier carcass weights at a younger age. However, if leanness is the most important grading criteria then selection must be based on the lowest LPRm value. The problem with selecting animals on the basis of their mature lipid to protein ratio, is that if the growing conditions are not ideal then the estimate of LPRm will be incorrect. Similarly, a particular pig breed may have undergone rigid selection on the basis of a low LPRm value but, when grown under less than ideal conditions, the pig may become as fat as a breed with a higher LPRm value that was grown in ideal conditions.

# CHAPTER 5

# PREDICTING THE DISTRIBUTION IN THE PARAMETERS USED TO DEFINE THE GENOTYPE

## 5.1 Introduction

All pig growth models to date (Roux, 1976; Whittemore and Fawcett, 1976; Philips and MacHardy, 1983; Bridges, Turner, Smith, Stahly and Louwer, 1986; Black, Campbell, Williams, James and Davies, 1986; Moughan, Smith and Pearson, 1987; Pomar, Harris and Minvielle, 1991; Ferguson, Gous and Emmans, 1994) have been designed to simulate the growth of an individual animal over time, so the description of the genotype, although defined in different ways by the above researchers, has not taken into account the variability that can be expected in a population of animals. Yet it is the population response to feed and the environment that is the ultimate goal in any simulation model - not the response of the individual.

However, to define the nutrient requirements of a population over time, it is important to understand first how an individual animal within the population will respond, at a time, to increasing dietary concentrations of the nutrient (Emmans and Fisher, 1986; Whittemore, 1993). For example, the relationship between protein growth and nutrient intake of an animal has been suggested to be linear, up to a maximum response, and then constant (Fisher, Morris and Jennings, 1973; Yen, Cole and Lewis, 1986a,b; Fuller, McWilliam, Wang and Giles, 1989; Batterham, Andersen, Baigent and White, 1990). This response has been defined as a linear-plateau relationship. Each animal will differ in its maintenance requirement (defined as the point at which the slope intersects the X axis) and its maximum protein growth (or plateau). The integration of the linear-plateau responses of a group of individuals will produce a curvilinear response. These responses are illustrated in Figure 5.1, where the effect of increasing amino acid intake on the protein growth of a number of individuals is shown, together with the integrated response over all animals.

In nutritional growth response experiments, it is important to understand the difference between the response of the 'average' animal and that of the population. The average animal is defined as that individual which has the average animal characteristics of the population and the response of the average individual is of a single animal. The population response is the mean of all the individuals within the population.

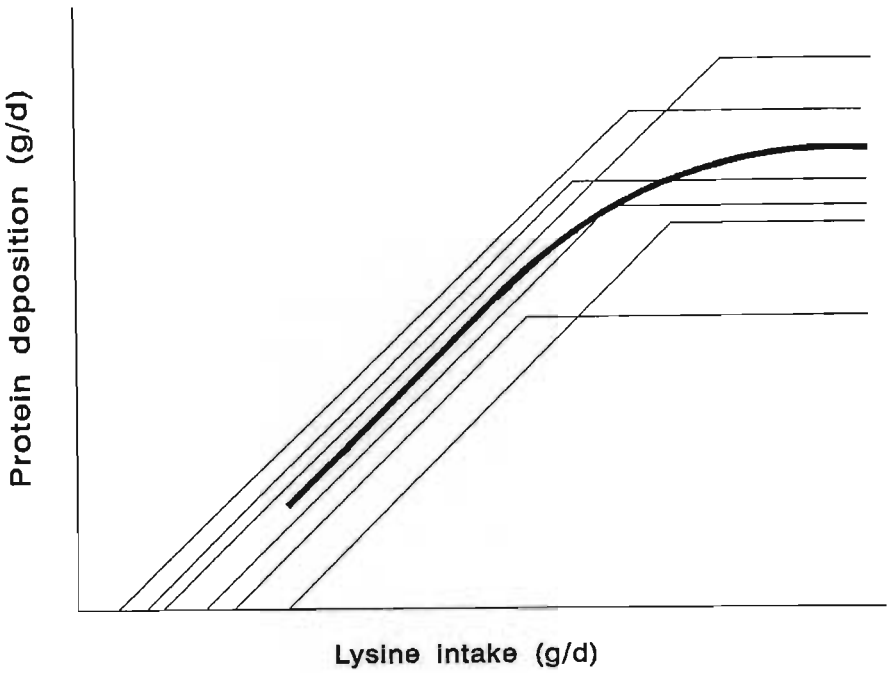


Figure 5.1 The response in protein deposition of individuals in a population (— ) and the mean population response (above maintenance) (━━ ) to increasing lysine intakes.

The models describe by Black *et al.* (1986) and Moughan *et al.* (1987) attempt to overcome the problem of predicting amino acid requirements by assuming a curvilinear response by the average individual to nutrient input. This is done by continually reducing the availability of the amino acids as the maximum rate of protein deposition is approached. However, this approach precludes any influence that the individuals within that population may have on the response to amino acid intakes, particularly when environmental conditions are not ideal. More recently Black *et al.* (1989) questioned the precision of the results obtained with this approach.

The only sensible approach to predicting the nutrient requirements of a population, using simulation models, is to repeat the simulation for a number of individuals representative of the population and then to average these results. This approach requires a knowledge of the parameters in the model that vary between animals, the nature of their distribution and the possible co-variances that may exist between parameters (Emmans and Fisher, 1986). Of all the current pig models only the model mentioned in Chapter 1 and described in detail by Ferguson (1989) can readily include variations in animal characteristics, because only a few parameters are required to describe the animal, and these parameters are both biologically meaningful and easy to measure. It would not be possible to introduce stochastic elements at the animal level into most of the existing models

either because the parameters have little biological meaning and it would therefore be difficult to measure the differences between genotypes, or the description of the animal is inadequate, such that the effect of variation would have little impact on the response of the animal.

To obtain estimates of the population structure it is important to determine the distribution of parameter values that might be expected to vary between individuals. In the model described by Ferguson (1989) the animal is defined by three parameters viz. the rate of maturing (B), the mature protein weight (Pm) and the lipid:protein ratio at maturity (LPRm). If B, Pm and LPRm can be used to describe an individual animal, and the nature of the distributions of these parameters is known, then it would theoretically be possible to simulate a population. It is also important to know if any correlations exist between these parameters. If there are, this will affect the nature and the description of the variation of the correlated parameters. Within a genotype there is likely to be a strong, inverse correlation between B and Pm, such that animals with a high Pm have a low B value (Emmans, 1988). Axiomatic to this is that larger animals will have a lower growth rate relative to body size (Taylor, 1968). The implications for modelling are that if the variability of B or Pm is changed then a corresponding change in the variability of the other parameter would be necessary. Errors of prediction will result if this correlation is ignored. Emmans and Fisher (1986) describe a scaled rate parameter ($B^{*}=B.Pm^{0.27}$) that is uncorrelated with Pm across genotypes and use of this parameter in a population model would, therefore, prevent such errors from occurring.

Currently, no data are available from which the distributions of $B^{*}$, Pm and LPRm can be estimated for pigs of a given sex and strain, although Emmans and Fisher (1986) and Emmans (1988) suggest, in the case of broilers, general coefficients of variation (CV) for $B^{*}$ of 0.02-0.04, and 0.06-0.10 for Pm. It would be impractical to determine experimentally the coefficients of variation and correlations between $B^{*}$, Pm and LPRm as a large number of widely different populations of pigs would have to be used and these would be required to be grown under similar conditions. As the population means, standard deviations and correlation coefficients would be estimated from samples of different populations, the sample size or number of pigs required to test whether the hypothesis is true, is related to the probability of incorrectly rejecting the null hypothesis (Ho) that there is no correlation between the parameters (Type I error or $\alpha$-error), the probability of incorrectly accepting Ho (Type II error or ß-error) and the value of the true correlation coefficient ($\rho$) if it is not equal to zero. Since confirmation is required that there is no correlation between the parameters, the chance of incorrectly accepting Ho or error Type II must be minimized so that the probability of incorrectly accepting Ho, when it is in fact false, is small (Rayner, 1967; Groebner and Shannon, 1989).

To increase the probability of a correct rejection of Ho let $\alpha=0.2$. Although this means that there would be a 20 % chance of incorrectly rejecting Ho if Ho is known to be true, it also means that the

probability of a correct rejection of Ho, when Ho is false, is increased. The net effect is a decrease in the ß-error and a lower probability of incorrectly accepting Ho .

To minimize error Type II (ß-error) let ß=0.05 and assume that the true population correlation coefficient (ρ) equals 0.15. For values of $\rho < 0.15$, finding the difference between ρ and zero becomes much more difficult and a much larger sample size is required for the same α and ß errors (0.2 and 0.05 respectively). For such values of ρ the correlations are likely to be small and probably unimportant.

The minimum number of animals required to test whether there are any correlations between the parameters is determined from Groebner and Shannon (1989) as follows:

$$n = \left( \frac{Z_\alpha - Z_ß}{0.5 \times \log_e\left(\frac{1+\rho}{1-\rho}\right)} \right)^2 + 3 \qquad (5.1)$$

where $Z_\alpha$ = standard normal variate associated with $\alpha = 0.2$
$Z_ß$ = standard normal variate associated with $ß = 0.05$
ρ = rho, the true population correlation coefficient > 0

Since the correlations could be negative or positive a two tailed test is required, which means that $Z_ß$ could be either a positive or a negative value. Substituting into this equation the probability values from Z-tables (Rayner, 1967) of $Z_\alpha$=1.282, $Z_ß$=-1.960 and ρ=0.15, results in the following:

$$n = \left( \frac{1.282 - (-1.960)}{0.5 \times \log_e\left(\frac{1+0.15}{1-0.15}\right)} \right)^2 + 3 \qquad (5.2)$$

n = 463

A sample size of 463 animals per population is required in order to test whether there are significant correlations between the parameters across different pig populations. Clearly, this is an impractical and costly exercise. To circumvent the problems of experimentation, simulation models are a viable alternative for estimating parameter variability. In using simulation modelling to estimate distributions of genetic parameters some basis for comparison must be available in order to determine whether the values are realistic or not. The data collected by direct measurement are prone to many errors, including the effect of weighing errors (differential gut fill, balance/reading errors), feed spillage, disease and inappropriate environmental effects. Also, small numbers of animals are often used in each replication, and the variation within the group is extrapolated from these small numbers to describe the population variance.

In the exercise reported here the simulation model outlined in Chapter 1 was used to estimate the statistical distributions of B*, Pm and LPRm and to measure the effect of these distributions on the

variability of average daily gain (ADG) and daily feed intake (FI). The analysis was in two parts. In the first, the effects of variation in each of the three parameters was measured on food intake and growth rate, and in the second part, comparisons were made between the variation determined in this way and those measured and subsequently published in the literature.

To conclude this discussion a comparison of the response to dietary lysine content is made between the average individual of a population and the mean of 100 pigs drawn from the same population as the individual pig, but using the CV's derived from the previous analysis. This comparison will highlight whether there are any differences between modelling at the level of the individual or population and whether the estimated CV values for $B^{\bullet}$, Pm and LPRm are adequate..

### 5.2 Method

As it is likely that only three parameters are needed to account for differences between genotypes, variation around the mean of each of these three parameters should describe all the individuals within a population. The estimates of normal independent distributions of these parameters suggested by Emmans and Fisher (1986) were used as the basis of the values chosen for this investigation.

Three coefficients of variation of both Pm and LPRm and four of $B^{\bullet}$ were chosen in a factorial arrangement (Table 5.1) with the three way interaction providing the estimate of error since there was no interaction between the factors. The values of the coefficients of variation of the three parameters were chosen to be less than, equal to and greater than the values estimated by Emmans and Fisher (1986). The three parameters were generated independently for a normally distributed population, to ensure that no correlations existed between them.

For each treatment a total of 465 individuals was generated, using the same population means over all treatments ($\mu B^{\bullet}$=0.0294 /d; $\mu$Pm=38.0 kg and $\mu$LPRm=2.5 g/g; average values for a typical, Large White X Landrace entire male), but using the CV's appropriate to each treatment in turn (Table 5.1). The genotypes of individuals within each treatment, thus defined, were then used to estimate the population response using the model to provide estimates of FI and ADG, and their respective standard errors, at 20, 40, 60 and 90 kg, and between 25 and 90 kg live weight. The starting weights of the simulations were randomly generated around a mean weight of 10 kg with a 10% variability. The reason for including data between 25 and 90 kg was that this weight range was the average body weight over which Standal and Vangen (1985), Cameron, Curran and Thompson (1988), Ellis, Chadwick, Smith and Laird (1988), Cameron (1990) and Mrote and Kennedy (1993) investigated growth performances in different populations of pigs. It was possible, therefore, to compare the results obtained in this exercise with those in the literature. The

composition of the feed was the same in all simulations. This contained 13.50 MJ digestible energy/kg, 160.0 g crude protein/kg and 10.0 g total lysine/kg (assumed the first limiting amino acid), this being similar to the feed used in those experiments with which results were compared.

The ADG's and FI's at 20, 40, 60 and 90 kg live weight were used to determine the effects of variation on the estimation of the genetic parameters. The mean and standard deviation of each of these measurements were determined for each treatment, from which coefficients of variation were calculated. The simulation model (Chapter 2) used in this exercise takes no account of so-called environmental variation therefore the calculated variations in ADG and FI are a result of true genetic variance in $B^*$, Pm and LPRm. Hence, the coefficients of variation ($CV_g$) of the two predicted traits are estimates of genetic variation and not phenotypic variation.

The variation in the data from real experiments comprises both genetic and environmental variations whereas the simulated results reflect genetic variation only. Therefore it is necessary, for meaningful comparisons to be made between simulated and actual values, to isolate only the genetic component in the actual results. As the heritability ($h^2$) of a trait is an estimate of the genetic proportion of the phenotypic variation , it was used to calculate the $CV_g$ of ADG's and FI 's from the real experiments. In the literature $h^2$ values for both ADG anf FI vary from 0.29 to a maximum of 0.62 (McPhee, Brennan and Duncalfe, 1979; Wyllie, Morton and Owen, 1979; Mrode and Kennedy, 1993; Whittemore, 1993; Cameron and Curran, 1994). To accomodate such a wide range of heritabilities the $CV_g$ values from the real experiments will be calculated using $h^2$ values of 0.3 and 0.6.

Analyses of variance were performed on the $CV_g$'s of ADG and FI at the above weights to ascertain to what extent each of the three parameters contributed to the variability in ADG and FI and also whether there were any significant interactions between them. Although this comparative technique is crude it does provide an estimate of the expected genetic variation of ADG and FI in a population of pigs from which the distribution of $B^*$, Pm and LPRm can be deduced.

After deriving the most appropriate CV's for $B^*$, Pm and LPRm it is important to consider whether or not introducing variability into the model will produce a different response than that of the average individual. To test if the simulated response would differ between the two, a simple lysine response trial between two live weights for an individual and for a population was simulated. The response to nine concentrations of dietary lysine (4, 5, 6, 7, 8, 9, 10, 11 and 12 g/kg) was simulated using a single male, and then again using 100 individuals drawn from a population with the same mean genetic parameters as the individual ($\mu B^*$=0.0294 /d; $\mu$Pm=38.0 kg and $\mu$LPRm=2.5 g/g), but using the suggested CV's ($B^*$= 2%; Pm = 7% and PRm = 10%). The starting weights of the simulations were randomly generated around a mean weight of 20 kg with a 10% variability. Digestible Energy (DE) content of all the feeds was kept constant at 14.0 MJ/kg and lysine was

formulated to be the most limiting amino acid. For this genotype and DE content of the diet , the lysine content required for maximum protein growth is 10g/kg. Food intake, average daily gain , protein retention and lipid retention results were obtained between 20 and 40 kg live weight for each of the lysine treatments for the average individual animal and the mean of the population. As previously discussed the simulated results of the population reflect genetic variation only. Whether genetic or phenotypic variation should be used to determine statistical significance between results from an individual or from a population is debatable, particularly as the results are derived from the same simulation model. If the individual results were from real data then it would be imperative to convert the estimated genetic variations in FI, ADG, PR and LR from the simulation model to phenotypic variations. However, to remain consistent with the discussion throughout this chapter genetic variation is preferred but phenotypic variation is shown. In this simulated trial $h^2$ was assumed to be 0.5 for both FI and ADG. The exact $\hat{h}$ value used is not critical to this discussion as it is the trends in response between the individual and the population that are important and not the exact statistical differences between the individual response and the mean of the population response.

## 5.3 Results and Discussion

### 5.3.1 The effects of parameter variation on ADG and FI

The effects of different estimates of the three population parameters on the mean and $CV_g$ of ADG and FI are presented in Table 5.1 for pigs between 25 and 90 kg live weight. See Appendix 1 for all the details of the results.

If any interactions were found to exist between B*, Pm and LPRm it would be extremely difficult to quantify the relationship between the variation of these parameters and the mean ADG and FI. To adjust the means of either FI or ADG would involve selecting a specific combination of B*, Pm and LPRm appropriate to the desired adjustment. This would clearly not be very practical. For this reason the interactions between parameters were fixed to be independent and uncorrelated (Table 5.2). This does not mean that no correlations between the parameters actually exist in a real population of pigs, but it is unlikely that they do.

The main effects of the different CV's of B*, Pm and LPRm on the means and $CV_g$'s of the means in the analyses of variance for ADG and for FI are shown in Tables 5.3 and 5.4 respectively.

To determine to what extent each of the three genetic parameters influenced the genetic variation in FI and ADG among individuals in the simulated populations, and whether any

trends were evident in the relative contributions of the CV's of the three parameter estimates with increasing live weight, genetic variability in feed intake and daily gains were examined within the simulated populations.

From Table 5.3 there are indications that the genetic variability in ADG is a function of body weight, as the effect of the parameters on the $CV_g$ of ADG differed over the range of live weights tested. When the CV of $B^*$ was increased from 1 to 6 percent the $CV_g$ of ADG increased by 84 percent at 20 kg live weight, but only by 29 percent at 90 kg live weight. Conversely, virtually no variation in ADG occurred at 20 kg live weight when the CV's of either Pm or LPRm were increased, yet significant increases occurred at 90 kg live weight.

Table 5.1. The effect of different estimates of three population parameters on the mean, s.d. and the genetic Coefficient of Variation ($CV_g$) of the mean average daily gain (ADG) and food intake between 25 and 90 kg live weight. The parameters of the population mean used in the simulations were $\mu$Pm=38.0 kg, $\mu B^*$=0.0294 /d and $\mu$LPRm=2.5 g/g and 465 individuals were simulated for each treatment mean.

| | Coefficient of Variation (%) | | | ADG | | | Food Intake | | |
|---|---|---|---|---|---|---|---|---|---|
| Treatment | $B^*$ | Pm | LPRm | mean (g/d) | s.d. | $CV_g$ (%) | mean (g/d) | s.d. | $CV_g$ (%) |
| 1 | 1 | 5 | 10 | 880 | 34.7 | 3.94 | 2088 | 122.2 | 5.88 |
| 2 | 1 | 5 | 15 | 878 | 37.0 | 4.21 | 2070 | 142.6 | 6.89 |
| 3 | 1 | 5 | 20 | 886 | 46.3 | 5.23 | 2095 | 183.4 | 8.75 |
| 4 | 1 | 10 | 10 | 881 | 47.1 | 5.35 | 2080 | 124.6 | 5.99 |
| 5 | 1 | 10 | 15 | 883 | 49.8 | 5.64 | 2078 | 153.0 | 7.36 |
| 6 | 1 | 10 | 20 | 885 | 57.5 | 6.50 | 2101 | 190.4 | 9.07 |
| 7 | 1 | 15 | 10 | 879 | 61.0 | 6.94 | 2063 | 125.1 | 6.06 |
| 8 | 1 | 15 | 15 | 881 | 66.6 | 7.56 | 2086 | 161.9 | 7.76 |
| 9 | 1 | 15 | 20 | 881 | 67.0 | 7.60 | 2085 | 197.8 | 9.49 |
| 10 | 2 | 5 | 10 | 882 | 40.4 | 4.58 | 2084 | 129.6 | 6.22 |
| 11 | 2 | 5 | 15 | 883 | 46.6 | 5.28 | 2079 | 160.5 | 7.72 |
| 12 | 2 | 5 | 20 | 883 | 49.4 | 5.59 | 2090 | 186.6 | 8.92 |
| 13 | 2 | 10 | 10 | 883 | 53.9 | 6.10 | 2093 | 143.1 | 6.84 |
| 14 | 2 | 10 | 15 | 882 | 56.2 | 6.37 | 2081 | 171.9 | 8.26 |
| 15 | 2 | 10 | 20 | 882 | 62.6 | 7.10 | 2094 | 201.3 | 9.61 |
| 16 | 2 | 15 | 10 | 876 | 66.0 | 7.53 | 2076 | 139.3 | 6.67 |
| 17 | 2 | 15 | 15 | 882 | 68.0 | 7.71 | 2087 | 171.8 | 8.23 |
| 18 | 2 | 15 | 20 | 871 | 70.5 | 8.09 | 2061 | 193.3 | 9.38 |
| 19 | 3 | 5 | 10 | 882 | 46.4 | 5.60 | 2082 | 147.0 | 7.06 |
| 20 | 3 | 5 | 15 | 882 | 53.6 | 6.08 | 2085 | 176.5 | 8.47 |
| 21 | 3 | 5 | 20 | 885 | 57.1 | 6.45 | 2091 | 199.1 | 9.52 |
| 22 | 3 | 10 | 10 | 880 | 62.7 | 7.13 | 2079 | 164.1 | 7.89 |
| 23 | 3 | 10 | 15 | 881 | 65.1 | 7.39 | 2085 | 189.6 | 9.09 |
| 24 | 3 | 10 | 20 | 885 | 68.3 | 7.72 | 2101 | 207.4 | 9.88 |
| 25 | 3 | 15 | 10 | 883 | 72.8 | 8.24 | 2084 | 161.1 | 7.73 |
| 26 | 3 | 15 | 15 | 875 | 74.5 | 8.51 | 2067 | 184.9 | 8.94 |
| 27 | 3 | 15 | 20 | 876 | 77.0 | 8.79 | 2077 | 204.2 | 9.83 |
| 28 | 6 | 5 | 10 | 893 | 84.8 | 9.50 | 2113 | 231.4 | 10.95 |
| 29 | 6 | 5 | 15 | 881 | 91.5 | 10.38 | 2081 | 264.0 | 12.69 |
| 30 | 6 | 5 | 20 | 880 | 93.9 | 10.67 | 2077 | 278.3 | 13.40 |
| 31 | 6 | 10 | 10 | 883 | 89.8 | 10.06 | 2091 | 230.7 | 11.03 |
| 32 | 6 | 10 | 15 | 880 | 88.8 | 10.21 | 2077 | 246.4 | 11.86 |
| 33 | 6 | 10 | 20 | 880 | 91.5 | 10.40 | 2083 | 262.9 | 12.62 |
| 34 | 6 | 15 | 10 | 878 | 93.9 | 10.69 | 2084 | 233.1 | 11.18 |
| 35 | 6 | 15 | 15 | 885 | 97.7 | 11.04 | 2093 | 248.3 | 11.86 |
| 36 | 6 | 15 | 20 | 880 | 104.5 | 11.88 | 2086 | 269.9 | 12.94 |

Table 5.2. The correlation coefficients (r) between the genetic parameters B, B*, Pm and LPRm in the populations simulated.

| | B* | Pm | LPRm |
|---|---|---|---|
| Pm | 0.000 | | |
| LPRm | -0.200 | -0.066 | |
| B | 0.815 | -0.570 | 0.015 |

At low CV's of B*, growth rates between individuals will be similar and therefore the range of ADG would be expected to be lower, particularly in young animals where the growth rate is less likely to be constrained by the environment than when the animal is growing at its maximum rate.

Table 5.3. Main effects of different Coefficients of Variation (CV) of B*, Pm and LPRm on the mean. s.d. and $CV_g$ of ADG at 20, 40, 60 and 90 kg live weight for a population of 465 pigs.

| | B* | ADG | | | Pm | ADG | | | LPRm | ADG | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Weight kg | CV (%) | mean (g/d) | s.d. | $CV_g$ (%) | CV (%) | mean (g/d) | s.d. | $CV_g$ (%) | CV (%) | mean (g/d) | s.d. | $CV_g$ (%) |
| 20 | 1 | 543 | 30.5 | 5.62 | 5 | 545 | 36.6 | 6.71 | 10 | 545 | 37.1 | 6.81 |
| 40 | | 787 | 40.5 | 5.14 | | 789 | 53.0 | 6.72 | | 787 | 54.5 | 6.93 |
| 60 | | 952 | 59.6 | 6.26 | | 953 | 64.9 | 6.81 | | 952 | 70.1 | 7.36 |
| 90 | | 1070 | 85.3 | 7.97 | | 1070 | 70.7 | 6.61 | | 1070 | 88.6 | 8.28 |
| 20 | 2 | 544 | 30.6 | 5.63 | 10 | 544 | 37.0 | 6.80 | 15 | 545 | 37.7 | 6.92 |
| 40 | | 787 | 46.3 | 5.88 | | 789 | 56.9 | 7.21 | | 788 | 57.1 | 7.25 |
| 60 | | 950 | 65.2 | 6.86 | | 953 | 75.3 | 7.90 | | 952 | 75.3 | 7.91 |
| 90 | | 1066 | 88.1 | 8.26 | | 1068 | 92.8 | 8.69 | | 1070 | 93.1 | 8.70 |
| 20 | 3 | 544 | 35.4 | 6.50 | 15 | 544 | 38.5 | 7.08 | 20 | 544 | 37.4 | 6.87 |
| 40 | | 787 | 54.5 | 6.93 | | 786 | 61.2 | 7.78 | | 789 | 59.5 | 7.54 |
| 60 | | 951 | 73.2 | 7.70 | | 949 | 86.6 | 9.13 | | 951 | 81.4 | 8.56 |
| 90 | | 1067 | 93.0 | 8.72 | | 1063 | 118.3 | 11.13 | | 1064 | 100.7 | 9.46 |
| 20 | 6 | 545 | 56.2 | 10.32 | | | | | | | | |
| 40 | | 790 | 86.8 | 10.99 | | | | | | | | |
| 60 | | 953 | 104.4 | 10.95 | | | | | | | | |
| 90 | | 1064 | 109.6 | 10.30 | | | | | | | | |

At a high CV of B* there is a greater probability of obtaining a number of very fast and very slow growing animals, which will result in a greater distribution of potential ADG's in a population. It would be expected therefore, that by increasing the CV of B* from 1% to 6% of the mean, the spread of ADG's will be considerably wider across all live weights. Whereas a wider range of potential ADG's are produced when the CV of B* is increased, nevertheless the actual ADG's are constrained to a narrower range because of the constraining effect of the physical environment. For example, those animals with the potential to grow fastest would require a lower environmental temperature than the slower-growing individuals, and, because in the model all pigs are subjected to only one temperature, the pigs with the potential to grow fastest would not be able achieve their potential and hence the narrower range of actual ADG's.

The genetic variation in feed intake largely followed that in live weight gain: as with ADG, the $CV_g$ of FI at 20 kg live weight increased significantly as the CV of B* was increased, with smaller differences also being evident at 90 kg (Table 5.4); whilst the increase in CV's of both Pm and LPRm had a curvilinear response on the $CV_g$ of FI, with differences between the chosen CV's occurring mainly at the heavier live weights (60 and 90 kg) (Table 5.4). Because of the intimate relationship between food intake and growth rate it is not surprising that the relationships between the $CV_g$'s of ADG and FI were so similar. The considerable increase in the $CV_g$ of FI at 40 kg compared with that at 20 kg is as a result of there being a greater opportunity for individuals within the population to attempt to express their genetic potential by the time they reach 40 kg than at 20 kg, where the differences in potential food intake are likely to be considerably smaller.

Table 5.4. Main effects of different Coefficients of Variation (CV) of B*, Pm and LPRm on the mean, s.d. and $CV_g$ of food intake at 20, 40, 60 and 90 kg live weight for a population of 465 pigs.

| | B* | Food Intake | | | Pm | Food Intake | | | LPRm | Food Intake | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Weight kg | CV (%) | mean (g/d) | s.d. | $CV_g$ (%) | CV (%) | mean (g/d) | s.d. | $CV_g$ (%) | CV (%) | mean (g/d) | s.d. | $CV_g$ (%) |
| 20 | 1 | 1050 | 57.1 | 5.44 | 5 | 1053 | 74.8 | 7.10 | 10 | 1053 | 73.7 | 7.00 |
| 40 | | 1709 | 124.6 | 7.29 | | 1713 | 157.8 | 9.21 | | 1709 | 141.5 | 8.28 |
| 60 | | 2332 | 190.1 | 8.15 | | 2337 | 224.8 | 9.62 | | 2252 | 184.7 | 8.20 |
| 90 | | 3010 | 256.1 | 8.51 | | 3011 | 264.4 | 8.78 | | 3015 | 242.4 | 8.04 |
| 20 | 2 | 1052 | 62.3 | 5.92 | 10 | 1052 | 74.2 | 7.05 | 15 | 1052 | 75.2 | 7.15 |
| 40 | | 1712 | 134.2 | 7.84 | | 1716 | 158.9 | 9.26 | | 1711 | 157.4 | 9.20 |
| 60 | | 2333 | 202.5 | 8.68 | | 2339 | 231.6 | 9.90 | | 2331 | 229.6 | 9.85 |
| 90 | | 3005 | 265.0 | 8.82 | | 3009 | 283.1 | 9.41 | | 3001 | 282.7 | 9.42 |
| 20 | 3 | 1052 | 70.6 | 6.71 | 15 | 1052 | 74.9 | 7.12 | 20 | 1051 | 74.8 | 7.12 |
| 40 | | 1713 | 149.7 | 8.74 | | 1713 | 155.7 | 9.09 | | 1722 | 178.4 | 10.07 |
| 60 | | 2334 | 220.1 | 9.43 | | 2245 | 221.6 | 9.87 | | 2338 | 264.7 | 11.32 |
| 90 | | 3005 | 276.8 | 9.21 | | 2993 | 304.4 | 10.17 | | 2997 | 327.0 | 10.91 |
| 20 | 6 | 1054 | 108.6 | 10.30 | | | | | | | | |
| 40 | | 1721 | 221.5 | 12.87 | | | | | | | | |
| 60 | | 2230 | 287.7 | 12.90 | | | | | | | | |
| 90 | | 2997 | 338.4 | 11.29 | | | | | | | | |

There were no significant interactions between the CV's of B* and LPRm or between Pm and LPRm on food intakes or daily gain at any of the live weights tested. There were, however, significant interactions ($P<0.05$) between the CV's of B* and Pm on the distribution of both FI and ADG, irrespective of live weight. As B* is used in the model to determine the potential rate of growth, it is expected that an increased variation in this parameter will affect the variation in daily gains and subsequent food intake. This effect is still apparent as the variability in mature size (Pm) is increased, as indicated by a significant B* x Pm interaction. The implications are that different combinations of the CV of B* and Pm, in particular, are likely to have different effects on the distribution of ADG and FI.

A CV of B* not greater than 3% will reduce the spread of genetic variation in ADG at low body weights whilst at higher body weights a similar response would be better achieved by reducing the variation in Pm.

The distribution of the variability in FI followed different trends to that of the variability in ADG. No significant differences were measured in the variation of FI as a result of varying the spread of Pm until 60 kg live weight. As body weight increases, the effect of variation in Pm on the distribution of FI remains constant. This is in contrast to the response in ADG where the variation in ADG is increased as the CV of Pm increases. When the CV of Pm is increased there is a concomitant increase in the range of potential FI's but this range is still constrained to a narrow limit because of the environmental constraints. Given that the environment remains constant, those individuals which have the potential to consume more food (of which there will be more as the CV of Pm increases) will be constrained by the amount of heat they can lose. Hence, the narrow range of FI's. Whilst the hot environment may result in similar FI's for both fast- and slow-growing animals, the ADG will be significantly different because individuals have different predispositions to depositing lean and fat tissue as a means of reducing the environmental heat demand. Hence, the greater the variation in Pm, the higher the probability of obtaining very divergent genotypes and therefore larger variations in ADG's particularly at higher body weights where the environment is limiting to a larger number of individuals in the population. The modelling implications are that as FI is less sensitive to changes in Pm so any changes in the CV of Pm will have little effect on the variation in the FI of the population.

If the selection objective were to reduce the genetic variability in FI, across all live weights, the CV of LPRm should be reduced. However, if one were interested only in young animals or animals with a live weight of less than 40 kg, then a reduction in the CV of B* would be more effective. Animals that have a high LPRm are more predisposed to having a higher appetite than those with a low LPRm, hence this parameter has a greater effect on variations in food intake, especially at heavier body weights, than does B*. The reason LPRm influences FI more at heavier body weights is because as the animal increases in size the energy requirements for lipid deposition are higher than for protein deposition (Campbell and Dunkin, 1983; Rinaldo and Le Dividich, 1991). The inherent fatness of the animal (as defined by LPRm) will therefore dominate the animal's requirements for energy and subsequent energy (food) intake. The greater the variability of LPRm the greater the genetic variability in FI in older animals (Table 5.4).

### 5.3.2 Estimation of parameter variation from literature comparisons

To determine which of the 36 treatments provided coefficients of variation of the three

parameters that most closely approximated the differences in genotype for both FI and ADG in the literature, the results were compared with data from studies on various populations of growing pigs published by Standal and Vangen (1985), Cameron *et al.* (1988), Ellis *et al.* (1988); Cameron (1990) and Mrode and Kennedy (1993) (Table 5.5).

An important point to consider when comparing the results of this exercise with those reported in the literature is that the CV's for ADG and FI of the different treatments, shown in Table 5.5, reflect more closely the potential growth characteristics of populations of pigs than could have been achieved by experimentation because of extraneous random variation. The response of a real population of pigs to a given food and environment is not only subject to variations in animal characteristics but also to variations in nutrient quality and quantity, environmental changes and sample size. Additional sources of variation could result from biological variations associated with factors other than $B^*$, Pm and LPRm, such as net efficiencies of amino acid and energy utilization, which are assumed constant in the model. A further cause of difference between the simulated and published results is that only a male genotype was simulated whereas the published data contains results from both males and females.

Table 5.5 provides a summary of the comparisons between the range of $CV_g$'s from real experiments and the treatments associated with the best estimated $CV_g$'s from the populations simulated. Standal and Vangen (1985) provide population estimates for Danish and Norwegian Landrace pigs. The calculated range of $CV_g$'s for ADG and FI for Danish Landrace pigs were 2.96-5.92% and 2.91-5.83% respectively, whilst for Norwegian Landrace pigs they were 2.55-5.10% and 2.82-5.63% respectively. Comparing these results with those shown in Table 5.5, it is evident that for both Danish and Norwegian Landrace pigs the results produced by Treatment 1 provided the closest overall estimate of genetic variability of the ADG and the FI.

The data from Cameron *et al.* (1988), Ellis *et al.* (1988) and Cameron (1990) showed considerably more phenotypic variation than those of Standal and Vangen (1985), with the data of Mrode and Kennedy (1993) somewhere in between. The differences are the result of combining entire males and females and the use of very different pig breeds, such as the British Landrace and the Duroc, in providing estimates of the population mean and standard error, and the standard errors given by Standal and Vangen (1985) were estimated and not calculated values .

Table 5.5. A comparison between the range of CVg's of ADG and FI in the literature and the best simulated estimates from the model , with the associated CV's of B', Pm and LPRm, for pigs grown between 25 and 90 kg live weight.

| Reference | Published range† of CVg (%) | | Best Simulated | Best Simulated CVg (%) | | CV (%) | | |
|---|---|---|---|---|---|---|---|---|
| | ADG | FI | Treatment(s) | ADG | FI | B' | Pm | LPRm |
| Strandal and Vangen (1985) | | | | | | | | |
| Danish Landrace | 2.96-5.92 | 2.91-5.83 | 1 | 3.94 | 5.88 | 1 | 5 | 10 |
| Norwegian Landrace | 2.55-5.10 | 2.82-5.63 | 1 | 3.94 | 5.88 | 1 | 5 | 10 |
| Cameron *et al.* (1988) | | | | | | | | |
| British Landrace | 3.38-6.76 | 3.78-6.56 | 10 | 4.58 | 6.22 | 2 | 5 | 10 |
| Large White | 3.31-6.62 | 3.62-7.23 | 10,13,19¶ | 4.58, 6.10, 5.60 | 6.22,6.84,7.06 | 2,2,3 | 5,10,5 | 10,10,10 |
| Ellis *et al.* (1988) | | | | | | | | |
| Large White | 3.16-6.32 | 3.76-7.52 | 10,13,19¶ | 4.58, 6.10, 5.60 | 6.22,6.64,7.06 | 2,2,3 | 5,10,5 | 10,10,10 |
| Cameron (1990) | | | | | | | | |
| Duroc/British Landrace‡ | 3.39-6.78 | 3.59-7.19 | 10,13,19¶ | 4.58, 6.10, 5.60 | 6.22,6.64,7.06 | 2,2,3 | 5,10,5 | 10,10,10 |
| Mrode and Kennedy (1993) | | | | | | | | |
| Yorkshire/Landrace/Duroc‡ | 3.25-6.49 | 3.33-6.67 | 10 | 4.58 | 6.22 | 2 | 5 | 10 |

† The range of CVg is calculated by multiplying the phenotypic variation by the lowest (0.3) and highest (0.6) $h^2$ values reported in the literature.

‡ The values obtained from published results are from means of combining all given breeds.

¶ These Treatments had CVg's of ADG and FI within the range of published CVg's. The simulated CV's for each respective Treatment are shown in adjacent columns.

The treatment that produced $CV_g$'s within the range of $CV_g$'s for ADG and FI for the British Landrace pigs of Cameron *et al.*. (1988) and Cameron (1990) was treatment 10 with CV values of B*, Pm and LPRm of 2%, 5% and 10% respectively. For the data of Large White pigs of Cameron *et al.* (1988), Ellis *et al.* (1988) and Cameron (1990) Treatments 10,13 and 19 were within range, with CV's of B* varying between 2 and 3%, and Pm between 5 and 10%. In all the treatments the CV of LPRm was 10%.

As discussed previously, the assumptions concerning B*, Pm and LPRm appear to have different effects on the variations in ADG and FI caused by genotypic differences. However, most of the simulated treatments within the range of the published $CV_g$'s of both ADG and FI, were similar within and between breeds.

### 5.3.3 Comparison between individual and population responses

The results of the comparison between the simulated response of the average individual and the mean of the population to dietary lysine content are shown in Table 5.6 and Figures 5.2 and 5.3.

Table 5.6 A comparison of response in food intake (FI),average daily gains(ADG), protein retention (PR) and lipid retention (LR) to nine dietary lysine contents between the average individual (Ind) and the mean of the population (Pop), and the percent differences (%diff) between the individual and population.

| Lysine | FI | | | ADG | | | PR | | | LR | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (g/kg) | Ind | Pop | %diff‡ | Ind | Pop | %diff‡ | Ind | Pop | %diff‡ | Ind | Pop | %diff‡ |
| 12 | 1462 | 1419 | 2.9*** | 664 | 658 | 0.9$^{NS}$ | 108 | 107 | 0.9* | 139 | 136 | 2.2$^{NS}$ |
| 11 | 1454 | 1411 | 3.0*** | 664 | 658 | 0.9$^{NS}$ | 108 | 107 | 0.9* | 139 | 136 | 2.2$^{NS}$ |
| 10 | 1448 | 1408 | 2.8*** | 664 | 660 | 0.6$^{NS}$ | 108 | 107 | 0.9* | 139 | 137 | 1.4$^{NS}$ |
| 9 | 1496 | 1458 | 2.5*** | 681 | 678 | 0.4$^{NS}$ | 108 | 106 | 1.9*** | 158 | 157 | 0.6$^{NS}$ |
| 8 | 1654 | 1605 | 3.0*** | 731 | 723 | 1.1* | 107 | 105 | 1.9*** | 210 | 205 | 2.4** |
| 7 | 1846 | 1777 | 3.7*** | 765 | 749 | 2.1*** | 104 | 100 | 3.8*** | 255 | 246 | 3.5*** |
| 6 | 1873 | 1809 | 3.4*** | 706 | 694 | 1.7** | 89 | 87 | 2.2*** | 267 | 259 | 3.0*** |
| 5 | 1823 | 1760 | 3.5*** | 612 | 604 | 1.3* | 71 | 70 | 1.4* | 263 | 256 | 2.7*** |
| 4 | 1752 | 1693 | 3.4*** | 517 | 512 | 1.0$^{NS}$ | 52 | 52 | 0.0$^{NS}$ | 254 | 249 | 2.8*** |
| $SEM_p$ | | 7.04 | | | 3.78 | | | 0.41 | | | 1.64 | |
| $SEM_g$ | | 4.98 | | | 2.67 | | | 0.30 | | | 1.43 | |
| $CV_g$(%) | | 3.13 | | | 4.05 | | | 3.23 | | | 7.22 | |

‡ % diff = (Ind-Pop)/Ind x100
$SEM_p$ Standard error of the mean using the estimate of the phenotypic variation ($\sigma_p^2 = \sigma_g^2 / h^2$
$SEM_g$ Standard error of the mean using the genetic variation
$CV_g$ Coefficient of genetic variation
NS Not significant; * P < 0.05; ** P < 0.01; *** P < 0.001;To determine statistical differences t-tests were conducted using $SEM_p$.

The results in Table 5.6 show that the $CV_g$'s for FI (3.13%) and ADG (4.05%) are within the acceptable range as indicated in Table 5.5. This result confirms that the recommended CV's for B*, Pm and LPRm of 2%, between 5-10% and 10% respectively, will provide an adequate description of the variability in the genetic parameters. If included in a simulation model, they will provide realistic predictions of the voluntary food intake and growth rate of a group of animals.

From Table 5.6 it is evident that there are significant differences in FI, ADG, PR and LR responses to dietary lysine intake between the average individual and the population, particularly when lysine is marginally deficient (6 to 8 g/kg). These results highlight the limitation of using deterministic models to predict the nutrient requirements of a group or population of animals because of the errors introduced in converting the predicted requirements of the average animal into requirements for the population.

Figure 5.2 illustrates just how different the response between the average individual and the population mean can be. Although the trend in food intake was similar the average individual consumed significantly more than the mean of the population. The trend for the average individual to exhibit a greater response in ADG, PR and LR to lysine intake than the mean of the population was also observed.

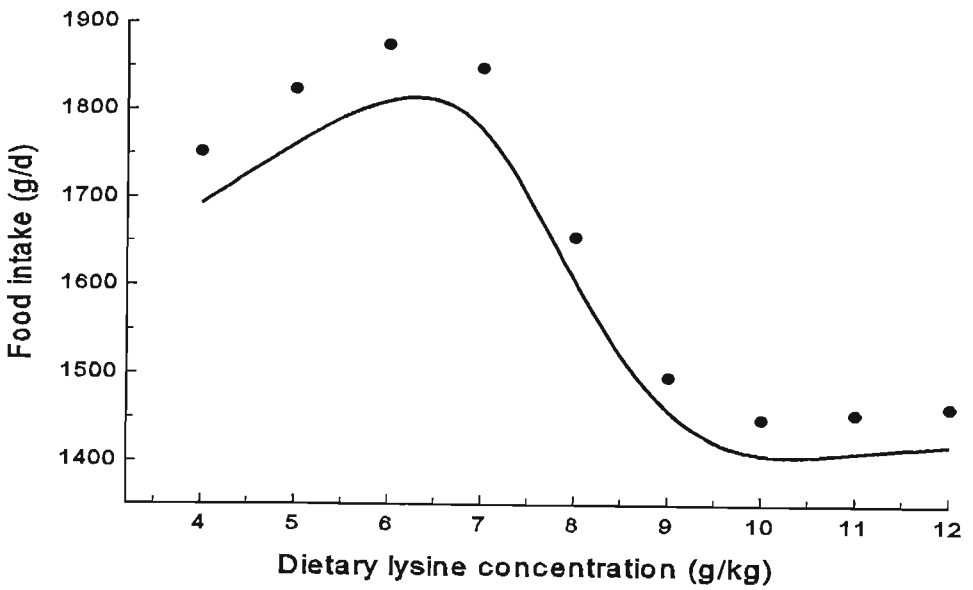


Figure 5.2 Comparison of simulated responses in food intake to dietary lysine content between an individual (●) and a population of 100 pigs (——) grown from 20 to 40 kg live weight.

In Figure 5.3 the relationship between lysine intake and protein growth in the average individual is adequately described by a linear-plateau model (Batterham *et al.*, 1990). It may be argued that there are other models that describe this relationship better but for the purposes of this discussion the linear-plateau model is adequate. However, the response of the population to lysine intake is better described by a curvilinear model (Bikker, 1994).

The reason for the differences in response between the average individual and the mean of the population is that the population response accounts for the different maintenance

requirements for protein and different maximum rates of protein deposition of all individuals in the population. In the case of the average individual, the response is of one animal with one maintenance requirement and one maximum protein deposition rate, even if these values are representative of the population average. Therefore, the cause-and-effect response of the average animal will always be different to the population response, even though this difference may be small as in this case (Curnow, 1973; Emmans and Fisher, 1986). This throws into doubt the accuracy of all deterministic models in which the response of an individual animal is simulated and believed to be representative of the population mean.

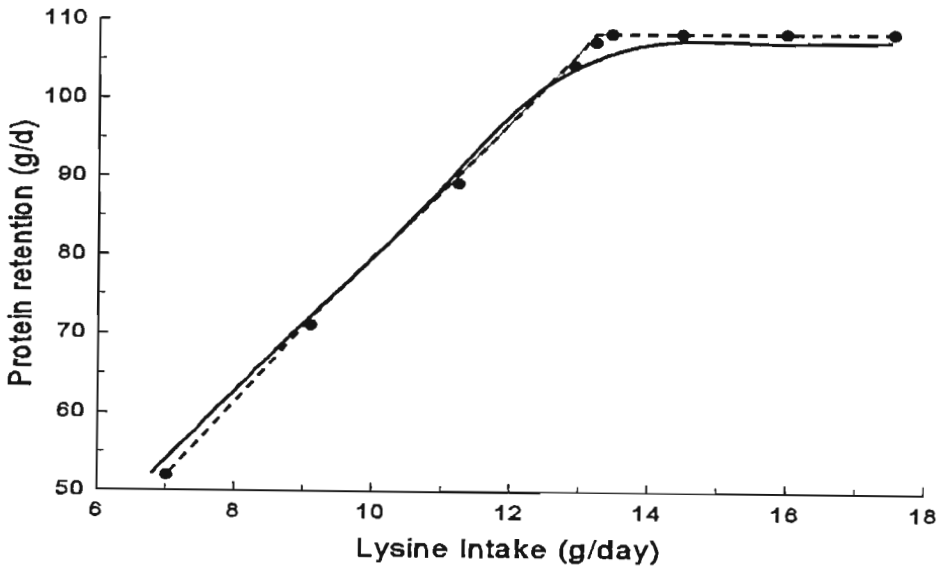


Figure 5.3 Comparison of the response in protein retention to lysine intake between the average individual (●) and the mean of a population (——) of 100 pigs grown between 20 and 40 kg live weight. The linear-plateau model is indicated by the dashed line (– –).

The extent of the errors introduced by translating requirements from the average animal to the population will depend on the genotype and variations in genetic parameters within a population, and the extent of the correlation between body weight (maintenance) and the potential growth rate of each animal. It is for this reason that estimates of the nutrient requirements of a population of animals are more meaningful than those of individuals when formulating diets to optimise the performance of a group of animals.

## 5.4 Conclusion

On the basis of a reasonable comparison with published data the results indicate that across a live weight range of 25 to 90 kg most, if not all, variability in ADG and FI from genetic differences can be accounted for when the CV of $B^*$ is between 1 and 3% (2% likely to be optimal), the CV of Pm between 5 and 10% (with values closer to 5% being optimum) and the CV of LPRm is 10%. These CV's were chosen.

The $CV_g$'s of both ADG and FI tend to increase with increasing variation in all three inherent parameters, the only exception being that the $CV_g$ of FI does not increase with increasing Pm. This trend is apparent across all body weights, but particularly so at heavier weights. The parameter that has the most profound effect on the genetic variation in FI is LPRm and in ADG it is Pm.

If the genotype is described, as in this thesis, by B, Pm and LPRm then it is useful to know their respective CV's as a population response can then be simulated. It is clear that there is a difference in the response when an individual and when a population is used in the simulation. Hence the value of knowing the CV's of these parameters.

The differences in response between the average individual and the mean of the population suggests that when formulating diets to optimise the performance of a group of animals the nutrient requirements of a population are more meaningful and preferred to those of an individual, even if the individual is the average individual in the population. The increased processing speed of computers make it possible to simulate responses of populations, but it is only where the description of the genotype allows a population to be described that it is possible to move from an individual to a population response.

CHAPTER 6

# DETERMINATION OF MAXIMUM HEAT LOSS AND TESTING THE INFLUENCE OF HEAT PRODUCTION ON VOLUNTARY FOOD INTAKE IN GROWING PIGS FED PROTEIN-DEFICIENT DIETS

## 6.1 Introduction

Central to the theory of voluntary food intake described in Chapter 1 is an estimate of the maximum amount of heat an animal can lose ($THL_{max}$) which constrains the desired food intake and hence reduce the growth rate below the potential of the animal. For this reason the most serious limitation in the simulation model is the inadequate description of $THL_{max}$. The current lack of data available to qualify and quantify $THL_{max}$ limits the application of the model and makes it difficult to properly test what effect heat production has on voluntary food intake and subsequent body tissue deposition, particularly in animals fed a protein-deficient feed. To achieve a reasonable level of accuracy of prediction, it is imperative that a more definitive function of $THL_{max}$ be determined. These problems must be suitably addressed in order for the theory to be successfully implemented into a simulation model to predict food intake and rate of growth in growing pigs.

It is well documented that the environment, and particularly ambient temperature, affects the voluntary food intake, growth and heat production of growing pigs (Fuller and Boyne, 1971; Verstegen *et al*, 1973; Close and Mount, 1978; Dauncey et al, 1983; LeDividich and Noblet, 1986; Campbell and Taverner, 1988; Rinaldo and LeDividich; 1991). What is not clear, however, is how the environmental temperature interacts with protein and energy intake to affect protein metabolism and body composition. This problem has been exacerbated by the recent developments of faster-growing and genetically leaner pigs and the use of intensive production systems in which many pigs are reared in a confined space.

Most studies relating the effects of temperature to the growth of pigs have been confined to the effect of low ambient temperatures on energy metabolism (Verstegen *et al.*, 1977, 1982; Close 1981,1987). Few authors have considered the influence of high temperatures on energy and protein metabolism and maximum heat loss (Campbell and Taverner, 1988; Rinaldo and Le Dividich, 1991). These latter two authors concentrated on the effects that high temperature and energy intake have on energy metabolism, with little regard to the relationship between temperature and protein intake on maximum heat loss. The question of assessing the maximum heat loss when pigs are fed sub-optimal protein diets has, surprisingly, not been addressed, although it is critical for optimal production in hot environments. The only work on how dietary protein and environmental temperature affects the growth performance of pigs was done using protein-adequate diets (Stahly *et al.*, 1981; Berschauer *et al.*, 1983). However, it is well

documented that dietary protein concentration, and particularly low protein to energy concentrations, is important in regulating protein and fat deposition, and heat production (Kyriazakis *et al.*, 1991a,b; Henry *et al.*, 1992; Kyriazakis and Emmans, 1992).

As improvements are continually being made to the inherent lean growth capacity of commercial pigs and to the way in which these animals are being fed, the optimal environment which will allow the animals to express their potential growth would be expected to be changing also. The question is how the optimal environment could be determined, and whether it maybe possible to predict this in the future as further changes are made to the potential growth rate of pigs. For the purposes of this discussion the optimum environment can be defined as the environmental conditions that allow the potential lean capacity of the pig to be realised. For practical purposes the optimum environment is defined by an estimate of the mean daily ambient temperature. Therefore, a hot environment can be defined as an environment in which the animal is unable to achieve its maximum rate of protein deposition because the air temperature is too high.

Improvements in the understanding of the relationships between tissue deposition, minimum and maximum total heat loss and nutrient intakes will also improve the way in which animals are reared. Once the factors that influence heat loss have been identified (e.g. energy and protein intake, rates of protein and lipid gain, amino acid balance in the feed etc.) and their relationships established, determining the partitioning of energy between fat and protein in both energy and protein limiting diets will be possible. Animals fed a protein-deficient diet will only achieve their maximum rate of protein retention if they can consume sufficient protein to meet their daily requirements. This can only be achieved if they can lose the heat produced from depositing body tissue and from the heat increment of feeding on such feed. A corollary to the above is that the amount of heat an animal can lose in a hot environment will determine the rate of protein deposition and, therefore, the importance of knowing the maximum heat loss capability of the animal. Modelling these relationships will make it possible to compensate for warm conditions by adjusting the protein to energy ratio in the feed and to design housing facilities that are more appropriate to the animals being housed therein.

An experiment was designed to measure the responses in tissue deposition, food intake and heat production over a range of dietary concentrations of crude protein and environmental temperatures. On the assumption that the heat stored in the body of an animal is negligible and therefore that heat loss is equal to heat produced, the results of the experiment were used to derive a function that would predict the maximum rate of heat loss of a given animal in a given environment. After including the new maximum heat loss function in the model described in Chapter 1, the results from the experiment were used to test the algorithm in a model designed to predict food intake, and subsequent growth performance in protein-limiting diets, and to determine the influence of heat production on voluntary food intake.

## 6.2 Materials and Method

### 6.2.1 Animals and Design

Ninety-nine entire male Large White x Landrace pigs were used in this 4 x 6 factorial experiment. The respective factors were four temperatures, 18°C, 22°C, 26°C and 30°C, and six dietary protein concentrations ranging from 1.2 to 0.48 of their amino acid requirements. The experiment started when the average live weight of the animals in each chamber reached 12 kg. To determine initial body composition, three pigs were allocated to an initial slaughter group and slaughtered at the start of the experiment. The remaining ninety-six pigs were randomly allocated to one of six dietary protein concentrations and four temperature treatments to ensure four pigs per treatment. For any given temperature each controlled environment chamber contained two animals per protein treatment. All animals were kept in their respective treatments until 30 kg live weight whereafter they were slaughtered.

### 6.2.2 Housing and Management

The pigs were penned individually in controlled-environment chambers that contained 12 pens. Each pen measuring 0.6m$^2$ had a reinforced-plastic floor with its own nipple drinker and metal feed bin. The chambers were designed to maintain temperature within 0.2°C. The four temperatures used were 18.1(±0.44)°C, 22.1(±0.23)°C, 25.9 (±0.34)°C and 29.8 (±0.35)°C and the respective relative humidities were 62.0 (±14.3) %, 66.4(±8.4) %, 72.1 (±5.2) % and 70.2 (±4.3) %. These temperatures were chosen to provide environments nominally called cold, cool, warm and hot. As there were only two controlled-environment chambers available, the four temperature treatments were spread over four different periods.

All animals were given free and continuous access to food and water. The animals were weighed once a week at 08 00 hr until they were within three kgs of the slaughter weight (30 kg) where-upon they were weighed every second day. Food intake was calculated by determining the difference in weight of the feeder at the beginning and end of each week.

### 6.2.3 Diets and Feeding

A summit-dilution technique (Fisher and Morris, 1970) was used to formulate the six protein treatments to ensure feeds were blended in the following proportions (summit:dilution): 100:0, 88:12, 76:24, 64:36, 52:48, 40:60 (Table 6.1).

Table 6.1. Dilution of Summit diet and the expected lysine concentrations and % of requirements of the protein diets.

| Treatment | Dilution (%) | % of requirement | lysine concentration (g/kg) |
|---|---|---|---|
| P1 | 0 | 120 | 14.4 |
| P2 | 12 | 106 | 12.7 |
| P3 | 24 | 91 | 10.9 |
| P4 | 36 | 77 | 9.2 |
| P5 | 48 | 62 | 7.4 |
| P6 | 60 | 48 | 5.8 |

A summit diet was formulated to contain 1.2 times the amino acid requirement for maximum lean growth between 12 and 30 kg body weight. The amino acids were balanced according the ideal protein balance with lysine as the reference amino acid (Wang and Fuller, 1989). The simulation model, outlined in Chapter 1, was used to predict the requirements for lysine between 12 and 30 kg live weight (12.0 g/kg) in a diet containing 15.0 MJ/kg DE. The summit diet was then formulated to contain 15.0 MJ/kg and 14.4 g/kg total lysine with all other amino acids balanced accordingly (Table 6.2).

A non-protein dilution feed was formulated to contain the same concentrations of all nutrients and energy other than amino acids (Table 6.2). The dilution diet was used to dilute the summit diet to ensure the correct levels of crude protein and amino acids for each protein treatment (P1 to P6).

Table 6.2. Constituents and calculated chemical composition of the Summit and Dilution diets.

| Ingredient (g/kg) | Summit | Dilution |
|---|---|---|
| Yellow Maize | 576.86 | - |
| Soyabean OC | 250.00 | - |
| Fish Meal | 126.78 | - |
| Maize Starch | - | 200.00 |
| Sugar | - | 577.82 |
| Sunflower Oil | 19.38 | 50.00 |
| Sunflower Husks | - | 116.25 |
| Monocalcium Phosphate | 9.05 | 38.36 |
| Limestone | 10.42 | 10.08 |
| Salt | 2.50 | 2.50 |
| Vit+Min Premix | 5.00 | 5.00 |
| Calculated Composition (g/kg): | | |
| DE (MJ/kg) | 15.0 | 15.0 |
| Crude protein (N x 6.25) | 230.0 | 0.0 |
| Lysine | 14.4 | 0.0 |

The results of the chemical analyses are shown in Table 6.3. The inclusion rate of vitamins and minerals was 1.5 times the normal to ensure that these nutrients were not limiting.

Table 6.3 The analysed chemical compositions of the Summit, Dilution and remaining diets.

| Nutrient (g/kg) | Summit (P1) | P2 | P3 | P4 | P5 | P6 | Dilution |
|---|---|---|---|---|---|---|---|
| Digestible Energy MJ/kg | 15.1 | 15.0 | 15.1 | 15.1 | 15.1 | 15.0 | 15.2 |
| Metabolizable Energy MJ/kg[§] | 14.4 | 14.4 | 14.6 | 14.6 | 14.7 | 14.7 | 15.1 |
| Crude Protein | 230.0 | 201.2 | 177.8 | 150.9 | 125.0 | 93.0 | < 1.0 |
| Dry Matter | 899.2 | 900.4 | 901.5 | 902.6 | 903.3 | 904.6 | 907.4 |
| Ash | 62.9 | 60.9 | 61.0 | 57.0 | 54.9 | 52.4 | 49.3 |
| Total Lysine | 14.6 | 12.5 | 11.0 | 9.0 | 7.8 | 5.9 | ND |
| Total Methionine and cystine | 8.9 | 7.6 | 6.7 | 5.5 | 4.8 | 3.6 | ND |
| Total Threonine | 9.0 | 7.7 | 6.8 | 5.6 | 5.0 | 3.7 | ND |
| ME:DCP (MJ/kg)[¶] | 78.3 | 89.4 | 102.3 | 121.1 | 147.0 | 197.5 | ND |

ND Not determined

[§] Calculated ME = DE*(0.997-0.000189*CP) (ARC, 1981)

[¶] ME:DCP = ME(MJ/kg) / (CP(kg/kg) x protein digestibility); protein digestibility = 0.80

### 6.2.4 Slaughter Procedure and Carcass Analysis

Pigs were killed by an intra peritoneal injection of 25 ml of Sodium Pentobarbitone (20%) (Euthatol™, Rhône Poulenc Group). The intestinal tract was removed and the contents of the stomach and intestines were emptied. The remaining empty carcass and gastrointestinal tract (referred together as the empty body) were stored in a plastic bag and frozen at -20°C. From the difference in weight before emptying and after emptying the gut-fill was determined. The frozen empty body was cut into smaller pieces and homogenized in a mincer. Each pig was then subsampled and duplicate samples were used for proximate analysis. The three pigs slaughtered at 12 kg live weight were analysed in triplicate.

Dry matter content was determined by freeze drying each sample for 72 hours. Nitrogen content of the dry matter was determined by auto analysis and the protein content calculated as nitrogen x 6.25. Lipid content was assessed by Soxhlet extraction of the freeze-dried samples with petroleum ether at 40 to 60°C for 6h. Ash was analysed by burning the samples in a muffle furnace at 550° for 4h. After individual analyses of each sample the two sample results were pooled to provide a single result per pig. Where there were differences in any component of more than 10% between duplicated samples a further sample was analysed.

### 6.2.5 Heat Loss

On the assumption that heat storage in young pigs is negligible, total heat lost is equal to total heat produced. Total heat loss (THL) is calculated from the equation:

$$THL = MEi - (23.8 \times PR + 39.6 \times LR) \qquad (MJ/d) \qquad (6.1)$$

where MEI = Metabolizable Energy intake (MJ/d)
PR = daily protein retention (kg/d)
LR = daily lipid retention (kg/d)

### 6.2.6 Statistical Analysis

The growth and food intake results were analysed by analysis of variance using a factorial design with protein concentration and temperature as factors. The effect of protein intake on protein deposition was determined with regression analysis using dummy variables to fit a broken-stick model (Minitab, 1994). Multiple regression analysis was used to determine the relationship between maximum heat loss and the size and state of the animal. Data were analysed using Minitab (1994).

### 6.2.7 Simulation model comparisons

Once the maximum heat loss equation had been determined and implemented into the simulation model the data from the experiment were used to test two components of the theory of food intake included in the simulation model partly described in Chapter 1. The two ideas to be tested were, firstly, do pigs attempt to maintain protein intake as the protein content of the food is decreased, and secondly, does the ability of the animal to lose heat limit the extent to which the pig can compensate for decreasing protein contents.

## 6.3 Results and Discussion

The composition of the initial slaughter group at 12.8 ( ±1.28) kg live weight was 11.43 (±0.610) kg empty body weight, 1.80 (±0.068)kg protein, 0.88 (±0.066) kg lipid, 8.11 (±0.591) kg moisture and 0.36 (±0.015) kg ash. At the end of the experiment, the animals on all treatments were slaughtered at 29.95 (±0.310) kg live weight. See Appendix 2 for detailed results of each pig.

### 6.3.1 The Effects of Heat Production on Growth and Voluntary Food Intake

#### 6.3.1.1 *Food intake and live weight changes*

The effects of temperature and protein concentration on the empty body weight (EBWT), gut fill, voluntary food intake (FI), average daily gain (ADG) and feed conversion ratio (FCR) are shown in Table 6.4.

There were no significant differences in the EBWT across the protein and temperature treatments. There were, however, significant differences ($P < 0.05$) in the gut fill across the six protein treatments. Although there was no statistical difference in gut fill between temperature treatments there is linear trend for gut fill to increase with decreasing temperatures. According to Close (1987) and Whittemore (1993) the lower critical

temperature for pigs between 10 and 30 kg is close to 26°C. At 18° C and 22 C the environmental heat demand, associated with an ambient temperature below the comfort zone, will cause the animal to increase its voluntary food intake (Verstegen *et al.*, 1982) and hence an increase in gut fill.

Table 6.4 The live weight (LWT), empty body weight (EBWT), food intake (FI), average daily gain (ADG) and food conversion efficiency (FCR) of pigs grown from 12 kg to 30 kg live weight on feeds differing in protein concentration at different temperatures.

| Temperature | Protein Treatment | EBWT (kg) | Gut fill (kg) | FI (kg/d) | Gut fill Index¶ | ADG (kg/d) | FCR |
|---|---|---|---|---|---|---|---|
| 18°C | P1 | 27.73 | 2.62 | 1.388 | 1.89 | 0.737 | 1.890 |
| | P2 | 27.15 | 2.48 | 1.392 | 1.79 | 0.775 | 1.798 |
| | P3 | 28.24 | 2.09 | 1.369 | 1.52 | 0.731 | 1.875 |
| | P4 | 28.58 | 2.00 | 1.408 | 1.41 | 0.662 | 2.137 |
| | P5 | 27.86 | 2.06 | 1.496 | 1.40 | 0.650 | 2.293 |
| | P6 | 27.51 | 1.71 | 1.318 | 1.30 | 0.508 | 2.595 |
| 22°C | P1 | 27.83 | 2.11 | 1.282 | 1.63 | 0.784 | 1.636 |
| | P2 | 28.38 | 2.34 | 1.291 | 1.84 | 0.764 | 1.694 |
| | P3 | 27.99 | 2.29 | 1.284 | 1.79 | 0.721 | 1.782 |
| | P4 | 28.00 | 2.12 | 1.381 | 1.55 | 0.673 | 2.054 |
| | P5 | 28.07 | 1.83 | 1.374 | 1.34 | 0.572 | 2.400 |
| | P6 | 28.41 | 1.61 | 1.288 | 1.25 | 0.519 | 2.500 |
| 26°C | P1 | 28.39 | 1.95 | 1.072 | 1.83 | 0.720 | 1.492 |
| | P2 | 28.27 | 1.97 | 1.093 | 1.81 | 0.722 | 1.516 |
| | P3 | 28.74 | 2.05 | 1.218 | 1.72 | 0.716 | 1.701 |
| | P4 | 29.14 | 1.63 | 1.390 | 1.17 | 0.724 | 1.935 |
| | P5 | 29.29 | 1.63 | 1.383 | 1.18 | 0.670 | 2.065 |
| | P6 | 28.21 | 1.71 | 1.319 | 1.29 | 0.573 | 2.302 |
| 30°C | P1 | 28.77 | 1.94 | 1.027 | 1.91 | 0.663 | 1.555 |
| | P2 | 29.05 | 1.78 | 1.093 | 1.60 | 0.641 | 1.713 |
| | P3 | 27.57 | 2.18 | 1.147 | 1.90 | 0.633 | 1.813 |
| | P4 | 28.82 | 1.74 | 1.209 | 1.47 | 0.638 | 1.894 |
| | P5 | 27.20 | 1.78 | 1.111 | 1.66 | 0.566 | 1.973 |
| | P6 | 27.88 | 1.42 | 1.038 | 1.40 | 0.393 | 2.659 |
| SED | | 0.766 | 0.373 | 0.081 | 0.317 | 0.037 | 0.121 |
| Means and SED of: | | | | | | | |
| Temperature: | | | | | | | |
| 18°C | | 27.84 | 2.16 | 1.395 | 1.55 | 0.677 | 2.098 |
| 22°C | | 28.11 | 2.05 | 1.317 | 1.56 | 0.672 | 2.011 |
| 26°C | | 28.69 | 1.82 | 1.246 | 1.50 | 0.680 | 1.868 |
| 30°C | | 28.21 | 1.81 | 1.104 | 1.65 | 0.589 | 1.934 |
| SED | | 0.313 | 0.152 | 0.033 | 0.130 | 0.015 | 0.050 |
| Protein: | | | | | | | |
| P1 | | 28.18 | 2.16 | 1.192 | 1.81 | 0.726 | 1.643 |
| P2 | | 28.21 | 2.14 | 1.217 | 1.76 | 0.725 | 1.680 |
| P3 | | 28.16 | 2.15 | 1.255 | 1.73 | 0.700 | 1.792 |
| P4 | | 28.63 | 1.87 | 1.347 | 1.40 | 0.674 | 2.005 |
| P5 | | 28.10 | 1.83 | 1.341 | 1.40 | 0.614 | 2.182 |
| P6 | | 28.00 | 1.61 | 1.240 | 1.31 | 0.498 | 2.514 |
| SED | | 0.383 | 0.187 | 0.040 | 0.159 | 0.019 | 0.061 |
| Significance of: | | | | | | | |
| Temperature (T) | | NS | NS | *** | NS | *** | *** |
| Protein (P) | | NS | * | *** | * | *** | *** |
| T x P | | NS | NS | NS | NS | NS | NS |

¶ Gut fill Index =Gut fill / FI
SED standard error of difference;
NS not significant; * P < 0.05; ** P < 0.01; *** P < 0.001

It is interesting to note that gut fill is a constant proportion of FI at all temperatures (±1.56),

but that this ratio varies with different protein concentrations (1.31 - 1.81). The constant ratio of gut fill to food intake over all temperatures suggests that rate of passage of food through the digestive tract is independent of environmental temperature and that the emptying of the digestive tract does not contribute towards the regulation of voluntary food intake. However, the converse is true for animals fed on different protein concentrations where the trend is for more rapid movement of digesta through the digestive tract as the protein concentration decreases.

Both gut fill and the gut fill:FI ratio decreased linearly with decreasing concentrations of dietary protein. However, this response may be confounded by the possible differences in digestibility or solubility of the feed, as the lower the protein concentration the greater the proportion of dilution diet and therefore, the greater the amount of sugar and starch. Both sugar and starch are very soluble and readily digestible ingredients and will therefore, result in an increase in the rate of passage through the digestive tract and a lower gut fill:FI ratio.

As there were no significant interactions between protein and temperature on FI, the main effects of these factors can be discussed separately.

The effects of dietary protein deficiency on food intake have been well documented (Campbell and Biden, 1978;Wyllie and Owen, 1978; Campbell and Dunkin, 1983a; Kyriazakis, Emmans and Whittemore, 1990; Kyriazakis *et al.*, 1991; Gatel, Buron and Fekete, 1992; Henry *et al.* 1992) but the responses have been quite varied. A possible explanation for the variation in response is due to the animals being housed at different temperatures, which is elaborated further on the basis of the results of this experiment.

The daily food intake over the live weight range of 12 to 30 kg increased as the protein content of the feed was decreased until a maximum rate of 1.347 (±0.120) kg/d on P4, where-after intakes declined (Figure 6.1). At the comfort temperature of 26°C, crude protein intake remained constant between 207 and 217 g/d for treatments P2 to P4. Protein intake was markedly lower on P5 (173 g/d) and P6 (123 g/d). This is consistent with the theory that pigs attempt to maintain a constant protein intake as the protein content of the feed is reduced (Kyriazakis *et al*, 1991a). However, a point is reached when the animal can no longer compensate for reduced dietary protein concentration and food intake will subsequently decline. This response was observed in animals fed either P5 or P6.

From the heat loss data, the dietary treatment that was responsible for the highest FI was also the treatment that had the highest THL and it was the protein concentration below which FI and THL declined. It would appear that the ambient temperature was responsible for limiting how much heat the animal could lose on protein-deficient diets. As a consequence

of a reduced protein intake, the rate of protein deposition decreased. Kyriazakis and Emmans (1991) alluded to the effect of temperature on protein intake and deposition to explain the marked improvement in the rate of protein deposition when a similar type of pig was grown in temperatures of 16°C as opposed to 22° C. In the current experiment, the regulation of protein intake at temperatures below 26°C was overridden by the requirement for energy as cold thermogenesis increased. This led to an over-consumption of protein at low temperatures.

It has been well documented that increasing the temperature above the thermoneutral zone results in a reduction in food intake and decreasing the temperature below the lower critical temperature causes an increase in voluntary food intake (Close and Mount, 1978; Verstegen *et al*, 1982; Rinaldo and Le Dividich, 1991; Nienaber *et al*, 1993). Similar results were obtained in this experiment (Table 6.4). Figure 6.1 illustrates the effect of dietary protein content on food intake for the different temperatures and the mean response for all temperatures. There was a linear decline in FI as the environmental temperature increased.

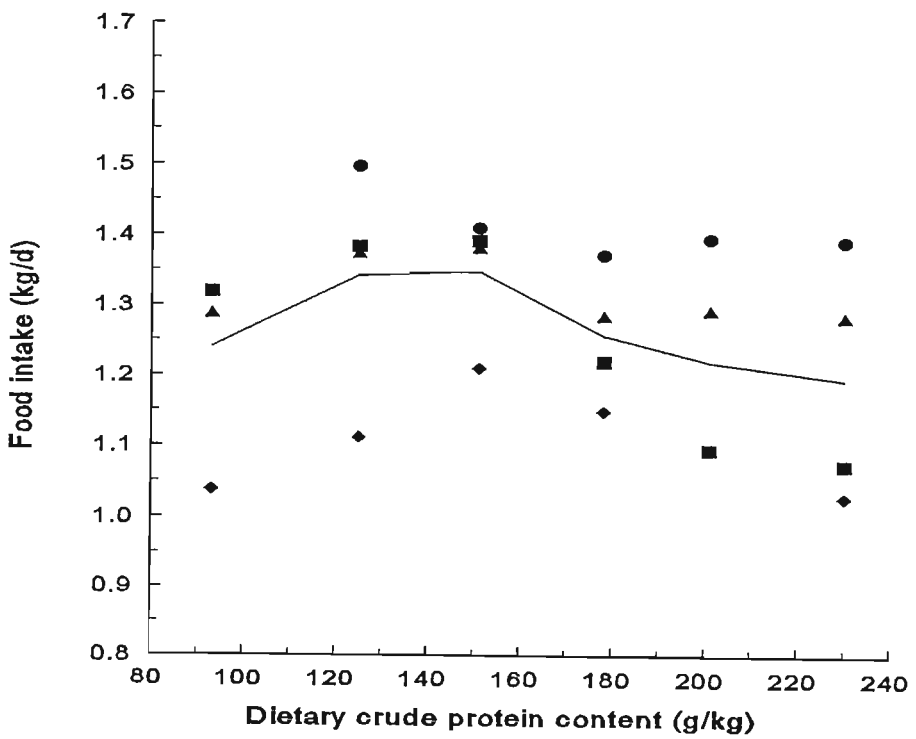


Figure 6.1 The effect of dietary protein concentration on the food intake of pigs grown from 12 to 30 kg live weight in four different temperatures. (● )18°C; ( ▲ ) 22°C; ( ■ ) 26°C; (♦ ) 30°C; ( — ) mean.

From Table 6.4 it can be calculated that for a 1 °C increase in temperature food intake was reduced by 19.6 g/d between 18°C and 22 °C, and 17.6 g/d. °C between 22 °C and 26 °C. However, there was a more pronounced decrease of 35.5 g/d.°C between 26°C and 30°C. If

26°C is assumed to be the comfort temperature for these pigs then for every 1°C below 26 °C an increase in voluntary food intake of 1.5% could be expected. Similarly, for every 1°C above 26°C food intake would be expected to decrease by 2.75%.

Although there were no significant interactions between the main effects of protein and temperature on food intake, at 18°C maximum food intake was achieved in pigs fed a diet containing 125g crude protein/ kg while at 30°C, maximum food intakes occurred in pigs fed 150g/kg. There were no differences in the response of FI to high dietary protein concentrations (P1 and P2) within a given temperature. However, as dietary protein concentration further decreased FI increased (Figure 6.1). The protein content below which FI increased depended on the temperature. At 18°C, 22°C, 26°C and 30°C the increase occurred on dietary treatment P4, P3, P2 and P1, respectively. Food intake would increase only if the additional heat increment of feeding did not result in THL exceeding the limit of the animal (defined by $THL_{max}$). This result provides support for the theory that an animal, fed a protein-deficient diet, will attempt to consume an amount of protein that would satisfy its requirement. The extent of the compensation is constrained by the ability of the animal to lose heat to the environment. The warmer the environment the lower the maximum amount of heat that can be lost, while a cooler environment would allow the animal to lose more heat.

Decreasing the protein concentration of the diet below 100% of the requirement of the animal (P2) resulted in significant ($P < 0.001$) decreases in ADG irrespective of the ambient temperature. The response to dietary protein was linear, with maximum ADG (0.726 g/d) attained in pigs fed P1 and the lowest ADG (0.498 g/d) in animals fed P6. As there were no interactions between temperature and protein supply on ADG, the response in growth rates to temperature was independent of protein supply. Temperature had a significant effect ($P < 0.001$) on the rate of daily gain but the effects were not linear. Maximum ADG of 0.680 kg/d was achieved at a temperature of 26°C. Above this temperature growth and food intake were depressed while below this temperature ADG's were insignificantly lower and food intakes were significantly higher ($P < 0.001$).

An increase in the supply of protein in the diet resulted in significant decreases ($P < 0.001$) in the amount of food required per unit of gain. This was to be expected, as the desired food intake of the animal will depend on the content of the first limiting nutrient which, in this experiment, was designed to be protein (actually lysine, with all amino acids balanced accordingly). As protein became less limiting so less food was required for maximum growth resulting in a reduction in FCR.

There was a curvilinear response in how much feed was required per unit of body weight gain as ambient temperature was increased, with the highest FCR (2.100 ± 0.072) being recorded

at 18°C and the lowest at 26°C (1.868 ± 0.083). Similar findings were observed by Rinaldo and Le Dividich (1991) and Nienaber, Hahn, Korthals and McDonald (1993). Like ADG, the response in FCR to temperature was independent of the protein concentration in the diet.

If maximum ADG and minimum FCR are the criteria used to determine the temperature of least thermoregulatory effort then the data from this experiment suggest that the optimal temperature for growing young pigs, between 12 and 30 kg live weight and fed ad libitum, is 26°C. This is similar to the upper limit of the range of comfort temperatures recommended by Whittemore (1993)and to the results of Rinaldo and Le Dividich (1991).

6.3.1.2 *Body composition*

The chemical composition of the empty body of pigs at 30 kg live weight is shown in Table 6.5. As was expected from previous experiments (Campbell, 1977; Campbell and Biden, 1978; Campbell and Dunkin, 1983; Kyriazakis *et al.*, 1991a and Kyriazakis and Emmans, 1991), there was a significant decrease ($P < 0.001$) in the protein content of the EBWT as the dietary protein concentration declined below 178g CP/kg (P3). There was a corresponding significant increase ($P < 0.001$) in the lipid weight as dietary protein diminished.

From Table 6.3 the implications are that, for the genotype of pig used in this experiment, a diet containing less than 90% of the protein requirements of the animal will not be sufficient to allow the animal to reach its potential protein weight, unless it was grown in temperatures of 22°C or less. From the response in food intake (Table 6.4) it would appear that the pigs did attempt to maintain their desired protein weight by eating more of the low protein diets. However, at P4, where a maximum intake occurred, the animals could not fully compensate for low protein concentrations and therefore, protein in the EBWT decreased.

There was an 18.6 % reduction in body protein between pigs fed on P6 as opposed to those on P1. The additional energy consumed in an attempt to satisfy their protein requirements resulted in a 115% increase in the lipid content of the empty body weight.

The significant interactions between protein and temperature on body protein ($P < 0.001$) and lipid ($P < 0.05$) contents suggest that although temperature, on its own, did not affect the protein weight, it did influence the response to decreasing dietary protein concentration. On the low protein diets ( P5 and P6) the lipid content increased with increasing temperature until a maximum at 26°C, whereafter there was a slight decrease at 30°C. The opposite trend was observed in the protein content of the body, with maximum protein weight being achieved on the three lowest protein diets at 18°C. The response in body moisture content to dietary protein concentration was independent of the ambient temperature and similarly the response in body ash to temperature was independent of crude protein content in the diet.

There were no significant differences in the protein contents of the empty body over the four different temperatures but there is a significant linear trend ($R^2$ = 0.92) with body protein content decreasing as environmental temperature decreases. Campbell and Taverner (1988) found that there were significant differences in body protein content, but in the opposite direction with pigs housed at 14°C and 32°C having 17.1% and 16.3% protein, respectively. The reason for the discrepancy is probably due to the wider temperature range used by Campbell and Taverner (1988) and that at 14°C there was less net energy available for protein deposition resulting in a lower protein content.

Table 6.5 The protein weight , lipid weight, moisture weight and ash weight of the empty body weight of pigs at 30 kg live weight , fed decreasing concentrations of protein at different temperatures.

| Temperature | Protein Treatment | Protein (kg) | Lipid (kg) | Moisture (kg) | Ash (kg) |
|---|---|---|---|---|---|
| 18°C | P1 | 4.598 | 3.395 | 18.592 | 0.803 |
| | P2 | 4..348 | 3.243 | 18.327 | 0.760 |
| | P3 | 4.578 | 3.780 | 18.737 | 0.853 |
| | P4 | 4.748 | 4.315 | 18.298 | 0.873 |
| | P5 | 4.315 | 5.275 | 17.190 | 0.810 |
| | P6 | 3.642 | 6.353 | 16.150 | 0.755 |
| 22°C | P1 | 4.388 | 2.933 | 19.463 | 0.795 |
| | P2 | 4.565 | 3.440 | 19.128 | 0.800 |
| | P3 | 4.620 | 3.715 | 18.647 | 0.835 |
| | P4 | 4.440 | 4.010 | 18.330 | 0.883 |
| | P5 | 4.308 | 5.008 | 17.392 | 0.903 |
| | P6 | 3.883 | 5.888 | 17.320 | 0.883 |
| 26°C | P1 | 4.680 | 2.808 | 19.665 | 0.930 |
| | P2 | 4.600 | 3.175 | 19.212 | 0.903 |
| | P3 | 4.685 | 3.933 | 19.022 | 0.948 |
| | P4 | 4.380 | 4.713 | 18.662 | 0.865 |
| | P5 | 4.283 | 5.438 | 18.312 | 0.950 |
| | P6 | 3.815 | 6.805 | 16.333 | 0.850 |
| 30°C | P1 | 4.948 | 2 858 | 19.932 | 0.878 |
| | P2 | 5.033 | 3.623 | 19.278 | 0.940 |
| | P3 | 4.560 | 3.583 | 18.300 | 0.900 |
| | P4 | 4.408 | 5.120 | 18.250 | 0.865 |
| | P5 | 3.948 | 5.303 | 16.985 | 0.828 |
| | P6 | 3.815 | 6.713 | 16.372 | 0.843 |
| SED | | 1.342 | 0.267 | 0.516 | 0.055 |
| Means and SED of: | | | | | |
| Temperature: | | | | | |
| 18°C | | 4.371 | 4.410 | 17.882 | 0.809 |
| 22°C | | 4.367 | 4.165 | 18.380 | 0.850 |
| 26°C | | 4.408 | 4.478 | 18.535 | 0.908 |
| 30°C | | 4.452 | 4.533 | 18.186 | 0.875 |
| SED | | 0.548 | 0.109 | 0.211 | 0.028 |
| Protein: | | | | | |
| P1 | | 4.653 | 2.998 | 19.413 | 0.851 |
| P2 | | 4.636 | 3.395 | 18.986 | 0.851 |
| P3 | | 4.611 | 3.753 | 18.677 | 0.884 |
| P4 | | 4.494 | 4.539 | 18.385 | 0.871 |
| P5 | | 4.213 | 5.256 | 17.470 | 0.873 |
| P6 | | 3.789 | 6.439 | 16.544 | 0.833 |
| SED | | 0.671 | 0.134 | 0.258 | 0.027 |
| Significance of: | | | | | |
| Temperature (T) | | NS | ** | * | *** |
| Protein (P) | | *** | *** | *** | NS |
| T x P | | *** | *** | NS | NS |

SED standard error of difference; NS not significant; * P < 0.05; ** P < 0.01; *** P < 0.001

With body lipid content there were significant differences between temperatures ($P < 0.01$), but there was no trend ($R^2 = 0.54$) for the level of fatness to change with a change in temperature. Rinaldo and Le Dividich (1991) and Campbell and Taverner (1988) observed decreasing concentrations of lipid as temperature increased. However, in their experiments energy and not protein was the most limiting nutrient and therefore excess lipid retention would not have occurred.

The response in body lipid was influenced by both protein and temperature as noted by a significant ($P < 0.05$) TxP interaction. The reason for the significant interaction is that at high protein contents (P1) there is a decrease in fatness as temperature increases, whereas with P5 and P6 fatness increases as temperature increases. So whereas there is no trend with the main effect of temperature, the significant interaction can be explained. The interaction between protein and temperature in lipid content suggests that at low protein contents the increase in energy intake, through an increase in food intake , at lower temperatures is used up in keeping the pig warm and not deposited as excess lipid.

The surprisingly low body moisture weight at 18°C was the main reason why of temperature had a significant effect ($P < 0.05$) on body moisture content. This was a consequence of the uncharacteristically high body lipid weight at 18°C. It was expected that less net energy would be available for lipid deposition in cold conditions as energy is repartitioned into cold thermogenesis.

The significant differences ($P < 0.05$) in body ash content across the four temperature treatments can probably be ascribed to the repartitioning of more net energy into maintaining homeothermy and less for bone growth at cold temperatures (18°C). This response diminishes with increasing temperature until at 26°C ash content is at a maximum.

6.3.1.3 *Protein and lipid retention*

The effects of dietary protein and ambient temperature on the rates of body tissue deposition are shown in Table 6.6. Decreasing the crude protein content of the diet below 90% of the requirement (P3) of the animal resulted in a significant decrease ($P < 0.05$) in PR. There were no significant differences in PR between P1, P2 and P3. However, there were significant increases ($P < 0.05$) in LR between P1 and P2, and between P1 and P3 (88.2, 103.6 and 113.0 g/d respectively).

The lack of any significant interaction between the protein content and temperature suggests that the response in PR to protein-deficient diets is independent of environmental temperature. This idea appears to contradict the idea that animals, fed on protein-deficient diets, will attempt to maintain their potential rate of protein growth provided the environment affords them the opportunity of losing excess heat generated by the overconsumption of other

nutrients. However, a closer look at the response to dietary protein concentration within each of the temperature treatments shows maximum PR (117.1 ±0.47 g/d) being attained on lower protein concentrations (P4) at 18°C than at 30°C (P2). It is evident that increasing protein concentrations are required to maximise PR as the environmental temperature increases. This response in PR to temperature in animals fed a protein-deficient diet does suggest that animals can only achieve maximum protein growth on protein-limiting diets if the environment is sufficiently cool to allow the extra heat increment of feeding to be dissipated.

Table 6.6 The daily rates of protein (PR), lipid (LR), moisture (WR) and ash (AR)deposition of the empty body of pigs grown between 12 and 30 kg live weight on feeds differing in protein concentration at different temperatures.

| Temperature | Protein Treatment | PR (g/d) | LR (g/d) | WR (g/d) | AR (g/d) |
|---|---|---|---|---|---|
| 18°C | P1 | 117.7 | 105.3 | 443.1 | 18.7 |
| | P2 | 117.9 | 114.4 | 472.7 | 18.6 |
| | P3 | 115.5 | 118.4 | 447.3 | 20.7 |
| | P4 | 108.7 | 125.7 | 380.8 | 19.3 |
| | P5 | 95.9 | 161.2 | 350.4 | 17.3 |
| | P6 | 57.8 | 163.7 | 252.7 | 12.3 |
| 22°C | P1 | 119.4 | 96.4 | 523.3 | 20.0 |
| | P2 | 118.5 | 109.3 | 471.5 | 18.2 |
| | P3 | 115.6 | 113.3 | 437.8 | 19.6 |
| | P4 | 102.9 | 124.6 | 398.6 | 20.5 |
| | P5 | 84.7 | 136.2 | 312.8 | 18.5 |
| | P6 | 62.5 | 154.1 | 278.9 | 15.5 |
| 26°C | P1 | 117.7 | 77.7 | 475.7 | 23.4 |
| | P2 | 115.6 | 94.2 | 460.9 | 22.5 |
| | P3 | 113.7 | 121.6 | 431.3 | 23.1 |
| | P4 | 104.7 | 158.0 | 425.0 | 20.5 |
| | P5 | 91.0 | 163.9 | 374.9 | 21.7 |
| | P6 | 63.5 | 193.1 | 256.7 | 15.5 |
| 30°C | P1 | 116.5 | 73.4 | 438.3 | 19.3 |
| | P2 | 114.9 | 96.5 | 399.5 | 20.8 |
| | P3 | 102.9 | 98.8 | 383.0 | 20.3 |
| | P4 | 94.0 | 150.0 | 366.2 | 18.3 |
| | P5 | 71.8 | 145.0 | 298.7 | 15.7 |
| | P6 | 47.9 | 143.7 | 195.8 | 11.5 |
| SED | | 4.86 | 11.61 | 24.98 | 2.02 |
| Means and SED of: | | | | | |
| Temperature: | | | | | |
| 18°C | | 102.2 | 131.5 | 391.2 | 17.8 |
| 22°C | | 100.6 | 122.3 | 403.8 | 18.7 |
| 26°C | | 101.0 | 134.7 | 404.1 | 21.1 |
| 30°C | | 91.3 | 117.9 | 346.9 | 17.7 |
| SED | | 1.98 | 4.74 | 10.20 | 0.83 |
| Protein: | | | | | |
| P1 | | 117.8 | 88.2 | 470.1 | 20.4 |
| P2 | | 116.7 | 103.6 | 451.1 | 20.0 |
| P3 | | 111.9 | 113.0 | 424.8 | 20.9 |
| P4 | | 102.6 | 139.6 | 392.7 | 19.7 |
| P5 | | 85.8 | 151.6 | 334.2 | 18.3 |
| P6 | | 57.9 | 163.6 | 246.0 | 13.7 |
| SED | | 2.43 | 5.81 | 12.49 | 1.01 |
| Significance of: | | | | | |
| Temperature (T) | | *** | ** | *** | *** |
| Protein (P) | | *** | *** | *** | *** |
| T x P | | NS | ** | NS | NS |

SED standard error of difference;
NS not significant; * P < 0.05; ** P < 0.01; *** P < 0.001

Although the main effect of temperature did cause significant differences ($P < 0.001$) in PR, there were no differences between animals at 18°C, 22°C and 26°C. Similarly there were no differences in the rate of LR, WR and AR between 18°C and 22°C. This suggests that in cold conditions when voluntary energy intake is sufficient to maintain a constant energy retention (PR and LR), both protein and lipid deposition are independent of environmental temperature. These findings support those of Rinaldo and Le Dividich (1991) that for pigs kept at temperatures below the lower critical temperature and fed ad libitum, temperature had no significance effect on protein and lipid deposition.

The reason for the overall significant effect of temperature on PR is due to the considerable reduction in PR at 30°C. There was a 9.6% decline in PR of pigs when grown at 30 C (91.3±5.30 g/d) as compared with that at 26°C (101.0 ±4.12 g/d). Similar results were shown by Campbell and Taverner (1988) between 14° C and 32°C, and Rinaldo and Le Dividich (1991) between 25°C and 31.5°C.

The reduction in PR at high temperatures is a consequence of the marked reduction in voluntary food intake and the resulting reduction in net energy available for tissue deposition. This is confirmed by the 12.6% decline in LR at 30°C (117.9 ±7.03 g/d) as compared with that at 26°C (134.7 ±9.19 g/d). Unlike the response at low temperatures, protein and lipid deposition are more dependent on the environmental temperature at high temperatures.

6.3.1.4 *Heat loss*

The total amount of heat lost (THL) across all treatments followed the same trend observed in the responses in food intake to protein-deficient diets and to different temperatures. The results are shown in Table 6.7.

The main effects of both protein and temperature treatments significantly affected THL ( $P < 0.05$ and $P < 0.001$, respectively). Within the protein treatments, there were no significant increases in THL between P1, P2 and P3, although pigs fed on P3 did produce more heat. Maximum THL occurred on diet P4 (11.88 ±0.403 MJ/d).

The protein treatment where maximum THL was observed corresponded with the protein treatment that resulted in pigs consuming the most food. However, the exact protein treatment responsible for maximum THL was not the same for all temperatures. Maximum heat output was observed in animals fed P5 at 18°C, P4 at 22°C and 26°C, and P3 at 30°C.

The similar responses in food intake and heat loss to dietary protein concentration and temperature show that one of the most important factors regulating the voluntary food intake of an animal is the maximum amount of heat that the animal can dissipate; the lower the ambient temperature, the greater the amount of heat the animal can lose. From Table 6.7 it

can be noted that there is a 36.6% increase in THL between animals kept at 18°C and those kept at 30°C. Although some of the additional heat produced in animals grown at 18°C is a result of cold thermogenesis, the potential exists for such animals to lose more heat when fed a diet with a high heat increment, such as P5 and P6, than those kept at higher temperatures. Pigs kept at 18°C in this experiment lost the greatest amount of heat (13.3 MJ/d) when fed diet P5 whereas those at 30°C lost the greatest amount of heat (10.5 MJ/d) on diet P3.

Table 6.7 Total heat loss (MJ/d) and the differences between these, for pigs grown between 12 and 30 kg live weight on feeds differing in protein concentration (P) at different temperatures(T).

| Temperature | Protein Treatment | THL (MJ/d) |
|---|---|---|
| 18°C | P1 | 13.095 |
| | P2 | 12.965 |
| | P3 | 12.747 |
| | P4 | 13.155 |
| | P5 | 13.323 |
| | P6 | 11.752 |
| 22°C | P1 | 11.920 |
| | P2 | 11.328 |
| | P3 | 11.413 |
| | P4 | 12.792 |
| | P5 | 12.760 |
| | P6 | 11.310 |
| 26°C | P1 | 9.655 |
| | P2 | 9.427 |
| | P3 | 10.438 |
| | P4 | 11.845 |
| | P5 | 11.797 |
| | P6 | 10.452 |
| 30°C | P1 | 9.193 |
| | P2 | 9.350 |
| | P3 | 10.540 |
| | P4 | 9.725 |
| | P5 | 8.977 |
| | P6 | 8.600 |
| SED | | 0.857 |
| Means and SED of: | | |
| Temperature: | | |
| 18°C | | 12.840 |
| 22°C | | 11.920 |
| 26°C | | 10.602 |
| 30°C | | 9.398 |
| SED | | 0.350 |
| Protein: | | |
| P1 | | 10.966 |
| P2 | | 10.767 |
| P3 | | 11.284 |
| P4 | | 11.879 |
| P5 | | 11.714 |
| P6 | | 10.529 |
| SED | | 0.428 |
| Significance of: | | |
| Temperature (T) | | *** |
| Protein (P) | | * |
| T x P | | NS |

SED standard error of difference; NS not significant; * P < 0.05; ** P < 0.01; *** P < 0.001
¶ Difference = (predicted-actual)/actual*100. The t-test (3 df) was used to test for significance.

It is clear from these results that, on marginally deficient feeds, pigs attempt to consume larger amounts of the feed in order to meet their requirement for the limiting nutrient (in this case, protein). They are prevented from achieving the desired intake by their inability to lose sufficient heat to the environment.

At grossly deficient protein concentrations the problem is exacerbated by the slow growth rate that is achieved as a result of the lack of protein. Similar findings were observed in previous experiments (Wethli, Morris and Shresta, 1975; Kyriazakis *et al.*, 1991a; Kyriazakis and Emmans 1992). This idea is substantiated by there being no corresponding decrease in EBWT with decreasing protein concentration and therefore dispelling the possibility that gut capacity was a limiting factor that could have exaggerated the reduction in food intake.

An interesting inference that can be made from the findings in this experiment is that part of the differences in results between compensatory growth trials in growing pigs may be attributed to the different ambient temperatures the pigs are exposed to during the compensatory phase (Wyllie, Speer, Ewan and Hays, 1969; Zimmerman and Khajarern, 1973; Shields and Mahan, 1980; Campbell and Dunkin, 1983). Pigs that are kept in cooler conditions during the replenishment phase have a greater chance of attaining their potential protein growth rate than animals kept in warmer conditions. Unfortunately many of the previous experiments did not include an estimate of the ambient temperature so confirming this idea is difficult.

#### 6.3.1.5 *Efficiency of protein utilisation*

From the protein retention data in Table 6.6 there is support for the proposal that at low levels of protein intakes the rate of protein retention is dependent on the rate of protein supply (Campbell, Taverner and Curic,1985a,b; Kyriazakis and Emmans, 1992). At high protein intakes (P1, P2 and P3) the rate of protein deposition remained constant and was probably close to the inherent potential of the animal, as energy intake was unlikely to be limiting in these feeds. The results from the simulation model confirm that the animals, which were fed diets P1, P2 and P3, retained protein close to their potential (118 vs 120 g/d, respectively, Tables 6.6 and 6.10) No additional protein gain was achieved by increasing the crude protein supply from 178 g/d to 230 g/d.

The efficiency of protein utilization can be determined from the ratio of protein retained and digested ideal protein intake (DIPI),as defined by Kyriazakis and Emmans (1992). The DIPI is defined by the equation:

$$DIPI = FI \times CP \times v \times d_{cp} \quad (g/d) \qquad (6.2)$$

where FI = food intake (g/d)
CP = crude protein (N x 6.25) content of the food (g/g)
$v$ = digestible protein relative to ideal protein
$d_{cp}$ = digestibility of CP

The value of *v* for all the diets was calculated to be close to 0.85. In a few instances it was higher but, according to Whittemore (1993), a *v* estimate of more than 0.85 is unlikely to occur in practice. The $d_{cp}$ is calculated to be 0.80. The simplest and most appropriate model to describe the relationship between protein retention (PR) and digestible ideal protein intake (DIPI) is a linear-plateau model (Batterham *et al.*, 1990). The regression equation fitted to data in the ascending part of the relationship was:

$$PR = -1.99\ (\pm\ 0.787\ ) + 0.766\ (\pm\ 0.0232)\ x\ DIPI \quad (g/d) \qquad (6.3)$$

Residual SD = 2.459; inflection point at 155.5 g DIPI/d.

The transition from the linear to a plateau phase occurred at 155.5 g DIPI/d with a maximum PR of 117.1 g/d. Figure 6.2 shows that for the genotype used in this experiment there is no advantage in supplying more than 155 g DIP/d between 12 and 30 kg live weight.

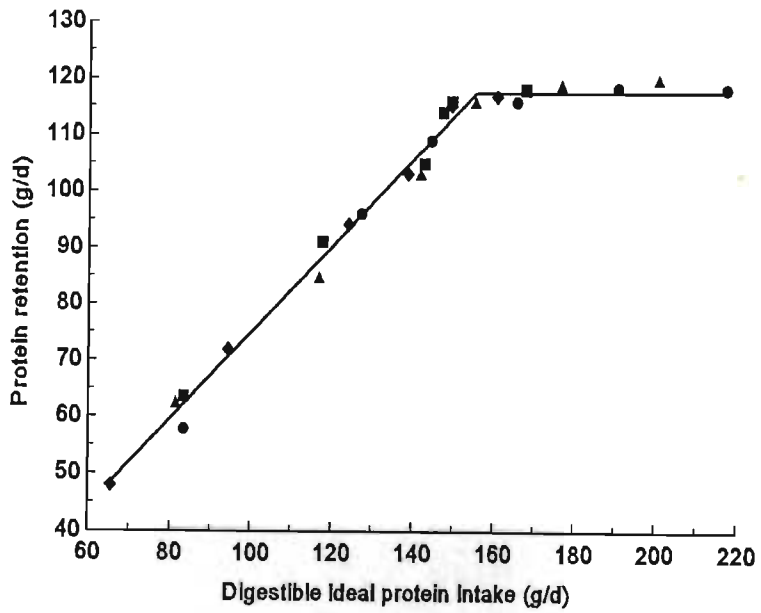


Figure 6.2 The daily rates of protein retention (PR) in pigs grown from 12 kg to 30 kg live weight on diets with different digestible ideal protein contents (DIPI) and housed in four different temperatures; at 18°C (●); 22°C (▲); 26°C (■); 36 C (♦). Solid line (—) represents fitting of linear-plateau model.

The slope of the linear phase (0.766 ± 0.023) provides an estimate of the apparent efficiency of ideal protein utilization. This estimate includes an amount of protein used for maintaining proteinaceous tissue and an amount for depositing new protein tissue. To calculate the net efficiency of ideal protein utilization above maintenance ($e_p$) the following equation of Kyriazakis and Emmans (1992) was used:

$$e_p = PR / (DIPI - MP) \qquad (6.4)$$

where PR = protein retention (g/d)
DIPI = digestible ideal protein intake (g/d)
MP = maintenance protein (4.00 x Protein weight (kg) )

The estimates of $e_p$ are presented in Table 6.8. There was a significant increase ($P < 0.001$) in $e_p$ with increasing ambient temperature and decreasing protein supply. The consequence of an increased demand for energy at low temperatures (18°C and 22 C) was an overconsumption of protein and a reduction in the efficiency of protein utilization. The extent to which $e_p$ was reduced at high protein concentrations decreased with increasing temperature. The lowest $e_p$ was recorded by pigs fed P1 at 18°C (0.593±0.022).

Table 6.8 The efficiencies of protein utilization (ep) of pigs grown between 12 and 30 kg live weight on feeds differing in protein concentration at different temperatures.

| Protein Treatment | 18°C | 22°C | 26°C | 30°C | P means | P SED |
|---|---|---|---|---|---|---|
| P1 | 0.593 | 0.643 | 0.769 | 0.815 | 0.705 | 0.020 |
| P2 | 0.663 | 0.725 | 0.851 | 0.858 | 0.774 | |
| P3 | 0.798 | 0.804 | 0.891 | 0.858 | 0.837 | |
| P4 | 0.870 | 0.801 | 0.828 | 0.874 | 0.843 | |
| P5 | 0.880 | 0.818 | 0.883 | 0.884 | 0.866 | |
| P6 | 0.823 | 0.891 | 0.862 | 0.880 | 0.864 | |
| T means and SED | 0.771 0.016 | 0.780 | 0.847 | 0.862 | | 0.040¶ |
| Significance of: | | | | | | |
| T | *** | | | | | |
| P | *** | | | | | |
| T x P | *** | | | | | |

SED standard error of difference;
¶ SED of values across all treatments
NS not significant; * P < 0.05; ** P < 0.01; *** P < 0.001

Within protein treatments there were no significant differences in $e_p$ between P3, P4, P5 and P6, with an average $e_p$ of 0.853 (±0.015). This result would imply that a maximum or plateau response in $e_p$ has been reached at a DIPI of 152 g/d and a ME:DCP of 102 MJ/kg. This is confirmed by the DIPI estimate of 155.5 g/d, at the inflection point of the linear-plateau model in Figure 6.2.

The implications of a significant T x P interaction are that the improved $e_p$, associated with pigs being fed protein-deficient diets at high temperatures, enabled the animals to reduce the heat increment of protein retention. Similarly, at low temperatures animals can compensate for an inadequate supply of protein by eating more and using the extra heat for maintaining homeothermy

The estimate of $e_p$ of 0.85 at 102 MJ ME/kg DCP is higher than that reported by Kyriazakis and Emmans (1992) of 0.83 at 73 MJ ME/kg DCP. Part of the reason for such a discrepancy is the significant T x P interaction and the subsequent improvement in $e_p$ at high temperatures (26°C and 30°C). Despite this difference the results in this experiment support the idea that $e_p$ has a maximum value when protein intake is limiting and energy supply is adequate (Bikker, 1994). Irrespective of the ambient temperature, at low protein intakes where protein is the limiting nutrient, the efficiency of protein utilization for protein deposition is constant and

independent of protein supply, as previously reported by Batterham *et al.* (1990) and by Bikker (1994). However, supplying protein above the requirement results in a significant decrease in $e_p$, the extent of this decrease being dependent on the ambient temperature. As a corollary, environmental temperature has a marked effect on $e_p$, but only when an excess of protein is supplied in the feed.

### 6.3.2 Determination of maximum heat loss

In the prediction of voluntary food intake one of the factors responsible for constraining intakes, as has been discussed above, is the amount of heat that can be lost by an animal to the environment. In order to improve the accuracy of such predictions, one of the objectives of this research was to derive an equation that would predict the maximum rate of heat loss of a given animal in a given environment.

An animal can be said to be losing the maximum possible amount of heat to the environment (THL = $THL_{max}$) when it is being offered a feed that is adequate in energy but limiting in some nutrient (in this case, protein), when gut capacity is not limiting intake, and where PR is less than PRmax. It can be assumed that gut capacity was not a constraining factor in this experiment. It is imperative therefore, in the determination of $THL_{max}$ that data be used only from treatments in which PR was significantly lower than the maximum PR. Table 6.9 shows which protein treatments were used from within different temperature treatments for this purpose. Appendix 3 provides a complete list of values used in the final regression analysis.

Table 6.9 The protein treatments within different temperature treatments that were used in the regression analysis to calculate maximum total heat loss.

| Temperature Treatment | Protein Treatment |
|---|---|
| 18°C | P5 and P6 |
| 22°C | P4, P5 and P6 |
| 26°C | P4, P5 and P6 |
| 30°C | P3, P4, P5 and P6 |

A further important consideration when predicting $THL_{max}$ from multiple regression analysis, is the choice of variables that should be included in the analysis. The method of selection adopted in this experiment was based on a "cause and effect " approach to maintain the "first principles" approach to modelling, as discussed in Chapter 1. Therefore, it is imperative that the derived function contains only variables that pertain to the current size and state of the animal and are independent of dietary factors, such as energy and protein intakes. The reason for the exclusion of the latter variables is that they are initially responsible for estimating the desired level of food intake and the subsequent amount of heat the animal would like to lose. An independent estimate of the maximum amount of heat the animal could lose is required to ensure that the predicted energy intake does not exceed an amount that would produce heat above that which the animal cannot lose.

According to Eckert, Randall and Augustine (1988) there are three main determinants of the rate of heat loss from the animal to its environment. These include the surface area of the animal, the difference in temperature between the body and the environment, and specific heat conductance of body tissue beneath the skin surface. In addition there is an amount of heat generated from the maintenance of vital organs (including the central nervous system, heart, liver and kidneys) to ensure that the animal survives. As proteinaceous tissue is the main source and site of continued maintenance in all the vital organs, it can be argued that heat produced for maintenance depends on body protein rather than body weight, which includes metabolically "inactive" tissue, such as lipid (Emmans and Fisher, 1986). Therefore, protein weight should be included as a possible variable.

Ambient temperature was included because of its physiological importance within homeotherms in regulating the transfer of heat from the animal to its environment ( Holmes and Close, 1977). However, the extent of the influence of temperature on thermoregulation is dependent on how low or high the ambient temperature is. At low temperatures the non-evaporative or sensible component of total heat loss is the dominant source because non-evaporative heat transfer is largely dependent on the temperature gradient between the animal and its immediate environment. As temperatures increase, the temperature gradient declines. This will result in sensible heat loss becoming less important and evaporative heat loss more so, until the ambient temperature reaches the body temperature (±38°C) at which point sensible heat loss would be zero. Evaporative heat loss varies with water vapour differences rather than temperature differences. Allowing for these physiological considerations, it would make more biological sense to use a transformed temperature value of 38-t (where *t* represents the mean ambient temperature). This scaled temperature variable is more reflective of the regulatory role of temperature than is ambient temperature alone. The greater the difference between the core temperature (38°C) and the ambient temperature the more heat the animal must produce to maintain homeothermy. Similarly, as the gradient diminishes with increased air temperature so less heat is transferred to the environment.

To encompass the effect of surface area on THL, empty body weight (EBWT) was incorporated rather than live weight, as gut-fill would increase the surface area but would not contribute towards heat transfer. As a pig increases in size its surface area also increases and therefore so does the ability to lose heat to the environment by both evaporative and sensible means (Bruce and Clarke, 1979). However, the proportional increase in surface area with increasing body weight is not linear but rather to the power 0.67 (Rubner, 1894). EBWT was scaled (by raising to the power 0.67) to estimate the effect of the size or surface area of the animal on heat loss.

Body lipid was included because of the role of subcutaneous fat in inhibiting the rate of heat transfer from within the animal to the environment. The high insulating properties of subcutaneous fat make it more difficult for the animal to lose heat despite the environmental temperature (Mount, 1979). It can be conjectured that as the animal becomes fatter, as a result of being fed a diet with a low protein to energy ratio, there would be an increase in susceptibility to heat stress and a decreased ability to lose heat.

As the rate of THL was determined between two live weights, it was appropriate for protein and lipid weight to be included as the mean of the starting and finishing protein and lipid weights respectively. It may be argued that the logarithmic mean would be more accurate than the arithmetic mean. However, preliminary analysis of the data suggested that the rates of lipid and protein retention were closer to linear than exponential rates over the period 12 to 30 kg live weight, so the arithmetic mean was used.

The variables initially considered in the regression analyses included temperature, scaled temperature (38-temperature), body lipid weight, body protein weight, EBWT and $EBWT^{0.67}$. Data were analysed by stepwise regression procedures to determine which variables most accurately account for $THL_{max}$. Data that were above or below two standard deviations about the mean were excluded from the analysis. This improved the $R^2$ (adjusted) from 60.1% to 82.0%. It may be argued that this practice could lead to a biased result that would disadvantage the particular treatment from which a replicate had been removed, and that it may result in legitimate data being incorrectly excluded and thus affecting the predicted response in $THL_{max}$. However, only four outliers, out of 48 data points, were excluded. Of these four data points, two were from treatment P5 , one from P4 and one from P6. With such a low exclusion rate it is unlikely that this procedure would introduce any bias for or against any variable. Two replicates from the 18°C temperature treatment and one each from the 26°C and 30°C treatments were removed.

The stepwise procedure excluded the intercept (constant term), temperature and body lipid weight because of their insignificant contribution toward the prediction of $THL_{max}$. The coefficients for the variables 38-T, protein weight and $EBWT^{0.67}$ were significantly different from zero and were therefore included in the equation. The resultant regression equation predicting the maximum amount of heat an animal can lose between 12 and 30 kg live weight is:

$$THL_{max} = 0.346(\pm 0.030) \times (38 - t) + 5.70(\pm 0.820) \times Pt - 1.37(\pm 0.340) \times EBWT^{0.67} \quad (MJ/d) \qquad (6.5)$$

Residual standard deviation = 0.842
where t = ambient temperature (°C)
Pt = body protein weight (kg)
$EBWT^{0.67}$ = Empty body weight raised to the power 0.67 (kg)

In comparing the predicted results from equation 6.5 with those observed in the experiment, comparisons are restricted to treatments in which PR was statistically less than PRmax, as only these treatments were included in the stepwise regression analysis. Comparisons of $THL_{max}$ observed in the experiment and $THL_{max}$ predicted by means of Equation 6.5 are shown both in Table 6.10 and Figure 6.3 .

Table 6.10 Comparison of estimated values of maximum total heat loss from experiment ($THL_{max}$) and predicted from Equation 6.5 ($pTHL_{max}$) and the percent differences.

| Temperature | Protein Treatment[§] | $THL_{max}$ (MJ/d) | SEM | $pTHL_{max}$ (MJ/d) | Difference[¶] (%) |
|---|---|---|---|---|---|
| 18°C | P5 | 14.680 | 0.841 | 14.301 | -2.58 |
| | P6 | 12.107 | 0.961 | 12.076 | -0.26 |
| 22°C | P4 | 12.792 | 0.387 | 13.299 | 3.96 |
| | P5 | 12.760 | 0.550 | 12.755 | -0.04 |
| | P6 | 11.310 | 0.339 | 11.617 | 2.71 |
| 26°C | P4 | 11.845 | 0.459 | 11.604 | -2.03 |
| | P5 | 11.477 | 0.673 | 11.254 | -1.94 |
| | P6 | 10.452 | 0.332 | 10.146 | -2.93 |
| 30°C | P3 | 10.540 | 0.228 | 10.688 | 1.40 |
| | P4 | 10.143 | 0.539 | 9.818 | -3.20 |
| | P5 | 8.977 | 0.892 | 9.069 | 1.02 |
| | P6 | 8.600 | 0.512 | 8.827 | 2.64 |

SEM standard error of mean;
[¶] Difference between predicted and actual = (predicted-actual)/actual*100.
[§] Only protein treatments that had PR values less than maximum PR.

Equation 6.5 produced results that slightly overestimated (< 4.0%) $THL_{max}$ at 22°C and underestimated (< 3.0%) $THL_{max}$ at 26°C in pigs fed protein-deficient diets. However, none of these differences was greater than one standard deviation about the mean.

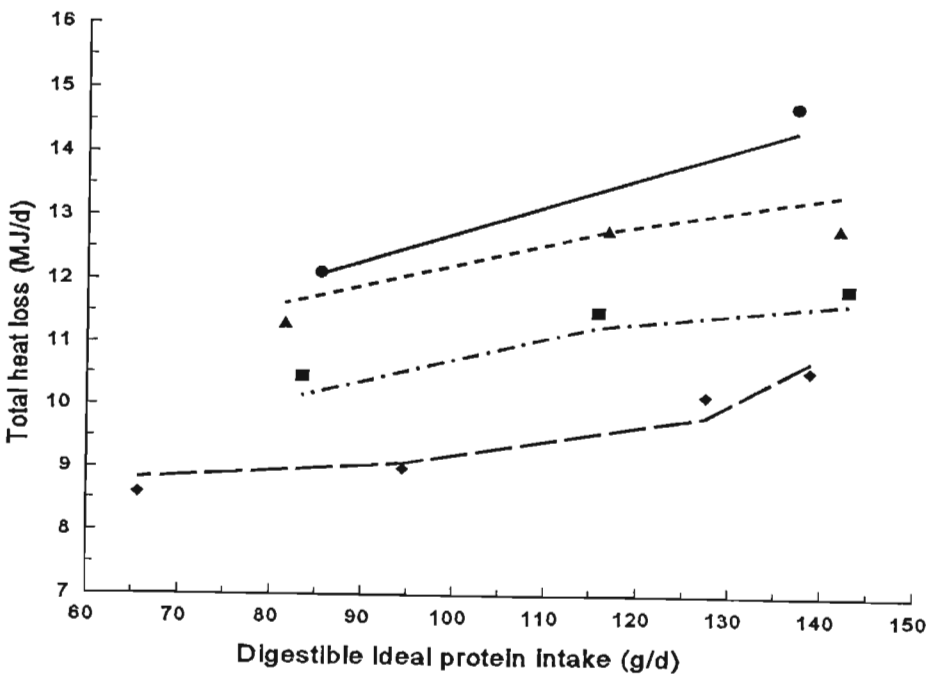


Figure 6.3 Comparison between predicted $THL_{max}$ and the actual THL in growing pigs between 12 and 30 kg live weight. Actual data at 18°C (●); 22°C (▲); 26°C (■); 30°C (♦); Predicted data at 18°C (—); 22°C (--); 26°C (-·-); 30°C (— —).

Central to the theory of voluntary food intake used in the simulation model in this thesis is the role of $THL_{max}$ in constraining the desired food intake and hence reducing the subsequent growth rates below the potential of the animal. The inclusion of Equation 6.5 in the model will improve the accuracy of the estimation of $THL_{max}$ and therefore improve the predicted estimates of food intake, body composition and rate of growth of body tissues. The next section considers in part, how effective the incorporation of Equation 6.5 into the simulation model is in predicting voluntary food intake and rate of growth in growing pigs.

### 6.3.3 Testing the effect of $THL_{max}$ on food intake and growth rates

The model described in Chapter 1 incorporates an algorithm that allows maximum protein retention to be attained only if the subsequent heat production is less than the maximum heat dissipation ability of the animal. To test whether the algorithm was adequate and applicable in predicting food intake, average daily gains and, protein and lipid growth over a range of protein and temperature treatments a series of simulations was conducted and the results compared with actual data from the experiment. Although it is inadvisable to use the same data for both determining the equation (Equation 6.5) and testing the equation there is no better data to test it on. The following results were derived after Equation 6.5 had been included in the simulation model.

#### 6.3.3.1 *Food intake and live weight changes*

The data in Table 6.4 were compared with the simulated results. The results are shown in Table 6.11. A comparison of the response in food intake between the simulation model and the experimental results is illustrated in Figure 6.4.

There were no significant difference between actual and predicted FI, even though the model predicted a 13.1% higher FI on P3 at 30°C than the actual value. Other than this treatment all other differences were less than 8% . The model predicted the same trends as reality and, in particular, the same protein concentration at which maximum food intake was realised. The high level of similarity in the results suggests that the algorithm predicting FI in the model is reasonably accurate over a wide range of dietary protein concentrations and temperatures. Figure 6.2 shows the simulated data following the same trend of increasing intake with decreasing protein content until a maximum whereafter intake declines.

Table 6.11 The simulated results of food intake (sFI), average daily gain (sADG) and feed conversion ratio (sFCR) for pigs grown from 12kg to 30 kg live weight on feeds differing in protein concentration at different temperatures.

| Temperature | Protein Treatment | sFI (kg/d) | Difference¶ (%) | sADG (kg/d) | Difference¶ (%) | sFCR | Difference¶ (%) |
|---|---|---|---|---|---|---|---|
| 18°C | P1 | 1.376 | -0.86 | 0.729 | 1.09 | 1.89 | 0.00 |
| | P2 | 1.357 | -2.51 | 0.726 | -6.20 | 1.87 | 3.89 |
| | P3 | 1.329 | -2.92 | 0.718 | -1.78 | 1.85 | -1.60 |
| | P4 | 1.445 | 2.62 | 0.760 | 14.80* | 1.90 | -11.09 |
| | P5 | 1.530 | 2.27 | 0.701 | 7.85 | 2.18 | -4.80 |
| | P6 | 1.367 | 3.71 | 0.502 | -1.18 | 2.72 | 5.02 |
| 22°C | P1 | 1.221 | -4.76 | 0.729 | -7.02 | 1.67 | 1.83 |
| | P2 | 1.228 | -4.88 | 0.736 | -3.66 | 1.67 | -1.18 |
| | P3 | 1.333 | 3.82 | 0.773 | 7.21 | 1.72 | -3.37 |
| | P4 | 1.475 | 6.81 | 0.759 | 12.48* | 1.95 | -4.88 |
| | P5 | 1.424 | 3.57 | 0.664 | 16.28* | 2.15 | -10.42 |
| | P6 | 1.320 | 2.48 | 0.505 | -2.70 | 2.61 | 4.40 |
| 26°C | P1 | 1.080 | 0.75 | 0.729 | 1.25 | 1.48 | -0.67 |
| | P2 | 1.128 | 3.20 | 0.748 | 3.60 | 1.51 | -0.66 |
| | P3 | 1.312 | 7.72 | 0.795 | 11.00 | 1.65 | 2.94 |
| | P4 | 1.412 | 1.58 | 0.734 | 1.38 | 1.92 | -0.78 |
| | P5 | 1.384 | 0.07 | 0.670 | 0.00 | 2.06 | 0.00 |
| | P6 | 1.281 | -2.12 | 0.522 | -8.90 | 2.47 | 8.69 |
| 30°C | P1 | 1.043 | 1.56 | 0.731 | 10.26 | 1.43 | -8.04 |
| | P2 | 1.159 | 6.04 | 0.767 | 19.66* | 1.51 | -11.70 |
| | P3 | 1.297 | 13.08 | 0.758 | 19.75* | 1.71 | -5.52 |
| | P4 | 1.270 | 5.04 | 0.674 | 5.81 | 1.89 | -0.21 |
| | P5 | 1.184 | 6.57 | 0.572 | 1.06 | 2.07 | 5.08 |
| | P6 | 1.089 | 4.91 | 0.423 | 7.63 | 2.57 | -3.35 |
| SEM | | | 0.057 | | 0.027 | | 0.086 |
| Means of: | | | | | | | |
| Temperature: | | | | | | | |
| 18°C | | 1.401 | | 0.689 | | 2.07 | |
| 22°C | | 1.334 | | 0.694 | | 1.96 | |
| 26°C | | 1.266 | | 0.700 | | 1.85 | |
| 30°C | | 1.174 | | 0.654** | | 1.86 | |
| SEM | | | 0.023 | | 0.011 | | 0.035 |
| Protein: | | | | | | | |
| P1 | | 1.180 | | 0.729 | | 1.62 | |
| P2 | | 1.218 | | 0.744 | | 1.64 | |
| P3 | | 1.318 | | 0.761* | | 1.73 | |
| P4 | | 1.401 | | 0.732* | | 1.92 | |
| P5 | | 1.381 | | 0.652 | | 2.12 | |
| P6 | | 1.264 | | 0.448 | | 2.59 | |
| SEM | | | 0.029 | | 0.013 | | 0.043 |

SEM Standard error of the mean from actual data
¶ Difference = (predicted-actual)/actual*100. The t-test (predicted-actual)/SEM with 3 df was used to test for significance.
* P < 0.05; ** P < 0.01; *** P < 0.001

Unlike the comparison of FI , the ADG comparisons were less accurate. Usually the model overestimated ADG. The reason for the significant differences between model and reality was the overestimation of daily lipid and moisture retention. This was particularly noticeable at high temperatures and in the marginally deficient protein diets (P3 and P4). These comparative results suggest that the allometric coefficients used in the model to describe the relationship between body protein and lipid, and body protein and moisture may be too high. However, the values used in the model are based on data collected from several experiments

and therefore it would be unreasonable to discard them because of the results of one experiment.

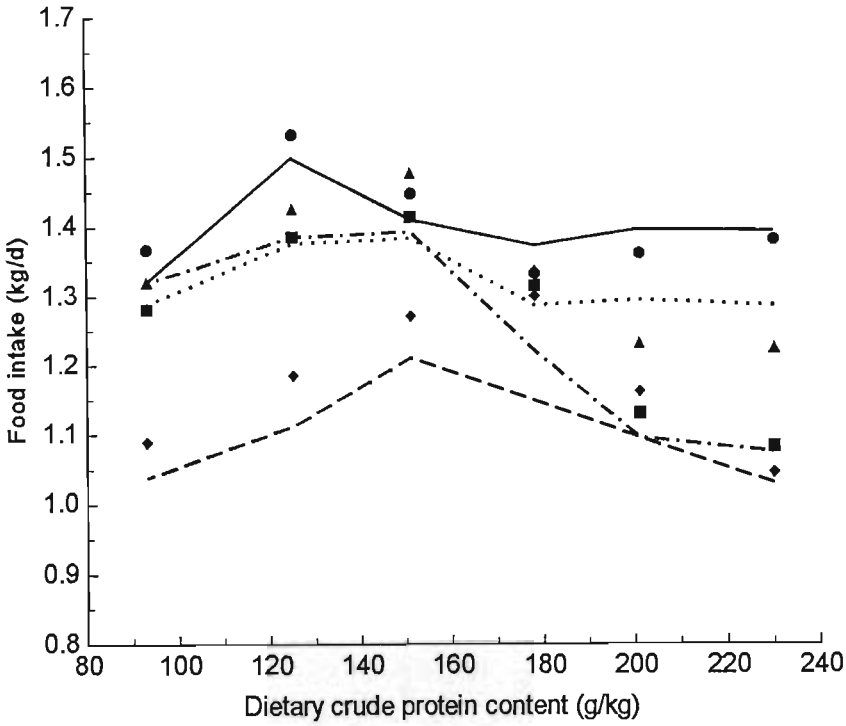


Figure 6.4 Comparing the simulated and actual response in food intake to dietary protein content in pigs grown from 12 kg to 30 kg live weight in four different temperatures. Actual data at 18°C (——); 22°C (· · · ·);26°C (- · -); 30°C (— — —); Simulated data at 18°C (●); 22°C (▲); 26°C (■); 30°C (♦).

There were no significant differences between sFCR and actual FCR. The greatest difference occurred on P2 at 30°C (-11.7%) but this result was not significant. The reason for no significant differences in FCR compared with the ADG results is that the effects of over- and underestimations of sADG were diminished or nullified by the over- and underestimation of sFI.

It is apparent from the comparison between actual and predicted results, in Table 6.11 and Figure 6.4, that the theory of voluntary food intake used in the model provides a good description of the response in growth and food intake to decreasing concentrations of dietary protein over a wide range of temperatures.

6.3.3.2 *Protein and lipid retention*

The results of the comparison between simulated protein (sPR) and lipid (sLR) growth rates and actual rates are shown in Table 6.12.

Table 6.12 The predicted daily rates of protein (sPR) and lipid (sLR) depositions in pigs grown between 12kg and 30 kg live weight on feeds differing in protein concentration at different temperatures, and the differences (%) between actual and predicted.

| Temperature | Protein Treatment | sPR (g/d) | Difference¶ (%) | sLR (g/d) | Difference¶ (%) |
|---|---|---|---|---|---|
| 18°C | P1 | 120 | 1.69 | 92 | -7.07 |
| | P2 | 119 | 0.85 | 94 | -12.96 |
| | P3 | 117 | 0.86 | 96 | -14.28 |
| | P4 | 115 | 5.50 | 141 | 11.90 |
| | P5 | 98 | 2.08 | 175 | 8.70 |
| | P6 | 62 | 6.89 | 162 | -1.22 |
| 22°C | P1 | 120 | 0.84 | 92 | -4.17 |
| | P2 | 120 | 0.84 | 98 | -10.09 |
| | P3 | 117 | 0.86 | 145 | 28.32 |
| | P4 | 108 | 4.85 | 179 | 43.20** |
| | P5 | 91 | 7.06 | 175 | 28.68* |
| | P6 | 62 | 0.00 | 169 | 9.74 |
| 26°C | P1 | 120 | 1.69 | 92 | 17.95 |
| | P2 | 119 | 2.59 | 115 | 22.34 |
| | P3 | 117 | 2.63 | 166 | 36.07* |
| | P4 | 104 | -0.95 | 179 | 13.29 |
| | P5 | 92 | 1.10 | 178 | 8.54 |
| | P6 | 65 | 1.56 | 169 | -12.44 |
| 30°C | P1 | 120 | 2.56 | 94 | 28.06 |
| | P2 | 120 | 4.34 | 127 | 30.93* |
| | P3 | 109 | 5.83 | 175 | 76.77*** |
| | P4 | 93 | -1.06 | 176 | 17.33 |
| | P5 | 75 | 4.17 | 168 | 15.86 |
| | P6 | 47 | -2.08 | 164 | 13.89 |
| SEM | | | 3.435 | | 8.210 |
| Means of: | | | | | |
| Temperature: | | | | | |
| 18°C | | 105 | | 127 | |
| 22°C | | 103 | | 143** | |
| 26°C | | 103 | | 149* | |
| 30°C | | 94 | | 151*** | |
| SEM | | | 1.402 | | 3.352 |
| Protein: | | | | | |
| P1 | | 120 | | 93 | |
| P2 | | 120 | | 109 | |
| P3 | | 115 | | 146** | |
| P4 | | 105 | | 169** | |
| P5 | | 89 | | 174* | |
| P6 | | 59 | | 166 | |
| SEM | | | 1.718 | | 4.105 |

SEM Standard error of the mean from actual data

¶ Difference = (predicted-actual)/actual*100. The t-test (predicted-actual)/SEM with 3 df was used to test for significance.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

There were no significant differences between sPR and actual protein growth (PR) and what differences there were between sPR and PR were less than 8%. Given that within pigs there is an 8 - 10% variation in the rate of protein retention and the coefficient of variation (CV) of PR was 23%, the results suggest that the algorithm used to describe protein growth in the model is accurate over a wide range of dietary protein concentrations and environmental temperatures. However, lipid growth was not as accurately predicted, particularly at marginally

deficient protein concentrations (P3 and P4). This can be attributed to the underestimation of how much heat was lost and the high variability in actual LR values (27% CV).

### 6.3.3.3 *Heat loss*

The results of the comparison between simulated THL and actual THL are shown in Table 6.13 and Figure 6.4.

Table 6.13 Simulated total heat loss (sTHL) (MJ/d) and the differences between simulated and actual THL for pigs grown between 12 and 30 kg live weight on feeds differing in protein concentration (P) at different temperatures(T).

| Temperature | Protein Treatment | pTHL (MJ/d) | Difference¶ (%) |
|---|---|---|---|
| 18°C | P1 | 13.399 | 2.36 |
| | P2 | 13.252 | 2.25 |
| | P3 | 12.947 | 1.54 |
| | P4 | 13.294 | 1.10 |
| | P5 | 13.467 | 1.10 |
| | P6 | 12.559 | 6.89 |
| 22°C | P1 | 11.230 | -5.79 |
| | P2 | 11.251 | -0.68 |
| | P3 | 11.309 | -0.91 |
| | P4 | 12.362 | -3.36 |
| | P5 | 12.158 | -4.72 |
| | P6 | 11.616 | 2.71 |
| 26°C | P1 | 9.264 | -4.05 |
| | P2 | 9.203 | -2.38 |
| | P3 | 10.182 | -2.45 |
| | P4 | 11.345 | -4.22 |
| | P5 | 11.289 | -4.31 |
| | P6 | 10.704 | 2.41 |
| 30°C | P1 | 8.667 | -5.72 |
| | P2 | 9.115 | 2.51 |
| | P3 | 9.646 | -8.48 |
| | P4 | 9.540 | -1.90 |
| | P5 | 9.099 | 1.36 |
| | P6 | 8.550 | -0.58 |
| SEM | | | 0.606 |
| Means of: | | | |
| Temperature: | | | |
| 18°C | | 13.151 | |
| 22°C | | 11.650 | |
| 26°C | | 10.332 | |
| 30°C | | 9.101 | |
| SEM | | | 0.247 |
| Protein: | | | |
| P1 | | 10.641 | |
| P2 | | 10.710 | |
| P3 | | 11.021 | |
| P4 | | 11.638 | |
| P5 | | 11.499 | |
| P6 | | 10.862 | |
| SEM | | | 0.303 |

SEM Standard error of the mean from actual data
¶ Difference = (predicted-actual)/actual*100
* P < 0.05; ** P < 0.01; *** P < 0.001 The t-test (predicted-actual)/SEM with 3 df was used to test for significance.

Comparisons between simulated and actual THL shows marked similarities, particularly at the highest and lowest temperature treatments (Figure 6.4). There were no significant differences between sTHL and THL across all treatments despite the result from pigs fed P3 at 30°C where actual THL was inexplicably high (10.540 ± 0.456 MJ/d). This result is, on average, 10% higher than P2 and P4 at 30°C.

A possible cause for such a high THL is the low rate of lipid deposition and therefore a marked reduction in the energy retained. The consequence of a low energy retention is an overestimation of heat loss. Incomplete extraction of lipid in the chemical analysis of the carcass samples would result in a low lipid concentration of the empty body weight and consequential reduction in the estimate of LR. At 22°C and 26°C the model underestimated, by no more than 4.7%, the amount of heat lost on low protein diets (P4 and P5). This difference was not statistically significant.

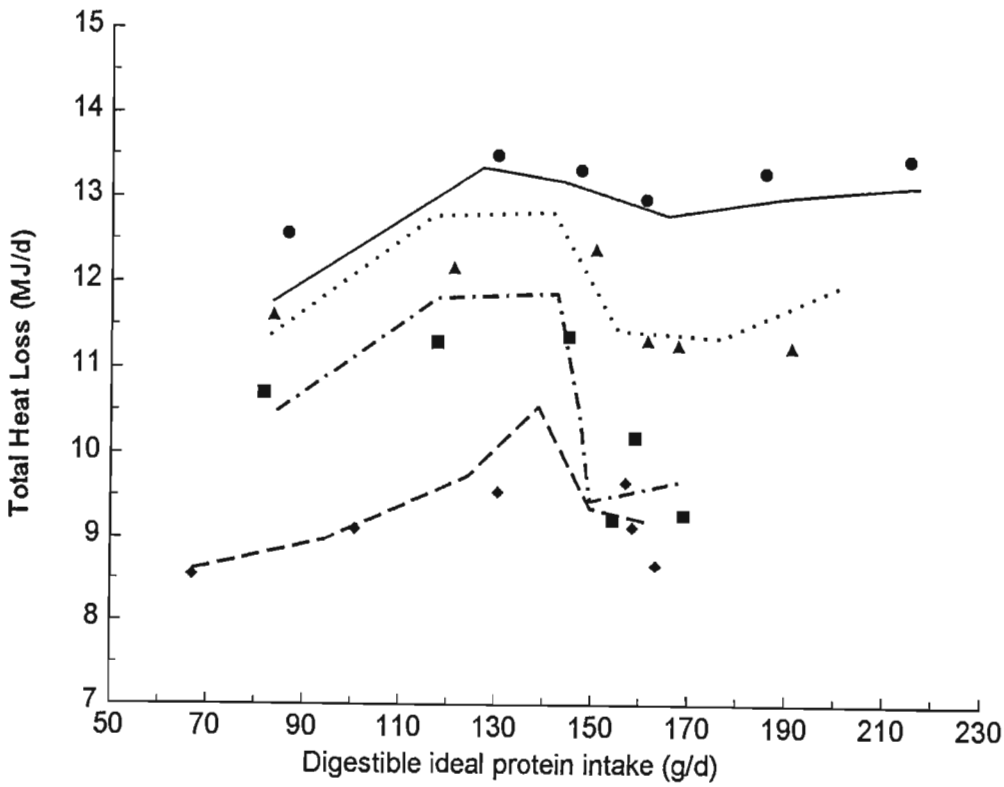


Figure 6.4 Comparing the simulated and actual response in total heat loss to dietary protein content in pigs grown from 12 kg to 30 kg live weight in four different temperatures. Actual data at 18°C (—); 22°C (····); 26°C (-··-); 30°C(— —) ; Simulated data at 18°C (●); 22°C (▲); 26°C (■); 30°C (♦).

### 6.4 Conclusion

Pigs fed a diet deficient in protein will attempt to maintain protein intake as the protein concentration declines until a point is reached when the animal can no longer compensate and food intake will decline. The extent of the compensation will depend on the maximum amount of heat the animal can lose. The lowest dietary protein concentration in which a pig can still maintain the maximum daily protein retention will depend on the ambient temperature. The lower the temperature the more heat can be lost and therefore, the lower the dietary protein level.

An independent estimate of maximum THL is required to limit the maximum food intake and growth rate of a young growing pig. Where such an estimate is included in a model it is possible to achieve high levels of accuracy in predicting voluntary food intake, protein retention and total heat loss in animals fed protein-deficient diets.

## SUMMARY

Predicting the performance of animals is a general problem in animal production and numerous approaches have been made to model the growth of pigs. This thesis explored new concepts and components for a simulation model to predict feed intake, amino acid requirements and body composition changes over time on the basis of the inherent potential protein growth rate of pigs varying in genotype. The potential protein growth rate of the animal is predicted each day based on its genotype and state, from which the potential growth rate of the other chemical components can be predicted and hence the nutrient requirements can be calculated. By considering the potential growth rate, the nutrient requirements, the nutrient supply (the composition of the feed) and the environment simultaneously, the constrained food intake can be predicted. If this is less than the desired food intake, the actual growth rate will be less than the potential growth rate. In either case, the growth rate of each of the chemical components can be predicted for that day. This final state of the animal at the end of the day becomes the initial state on the next day, and the process is repeated.

Part of the solution to the problem of predicting growth is an adequate description of the animal. Numerous methods have been employed to describe the genotype and there is an increasing demand for variables that will provide an adequate description of the animal. However a large number of parameters is undesirable as it is difficult and sometimes impossible to obtain such information from data pertaining to current pig populations. This thesis presented a simple approach to describe the potential rate of growth of body protein using a Gompertz equation, and to predict the growth of the other chemical components of the body using allometry. An experimental procedure was proposed that will predict values for the parameters of the Gompertz function under non-limiting conditions. The genetic worth of pigs can be estimated by means of three genetic parameters viz. mature body protein weight (Pm), the rate of maturing (B) and an inherent fat content, defined in terms of a lipid to protein ratio at maturity (LPRm). These three inherent growth characteristics have been shown to describe the potential growth rate of animals. It is recommended that these parameters become part of any system that describes the genetic ability of a breed or strain of pig. Already some simulation models rely on an estimate of Pm to describe the type of genotype used in the model (Moughan *et al.*, 1987 and Pomar *et al.*, 1991).

The ability to define a genotype in terms of a few meaningful biological characteristics is desirable for a number of reasons. Firstly, if the nature of the their distribution is known then deterministic models can readily be transformed into population models. Population models are more accurate and more useful in estimating nutrient requirements than models based on the average individual.

Secondly, a more definitive strategy for the genetic selection of improved strains of pigs would result, as would a more accurate means of predicting growth performances.

The genetic parameters of individuals will vary within a group or population of animals. It is this variation between individuals that allows genetic selection to be made. To quantify and qualify the relationships between these parameters is important as well as being difficult. It is important that the nature of the distribution of variation is known so as to quantify the spread or standard deviation about the mean of the population. All pig nutrition models to date predict growth responses of either an individual animal or the average animal of a given population over time. Translating the predicted nutrient requirements from the average animal to the population introduces a number of errors as the cause-and-effect response of the average animal is different to the population response. To overcome the problem of estimating the requirements for a given population using models it is necessary to simulate a number of individuals representative of a population and then average these results. This approach however, requires a knowledge of those animal characteristics that vary between individuals and the nature of their distribution. As no data exists from which the nature of the distribution of B or a scaled version of B ($B^*$), Pm and LPRm can be estimated for pigs of different strains and sexes, and due to the impracticality of determining this variability by experimentation, the proposed model was used to estimate the variations within each parameter.

In addition this thesis quantified the subsequent effects these distributions have on the genetic variability of average daily gains (ADG) and daily food intake (FI) over a live weight range of 20 to 90kg. Comparisons were made between the genetic variation determined by modelling and those published in the literature. The results indicated a coefficient of variation for $B^*$, Pm and LPRm of between 1-3%, 5-10% and 10% respectively. An increase in the variability of all three parameters resulted in an increase in the variation in ADG whilst only an increase in the variation of $B^*$ and LPRm affected the distribution of FI.

One of the problems associated with models that predict voluntary food intake is the relationship between desired food intake, protein and lipid retention, and heat loss. This is particulalry relevant when pigs are fed rations containing low protein:energy ratios in warm to hot environments. To overcome this problem an experiment was conducted to investigate the effects that protein-deficient diets have on food intake and growth rates, in different temperatures and to determine the maximum heat an animal can lose. Pigs that were fed a protein-deficient attempedt to maintain maximum protein retention by eating more until a protein concentration was reached when tha naimal could no longer compensate and food intake and protein retention declined. The

ability to compensate depended on the maximum amount of heat the animal could lose. Therefore, the lowest dietary protein concentration in which a pig can maintain its maximum daily protein retention will depend on the ambient temperature. The lower the temperature the more heat the pig can dissipate and therefore, the lower the dietary protein level at which maximum protein deposition can occur.

An independent estimate of maximum THL was determined to limit the maximum food intake and growth rate of a young growing pig. Inclusion of such an estimate in the model resulted in very close estimates of voluntary food intake, protein retention and total heat loss in animals fed a range of protein diets.

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APPENDIX 1

Treatment 1: B*=1% Pmat=5% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.066 | 0.8264 | 296 | 21.938 | 351 | 31.684 |
| 42 | 10.236 | 0.9707 | 354 | 23.965 | 441 | 41.293 |
| 49 | 12.910 | 1.1351 | 415 | 25.710 | 557 | 49.009 |
| 56 | 16.022 | 1.3225 | 481 | 27.277 | 688 | 60.526 |
| 63 | 19.604 | 1.5099 | 548 | 28.502 | 838 | 68.884 |
| 70 | 23.638 | 1.6913 | 616 | 29.566 | 1002 | 77.598 |
| 77 | 28.128 | 1.8843 | 683 | 30.500 | 1178 | 86.079 |
| 84 | 33.100 | 2.1012 | 748 | 31.501 | 1363 | 94.477 |
| 91 | 38.546 | 2.3131 | 811 | 32.635 | 1553 | 102.829 |
| 98 | 44.376 | 2.4978 | 868 | 34.099 | 1744 | 111.234 |
| 105 | 50.604 | 2.6798 | 920 | 36.015 | 1933 | 119.695 |
| 112 | 57.192 | 2.8381 | 966 | 38.339 | 2115 | 128.374 |
| 119 | 64.100 | 3.0569 | 1005 | 41.114 | 2289 | 135.952 |
| 126 | 71.218 | 3.2729 | 1036 | 44.230 | 2449 | 145.212 |
| 133 | 78.562 | 3.5042 | 1060 | 47.486 | 2594 | 154.870 |
| 140 | 85.412 | 3.2140 | 1070 | 47.743 | 2702 | 148.721 |
| 147 | 88.775 | 1.8875 | 1044 | 45.683 | 2676 | 131.510 |

Treatment 2: B*=1% Pmat=5% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.076 | 0.8876 | 295 | 23.592 | 351 | 34.160 |
| 42 | 10.264 | 1.0567 | 353 | 25.809 | 440 | 44.462 |
| 49 | 12.890 | 1.2218 | 415 | 27.857 | 557 | 53.271 |
| 56 | 16.010 | 1.4374 | 480 | 29.730 | 687 | 66.618 |
| 63 | 19.566 | 1.6269 | 548 | 31.511 | 837 | 77.205 |
| 70 | 23.596 | 1.8109 | 616 | 33.292 | 1001 | 89.695 |
| 77 | 28.114 | 2.0340 | 683 | 35.197 | 1177 | 102.170 |
| 84 | 33.078 | 2.2870 | 748 | 37.408 | 1362 | 116.072 |
| 91 | 38.526 | 2.4999 | 811 | 40.097 | 1552 | 130.369 |
| 98 | 44.378 | 2.7368 | 868 | 43.239 | 1743 | 145.937 |
| 105 | 50.610 | 3.0153 | 921 | 46.940 | 1932 | 161.046 |
| 112 | 57.200 | 3.2535 | 967 | 51.034 | 2115 | 177.754 |
| 119 | 64.102 | 3.5277 | 1006 | 55.468 | 2290 | 190.237 |
| 126 | 71.226 | 3.8472 | 1037 | 60.042 | 2451 | 206.875 |
| 133 | 78.492 | 4.1079 | 1060 | 63.687 | 2592 | 223.010 |
| 140 | 84.859 | 3.5370 | 1064 | 60.809 | 2676 | 210.780 |
| 147 | 88.231 | 2.1228 | 1023 | 51.505 | 2604 | 179.055 |

Treatment 3: B* = 1% Pmat = 5% LPmat = 20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.056 | 0.8980 | 295 | 23.350 | 341 | 36.290 |
| 42 | 10.234 | 1.0185 | 353 | 25.776 | 440 | 45.330 |
| 49 | 12.910 | 1.2020 | 415 | 28.086 | 553 | 59.148 |
| 56 | 16.008 | 1.4014 | 480 | 30.438 | 687 | 71.230 |
| 63 | 19.542 | 1.5929 | 548 | 32.931 | 837 | 85.659 |
| 70 | 23.612 | 1.8199 | 616 | 35.662 | 1002 | 101.338 |
| 77 | 28.078 | 2.0249 | 684 | 38.877 | 1178 | 119.147 |
| 84 | 33.100 | 2.3110 | 749 | 42.595 | 1364 | 138.396 |
| 91 | 38.514 | 2.5618 | 812 | 47.016 | 1555 | 159.555 |
| 98 | 44.394 | 2.8508 | 870 | 51.971 | 1748 | 181.457 |
| 105 | 50.668 | 3.1461 | 923 | 57.500 | 1938 | 204.641 |
| 112 | 57.226 | 3.4697 | 969 | 63.402 | 2123 | 226.824 |
| 119 | 64.160 | 3.8439 | 1009 | 69.508 | 2297 | 250.301 |
| 126 | 71.332 | 4.2598 | 1041 | 75.558 | 2463 | 266.859 |
| 133 | 78.688 | 4.6894 | 1065 | 81.483 | 2611 | 288.011 |
| 140 | 86.124 | 5.1184 | 1080 | 86.169 | 2735 | 311.638 |
| 147 | 92.821 | 4.9260 | 1078 | 84.714 | 2804 | 301.424 |
| 154 | 96.312 | 3.5008 | 1026 | 68.139 | 2692 | 224.531 |
| 161 | 98.033 | 2.7677 | 947 | 61.783 | 2509 | 191.051 |
| 168 | 97.500 | 2.9496 | 830 | 53.124 | 2210 | 150.556 |

Treatment 4: B* = 1% Pmat = 10% LPmat = 10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.053 | 0.8355 | 295 | 21.829 | 353 | 34.207 |
| 42 | 10.207 | 0.9519 | 353 | 23.808 | 443 | 45.071 |
| 49 | 12.867 | 1.1293 | 414 | 25.635 | 560 | 53.164 |
| 56 | 15.980 | 1.3056 | 479 | 27.502 | 690 | 65.081 |
| 63 | 19.524 | 1.4931 | 545 | 29.632 | 839 | 72.914 |
| 70 | 23.540 | 1.6910 | 613 | 32.333 | 1001 | 81.444 |
| 77 | 28.057 | 1.8961 | 679 | 35.946 | 1176 | 88.567 |
| 84 | 32.996 | 2.1232 | 744 | 40.682 | 1359 | 95.735 |
| 91 | 38.382 | 2.3389 | 805 | 46.784 | 1547 | 103.446 |
| 98 | 44.172 | 2.6238 | 862 | 54.098 | 1735 | 112.622 |
| 105 | 50.362 | 2.9067 | 913 | 62.527 | 1921 | 123.998 |
| 112 | 56.916 | 3.2535 | 958 | 71.797 | 2100 | 138.320 |
| 119 | 63.722 | 3.6771 | 996 | 81.630 | 2271 | 154.118 |
| 126 | 70.783 | 4.1303 | 1026 | 91.722 | 2428 | 174.170 |
| 133 | 77.979 | 4.5964 | 1048 | 101.085 | 2568 | 196.073 |
| 140 | 84.095 | 4.1813 | 1042 | 98.883 | 2647 | 187.546 |

Treatment 5: B* = 1% Pmat = 10% LPmat = 15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.120 | 0.8527 | 297 | 22.138 | 345 | 36.210 |
| 42 | 10.314 | 0.9743 | 355 | 24.202 | 444 | 44.521 |
| 49 | 12.982 | 1.1420 | 417 | 26.121 | 558 | 56.952 |
| 56 | 16.110 | 1.3317 | 482 | 27.986 | 692 | 66.939 |
| 63 | 19.662 | 1.5140 | 550 | 29.995 | 842 | 78.421 |
| 70 | 23.724 | 1.7326 | 618 | 32.252 | 1007 | 90.108 |
| 77 | 28.248 | 1.9292 | 685 | 35.068 | 1184 | 102.657 |
| 84 | 33.236 | 2.1451 | 750 | 38.592 | 1369 | 116.148 |
| 91 | 38.684 | 2.3765 | 813 | 42.963 | 1559 | 130.670 |
| 98 | 44.558 | 2.6124 | 870 | 48.197 | 1751 | 146.226 |
| 105 | 50.820 | 2.8852 | 923 | 54.214 | 1940 | 162.898 |
| 112 | 57.410 | 3.1960 | 969 | 60.847 | 2124 | 179.901 |
| 119 | 64.326 | 3.4998 | 1008 | 67.866 | 2297 | 198.396 |
| 126 | 71.470 | 3.8981 | 1039 | 75.112 | 2460 | 213.100 |
| 133 | 78.812 | 4.3367 | 1063 | 82.314 | 2606 | 231.762 |
| 140 | 86.265 | 4.7031 | 1079 | 88.693 | 2731 | 251.578 |

Treatment 6: B* = 1% Pmat = 10% LPmat = 20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.740 | 0.9198 | 311 | 23.895 | 401 | 46.982 |
| 42 | 11.020 | 1.0909 | 366 | 25.988 | 506 | 60.692 |
| 49 | 13.762 | 1.2265 | 424 | 28.156 | 630 | 72.645 |
| 56 | 16.912 | 1.4465 | 483 | 30.494 | 767 | 86.907 |
| 63 | 20.444 | 1.6298 | 543 | 33.281 | 918 | 101.446 |
| 70 | 24.446 | 1.8444 | 601 | 36.729 | 1078 | 117.756 |
| 77 | 28.812 | 2.0759 | 657 | 40.920 | 1244 | 134.667 |
| 84 | 33.588 | 2.3197 | 709 | 45.944 | 1413 | 153.243 |
| 91 | 38.690 | 2.5968 | 756 | 51.758 | 1581 | 171.520 |
| 98 | 44.126 | 2.8808 | 798 | 58.168 | 1744 | 191.731 |
| 105 | 49.826 | 3.2405 | 834 | 64.971 | 1901 | 208.652 |
| 112 | 55.712 | 3.5876 | 862 | 71.953 | 2044 | 228.762 |
| 119 | 61.814 | 4.0104 | 884 | 78.865 | 2183 | 237.517 |
| 126 | 68.052 | 4.4834 | 898 | 85.515 | 2299 | 254.589 |
| 133 | 74.382 | 4.9913 | 906 | 91.736 | 2386 | 287.240 |
| 140 | 80.210 | 5.0916 | 900 | 92.188 | 2443 | 280.015 |
| 147 | 84.223 | 4.3542 | 861 | 82.431 | 2401 | 238.977 |

Treatment 7: B*=1% Pmat=15% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.786 | 0.9327 | 312 | 23.480 | 403 | 46.090 |
| 42 | 11.058 | 1.0923 | 367 | 25.156 | 508 | 57.042 |
| 49 | 13.816 | 1.2382 | 424 | 26.774 | 632 | 64.950 |
| 56 | 16.970 | 1.4245 | 483 | 28.640 | 769 | 72.759 |
| 63 | 20.534 | 1.6353 | 542 | 31.140 | 918 | 79.503 |
| 70 | 24.500 | 1.8365 | 600 | 34.555 | 1076 | 85.787 |
| 77 | 28.850 | 2.0277 | 655 | 39.174 | 1240 | 92.265 |
| 84 | 33.580 | 2.2551 | 706 | 45.111 | 1407 | 99.765 |
| 91 | 38.670 | 2.5088 | 752 | 52.210 | 1571 | 109.183 |
| 98 | 44.090 | 2.7967 | 793 | 60.226 | 1731 | 121.312 |
| 105 | 49.720 | 3.1300 | 828 | 68.988 | 1883 | 136.349 |
| 112 | 55.624 | 3.5122 | 856 | 78.082 | 2024 | 154.464 |
| 119 | 61.690 | 3.9787 | 877 | 87.262 | 2157 | 167.146 |
| 126 | 67.862 | 4.5131 | 890 | 96.209 | 2272 | 187.136 |
| 133 | 74.116 | 5.0812 | 898 | 104.729 | 2361 | 220.586 |
| 140 | 80.055 | 5.4202 | 893 | 108.932 | 2429 | 232.076 |
| 147 | 83.756 | 4.7792 | 843 | 97.520 | 2392 | 208.182 |

Treatment 8: B*=1% Pmat=15% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.080 | 0.8895 | 296 | 23.385 | 353 | 36.590 |
| 42 | 10.262 | 1.0428 | 354 | 25.690 | 443 | 48.221 |
| 49 | 12.950 | 1.2126 | 415 | 27.983 | 560 | 57.738 |
| 56 | 16.038 | 1.4030 | 480 | 30.429 | 689 | 72.018 |
| 63 | 19.598 | 1.6425 | 547 | 33.231 | 838 | 82.594 |
| 70 | 23.632 | 1.8285 | 614 | 36.689 | 1000 | 95.114 |
| 77 | 28.116 | 2.0579 | 681 | 41.075 | 1175 | 106.852 |
| 84 | 33.092 | 2.3372 | 746 | 46.619 | 1357 | 119.817 |
| 91 | 38.492 | 2.6283 | 807 | 53.391 | 1545 | 133.565 |
| 98 | 44.322 | 2.9332 | 864 | 61.336 | 1733 | 149.274 |
| 105 | 50.536 | 3.2922 | 916 | 70.317 | 1919 | 166.071 |
| 112 | 57.050 | 3.7115 | 961 | 80.078 | 2099 | 186.027 |
| 119 | 63.918 | 4.1946 | 999 | 90.300 | 2271 | 203.327 |
| 126 | 70.942 | 4.6260 | 1029 | 99.636 | 2427 | 223.467 |
| 133 | 78.137 | 5.1543 | 1050 | 108.525 | 2563 | 247.254 |
| 140 | 83.650 | 4.5424 | 1035 | 103.498 | 2614 | 228.600 |

Treatment 9: B*=1% Pmat=15% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.106 | 0.8901 | 295 | 23.771 | 346 | 40.531 |
| 42 | 10.286 | 1.0538 | 352 | 26.184 | 446 | 50.126 |
| 49 | 12.972 | 1.2451 | 414 | 28.597 | 559 | 64.690 |
| 56 | 16.038 | 1.4299 | 479 | 31.228 | 694 | 76.657 |
| 63 | 19.574 | 1.6401 | 546 | 34.300 | 845 | 90.930 |
| 70 | 23.604 | 1.8542 | 614 | 38.142 | 1013 | 105.375 |
| 77 | 28.116 | 2.1193 | 683 | 43.045 | 1192 | 121.633 |
| 84 | 33.096 | 2.3618 | 750 | 49.258 | 1382 | 139.347 |
| 91 | 38.548 | 2.7015 | 814 | 56.771 | 1578 | 159.372 |
| 98 | 44.426 | 3.0058 | 874 | 65.621 | 1777 | 181.207 |
| 105 | 50.702 | 3.4142 | 929 | 75.569 | 1974 | 205.905 |
| 112 | 57.346 | 3.8595 | 978 | 86.355 | 2167 | 230.867 |
| 119 | 64.356 | 4.3849 | 1021 | 97.746 | 2350 | 259.796 |
| 126 | 71.588 | 5.0009 | 1056 | 109.395 | 2524 | 284.523 |
| 133 | 78.933 | 5.5420 | 1081 | 118.748 | 2674 | 307.875 |
| 140 | 84.080 | 4.8678 | 1055 | 107.259 | 2688 | 280.024 |
| 147 | 86.242 | 3.9192 | 975 | 97.426 | 2557 | 245.862 |

Treatment 10: B*=2% Pmat=5% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.192 | 0.8583 | 297 | 24.190 | 347 | 36.352 |
| 42 | 10.400 | 1.0537 | 355 | 26.995 | 447 | 44.734 |
| 49 | 13.062 | 1.2054 | 417 | 29.705 | 562 | 57.337 |
| 56 | 16.182 | 1.4258 | 482 | 32.384 | 698 | 67.492 |
| 63 | 19.746 | 1.6477 | 550 | 34.888 | 851 | 78.842 |
| 70 | 23.802 | 1.8756 | 619 | 37.289 | 1019 | 90.115 |
| 77 | 28.352 | 2.1045 | 688 | 39.598 | 1201 | 101.712 |
| 84 | 33.386 | 2.3875 | 755 | 41.761 | 1392 | 113.397 |
| 91 | 38.842 | 2.6418 | 820 | 43.922 | 1590 | 125.083 |
| 98 | 44.782 | 2.9037 | 880 | 46.048 | 1790 | 136.631 |
| 105 | 51.118 | 3.1825 | 936 | 48.228 | 1988 | 147.955 |
| 112 | 57.822 | 3.4535 | 985 | 50.527 | 2181 | 158.975 |
| 119 | 64.830 | 3.7801 | 1028 | 52.941 | 2366 | 169.588 |
| 126 | 72.166 | 4.0634 | 1063 | 55.423 | 2538 | 179.345 |
| 133 | 79.539 | 4.1630 | 1089 | 56.424 | 2692 | 184.408 |
| 140 | 85.720 | 3.4476 | 1095 | 53.430 | 2781 | 169.785 |

Treatment 11: B*=2% Pmat=5% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.076 | 0.8364 | 296 | 22.953 | 351 | 32.728 |
| 42 | 10.246 | 1.0037 | 353 | 25.547 | 440 | 43.106 |
| 49 | 12.910 | 1.1613 | 415 | 28.090 | 556 | 52.260 |
| 56 | 16.014 | 1.3702 | 480 | 30.642 | 686 | 66.602 |
| 63 | 19.560 | 1.5567 | 547 | 33.206 | 836 | 78.097 |
| 70 | 23.612 | 1.7617 | 615 | 35.876 | 998 | 92.231 |
| 77 | 28.126 | 1.9824 | 682 | 38.659 | 1174 | 106.146 |
| 84 | 33.086 | 2.2612 | 747 | 41.636 | 1358 | 121.551 |
| 91 | 38.490 | 2.5017 | 809 | 44.814 | 1547 | 137.066 |
| 98 | 44.372 | 2.7656 | 867 | 48.258 | 1737 | 153.867 |
| 105 | 50.556 | 3.0610 | 919 | 51.934 | 1925 | 169.279 |
| 112 | 57.158 | 3.3387 | 964 | 55.735 | 2106 | 186.606 |
| 119 | 64.014 | 3.6798 | 1003 | 59.648 | 2281 | 197.679 |
| 126 | 71.156 | 3.9945 | 1034 | 63.610 | 2440 | 213.997 |
| 133 | 78.439 | 4.3155 | 1057 | 67.109 | 2581 | 232.648 |
| 140 | 84.648 | 3.8408 | 1058 | 62.827 | 2656 | 216.692 |

Treatment 12: B*=2% Pmat=5% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.048 | 0.9227 | 295 | 24.638 | 340 | 37.898 |
| 42 | 10.218 | 1.0662 | 353 | 27.237 | 439 | 47.138 |
| 49 | 12.886 | 1.2697 | 414 | 29.848 | 551 | 61.679 |
| 56 | 15.964 | 1.4625 | 479 | 32.554 | 684 | 74.113 |
| 63 | 19.540 | 1.6823 | 546 | 35.439 | 832 | 89.922 |
| 70 | 23.572 | 1.8995 | 614 | 38.621 | 995 | 106.271 |
| 77 | 28.062 | 2.1530 | 681 | 42.225 | 1170 | 125.193 |
| 84 | 33.010 | 2.4037 | 746 | 46.316 | 1353 | 145.245 |
| 91 | 38.458 | 2.6763 | 808 | 50.889 | 1542 | 167.285 |
| 98 | 44.250 | 2.9815 | 865 | 55.979 | 1732 | 189.386 |
| 105 | 50.474 | 3.2935 | 917 | 61.400 | 1919 | 213.312 |
| 112 | 57.040 | 3.6880 | 963 | 67.083 | 2101 | 234.129 |
| 119 | 63.926 | 4.0691 | 1001 | 72.821 | 2272 | 257.862 |
| 126 | 71.008 | 4.4980 | 1032 | 78.482 | 2437 | 271.605 |
| 133 | 78.279 | 4.8867 | 1055 | 83.040 | 2579 | 288.523 |
| 140 | 84.279 | 4.4793 | 1051 | 78.927 | 2627 | 280.275 |
| 147 | 86.771 | 3.2852 | 998 | 71.009 | 2500 | 246.363 |
| 154 | 88.395 | 2.3543 | 924 | 53.494 | 2308 | 175.849 |

Treatment 13: B*=2% Pmat=10% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.110 | 0.8338 | 296 | 23.192 | 352 | 32.994 |
| 42 | 10.276 | 0.9888 | 354 | 25.906 | 442 | 43.286 |
| 49 | 12.944 | 1.1831 | 416 | 28.591 | 559 | 51.905 |
| 56 | 16.040 | 1.3777 | 481 | 31.342 | 690 | 64.863 |
| 63 | 19.620 | 1.5635 | 549 | 34.173 | 840 | 74.726 |
| 70 | 23.650 | 1.7894 | 617 | 37.161 | 1005 | 85.766 |
| 77 | 28.156 | 2.0689 | 684 | 40.404 | 1181 | 96.382 |
| 84 | 33.178 | 2.2997 | 749 | 44.019 | 1366 | 107.464 |
| 91 | 38.604 | 2.5683 | 812 | 47.987 | 1556 | 118.694 |
| 98 | 44.472 | 2.8903 | 869 | 52.437 | 1748 | 130.426 |
| 105 | 50.670 | 3.2065 | 921 | 57.297 | 1936 | 142.410 |
| 112 | 57.286 | 3.5283 | 967 | 62.574 | 2119 | 155.254 |
| 119 | 64.154 | 3.9024 | 1006 | 68.052 | 2292 | 166.541 |
| 126 | 71.324 | 4.3235 | 1037 | 73.748 | 2452 | 180.850 |
| 133 | 78.592 | 4.6200 | 1060 | 78.101 | 2595 | 192.727 |
| 140 | 84.802 | 4.2554 | 1060 | 75.539 | 2681 | 184.265 |

Treatment 14: B*=2% Pmat=10% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.070 | 0.8687 | 295 | 22.850 | 351 | 34.012 |
| 42 | 10.242 | 1.0047 | 353 | 25.167 | 440 | 44.176 |
| 49 | 12.892 | 1.1896 | 415 | 27.539 | 556 | 52.862 |
| 56 | 15.996 | 1.3798 | 480 | 29.941 | 685 | 66.301 |
| 63 | 19.574 | 1.5638 | 547 | 32.589 | 835 | 76.683 |
| 70 | 23.588 | 1.7801 | 615 | 35.558 | 998 | 89.241 |
| 77 | 28.058 | 2.0086 | 682 | 39.060 | 1173 | 101.441 |
| 84 | 33.056 | 2.2042 | 748 | 43.179 | 1357 | 115.197 |
| 91 | 38.498 | 2.4751 | 810 | 47.983 | 1546 | 129.385 |
| 98 | 44.338 | 2.7992 | 867 | 53.446 | 1737 | 145.169 |
| 105 | 50.560 | 3.0811 | 920 | 59.512 | 1925 | 160.726 |
| 112 | 57.138 | 3.4261 | 966 | 66.058 | 2107 | 178.718 |
| 119 | 64.018 | 3.7919 | 1005 | 72.917 | 2283 | 192.457 |
| 126 | 71.148 | 4.2054 | 1036 | 79.856 | 2443 | 211.563 |
| 133 | 78.471 | 4.6133 | 1060 | 86.296 | 2586 | 234.207 |
| 140 | 84.587 | 4.2436 | 1057 | 83.548 | 2659 | 220.728 |

Treatment 15: B*=2% Pmat=10% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.044 | 0.8576 | 294 | 23.614 | 349 | 35.028 |
| 42 | 10.194 | 1.0151 | 352 | 26.357 | 439 | 46.812 |
| 49 | 12.864 | 1.1935 | 413 | 29.193 | 555 | 57.472 |
| 56 | 15.934 | 1.3818 | 478 | 32.121 | 683 | 74.435 |
| 63 | 19.492 | 1.5821 | 545 | 35.333 | 832 | 88.332 |
| 70 | 23.482 | 1.8167 | 612 | 38.960 | 993 | 106.559 |
| 77 | 27.978 | 2.0459 | 679 | 43.136 | 1168 | 123.730 |
| 84 | 32.924 | 2.3318 | 744 | 48.014 | 1350 | 144.364 |
| 91 | 38.318 | 2.6227 | 805 | 53.617 | 1539 | 164.129 |
| 98 | 44.132 | 2.9400 | 863 | 59.901 | 1728 | 187.175 |
| 105 | 50.342 | 3.2709 | 915 | 66.817 | 1916 | 207.370 |
| 112 | 56.868 | 3.6815 | 960 | 74.228 | 2096 | 231.969 |
| 119 | 63.694 | 4.1258 | 999 | 81.863 | 2273 | 248.223 |
| 126 | 70.816 | 4.6105 | 1030 | 89.668 | 2431 | 272.239 |
| 133 | 78.012 | 4.9810 | 1052 | 96.068 | 2566 | 299.216 |
| 140 | 83.953 | 4.4376 | 1045 | 89.170 | 2620 | 272.731 |
| 147 | 86.761 | 3.2690 | 986 | 77.420 | 2513 | 234.327 |

Treatment 16: B*=2% Pmat=15% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.050 | 0.8769 | 295 | 24.774 | 351 | 37.237 |
| 42 | 10.222 | 1.0483 | 352 | 27.508 | 441 | 48.816 |
| 49 | 12.894 | 1.2704 | 414 | 30.182 | 558 | 58.245 |
| 56 | 15.978 | 1.4442 | 479 | 32.900 | 686 | 72.439 |
| 63 | 19.512 | 1.6827 | 545 | 35.757 | 835 | 82.362 |
| 70 | 23.554 | 1.9053 | 613 | 38.981 | 997 | 94.054 |
| 77 | 28.036 | 2.1307 | 680 | 42.735 | 1172 | 103.846 |
| 84 | 32.998 | 2.4153 | 745 | 47.227 | 1354 | 114.077 |
| 91 | 38.374 | 2.7168 | 806 | 52.613 | 1542 | 124.048 |
| 98 | 44.224 | 3.0219 | 864 | 58.921 | 1731 | 135.001 |
| 105 | 50.406 | 3.3586 | 916 | 66.118 | 1918 | 146.653 |
| 112 | 56.970 | 3.7305 | 961 | 74.121 | 2099 | 160.516 |
| 119 | 63.830 | 4.1414 | 1000 | 82.661 | 2271 | 173.546 |
| 126 | 70.936 | 4.6333 | 1031 | 91.580 | 2430 | 191.553 |
| 133 | 78.073 | 4.9718 | 1053 | 98.793 | 2568 | 206.988 |
| 140 | 83.852 | 4.2732 | 1042 | 90.805 | 2637 | 187.266 |
| 147 | 87.161 | 3.3096 | 991 | 91.115 | 2600 | 171.334 |

Treatment 17: B*=2% Pmat=15% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.070 | 0.8547 | 296 | 23.015 | 352 | 34.860 |
| 42 | 10.264 | 1.0002 | 353 | 25.628 | 442 | 45.818 |
| 49 | 12.920 | 1.1800 | 415 | 28.433 | 558 | 55.010 |
| 56 | 16.036 | 1.3750 | 479 | 31.552 | 687 | 69.285 |
| 63 | 19.580 | 1.5801 | 546 | 35.220 | 836 | 80.328 |
| 70 | 23.608 | 1.8289 | 613 | 39.601 | 997 | 94.249 |
| 77 | 28.088 | 2.0825 | 680 | 44.854 | 1172 | 107.660 |
| 84 | 33.050 | 2.3096 | 745 | 51.124 | 1354 | 123.327 |
| 91 | 38.420 | 2.6400 | 806 | 58.447 | 1541 | 139.642 |
| 98 | 44.252 | 3.0064 | 863 | 66.681 | 1730 | 158.708 |
| 105 | 50.448 | 3.4303 | 914 | 75.707 | 1916 | 177.591 |
| 112 | 56.998 | 3.8781 | 960 | 85.346 | 2096 | 200.646 |
| 119 | 63.866 | 4.3733 | 998 | 95.316 | 2270 | 218.884 |
| 126 | 70.930 | 5.0007 | 1029 | 105.365 | 2428 | 244.366 |
| 133 | 78.038 | 5.4439 | 1050 | 112.490 | 2560 | 267.132 |
| 140 | 83.348 | 4.7973 | 1031 | 104.839 | 2603 | 247.793 |
| 147 | 86.246 | 3.6961 | 958 | 84.837 | 2518 | 196.015 |
| 154 | 87.491 | 2.9407 | 866 | 68.820 | 2384 | 158.555 |

Treatment 18: B*=2% Pmat=15% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.044 | 0.8530 | 295 | 23.161 | 351 | 36.330 |
| 42 | 10.216 | 1.0215 | 353 | 25.754 | 441 | 48.475 |
| 49 | 12.900 | 1.1596 | 415 | 28.475 | 558 | 58.955 |
| 56 | 15.962 | 1.3814 | 480 | 31.434 | 686 | 74.978 |
| 63 | 19.566 | 1.5526 | 546 | 34.954 | 835 | 87.723 |
| 70 | 23.588 | 1.7958 | 614 | 39.239 | 997 | 104.100 |
| 77 | 28.100 | 2.0382 | 681 | 44.496 | 1171 | 119.433 |
| 84 | 33.054 | 2.3379 | 746 | 50.947 | 1354 | 138.032 |
| 91 | 38.448 | 2.6163 | 807 | 58.587 | 1542 | 156.095 |
| 98 | 44.290 | 2.9501 | 865 | 67.352 | 1731 | 178.200 |
| 105 | 50.492 | 3.3562 | 917 | 77.104 | 1919 | 198.351 |
| 112 | 57.058 | 3.7910 | 962 | 87.521 | 2099 | 223.999 |
| 119 | 63.900 | 4.3187 | 1001 | 98.434 | 2275 | 242.822 |
| 126 | 71.012 | 4.9226 | 1032 | 109.497 | 2434 | 270.342 |
| 133 | 78.167 | 5.4152 | 1054 | 118.746 | 2568 | 303.800 |
| 140 | 83.604 | 4.8167 | 1036 | 111.417 | 2605 | 278.193 |
| 147 | 85.952 | 3.7535 | 953 | 97.871 | 2489 | 246.063 |

Treatment 19: B*=3% Pmat=5% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.038 | 0.8911 | 295 | 24.545 | 350 | 33.274 |
| 42 | 10.252 | 1.0367 | 353 | 27.756 | 440 | 43.897 |
| 49 | 12.876 | 1.2229 | 415 | 31.071 | 557 | 53.197 |
| 56 | 15.982 | 1.4261 | 481 | 34.394 | 687 | 67.352 |
| 63 | 19.544 | 1.6227 | 548 | 37.704 | 837 | 78.507 |
| 70 | 23.600 | 1.8982 | 616 | 40.913 | 1000 | 91.796 |
| 77 | 28.092 | 2.1505 | 683 | 43.941 | 1176 | 104.160 |
| 84 | 33.048 | 2.4490 | 749 | 46.822 | 1361 | 117.063 |
| 91 | 38.518 | 2.7497 | 811 | 49.503 | 1551 | 129.414 |
| 98 | 44.360 | 3.0280 | 869 | 51.958 | 1742 | 141.586 |
| 105 | 50.606 | 3.3474 | 921 | 54.174 | 1930 | 152.630 |
| 112 | 57.212 | 3.7000 | 966 | 56.164 | 2112 | 163.654 |
| 119 | 64.064 | 4.0423 | 1005 | 57.985 | 2286 | 170.911 |
| 126 | 71.202 | 4.3440 | 1036 | 59.667 | 2445 | 180.283 |
| 133 | 78.490 | 4.6396 | 1059 | 60.470 | 2587 | 187.197 |
| 140 | 84.616 | 4.0902 | 1061 | 54.028 | 2671 | 166.335 |
| 147 | 87.453 | 2.7454 | 1026 | 43.083 | 2633 | 131.288 |
| 154 | 89.654 | 0.9356 | 991 | 38.365 | 2583 | 89.892 |

Treatment 20: B*=3% Pmat=5% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.086 | 0.8556 | 295 | 23.638 | 351 | 32.565 |
| 42 | 10.250 | 0.9967 | 352 | 26.808 | 440 | 43.275 |
| 49 | 12.910 | 1.1784 | 414 | 30.148 | 556 | 52.988 |
| 56 | 15.990 | 1.3615 | 479 | 33.668 | 684 | 68.421 |
| 63 | 19.552 | 1.5850 | 546 | 37.311 | 834 | 81.203 |
| 70 | 23.588 | 1.8168 | 613 | 41.117 | 996 | 97.306 |
| 77 | 28.084 | 2.0692 | 680 | 45.028 | 1171 | 113.123 |
| 84 | 33.032 | 2.3541 | 745 | 48.986 | 1354 | 130.822 |
| 91 | 38.406 | 2.6532 | 807 | 53.029 | 1542 | 148.248 |
| 98 | 44.228 | 2.9593 | 864 | 57.107 | 1732 | 167.153 |
| 105 | 50.432 | 3.3382 | 916 | 61.066 | 1920 | 183.982 |
| 112 | 56.998 | 3.6667 | 961 | 65.037 | 2100 | 202.788 |
| 119 | 63.834 | 4.0654 | 1000 | 68.810 | 2275 | 214.529 |
| 126 | 70.962 | 4.4637 | 1031 | 72.471 | 2434 | 231.602 |
| 133 | 78.202 | 4.8504 | 1054 | 75.213 | 2573 | 250.215 |
| 140 | 84.148 | 4.1618 | 1053 | 68.234 | 2643 | 228.569 |
| 147 | 87.399 | 2.8352 | 1015 | 60.597 | 2586 | 197.625 |

Treatment 21: B*=3% Pmat=5% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.116 | 0.8172 | 297 | 23.967 | 345 | 35.698 |
| 42 | 10.318 | 0.9833 | 355 | 27.598 | 444 | 45.687 |
| 49 | 12.998 | 1.1544 | 417 | 31.563 | 558 | 61.498 |
| 56 | 16.112 | 1.3547 | 483 | 35.841 | 693 | 76.107 |
| 63 | 19.696 | 1.6152 | 550 | 40.444 | 843 | 94.674 |
| 70 | 23.746 | 1.8483 | 618 | 45.333 | 1009 | 114.165 |
| 77 | 28.292 | 2.1457 | 686 | 50.473 | 1186 | 136.435 |
| 84 | 33.304 | 2.4518 | 752 | 55.766 | 1372 | 159.528 |
| 91 | 38.730 | 2.8116 | 814 | 61.193 | 1564 | 184.507 |
| 98 | 44.598 | 3.1876 | 872 | 66.659 | 1757 | 208.864 |
| 105 | 50.884 | 3.6167 | 924 | 72.032 | 1946 | 234.621 |
| 112 | 57.482 | 4.0796 | 970 | 77.306 | 2132 | 256.516 |
| 119 | 64.390 | 4.5475 | 1009 | 82.355 | 2306 | 280.459 |
| 126 | 71.566 | 5.0680 | 1041 | 87.052 | 2472 | 294.758 |
| 133 | 78.712 | 5.3959 | 1062 | 88.914 | 2608 | 305.322 |
| 140 | 83.916 | 4.6049 | 1047 | 77.507 | 2616 | 272.518 |

Treatment 22: B*=3% Pmat=10% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.020 | 0.8080 | 295 | 23.029 | 350 | 31.685 |
| 42 | 10.204 | 0.9339 | 352 | 26.305 | 439 | 42.414 |
| 49 | 12.842 | 1.1115 | 414 | 29.850 | 556 | 51.860 |
| 56 | 15.952 | 1.3119 | 480 | 33.552 | 686 | 66.481 |
| 63 | 19.476 | 1.5252 | 547 | 37.487 | 836 | 78.065 |
| 70 | 23.538 | 1.7728 | 615 | 41.610 | 999 | 92.010 |
| 77 | 28.040 | 2.0579 | 682 | 45.956 | 1176 | 105.090 |
| 84 | 33.006 | 2.3514 | 748 | 50.500 | 1360 | 119.220 |
| 91 | 38.456 | 2.6378 | 810 | 55.246 | 1550 | 132.827 |
| 98 | 44.284 | 3.0069 | 868 | 60.181 | 1741 | 147.198 |
| 105 | 50.480 | 3.3765 | 920 | 65.395 | 1930 | 160.875 |
| 112 | 57.088 | 3.7620 | 966 | 70.749 | 2112 | 175.420 |
| 119 | 63.974 | 4.2015 | 1005 | 76.213 | 2286 | 187.466 |
| 126 | 71.084 | 4.6747 | 1036 | 81.753 | 2446 | 202.444 |
| 133 | 78.285 | 4.9605 | 1057 | 84.439 | 2583 | 209.593 |
| 140 | 84.221 | 4.3623 | 1052 | 77.181 | 2656 | 186.545 |

Treatment 23: B*=3% Pmat=10% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.048 | 0.8667 | 295 | 24.709 | 351 | 34.394 |
| 42 | 10.256 | 1.0102 | 353 | 28.171 | 441 | 46.039 |
| 49 | 12.904 | 1.2156 | 415 | 31.913 | 557 | 56.527 |
| 56 | 16.018 | 1.4006 | 480 | 35.874 | 687 | 72.867 |
| 63 | 19.572 | 1.6438 | 547 | 40.152 | 836 | 86.393 |
| 70 | 23.590 | 1.9134 | 615 | 44.698 | 999 | 103.288 |
| 77 | 28.080 | 2.1935 | 682 | 49.534 | 1174 | 119.648 |
| 84 | 33.028 | 2.5027 | 747 | 54.641 | 1357 | 138.063 |
| 91 | 38.478 | 2.8555 | 808 | 60.045 | 1546 | 156.280 |
| 98 | 44.302 | 3.2298 | 865 | 65.733 | 1736 | 176.037 |
| 105 | 50.492 | 3.6144 | 917 | 71.603 | 1923 | 194.509 |
| 112 | 57.058 | 4.0812 | 962 | 77.611 | 2104 | 214.824 |
| 119 | 63.924 | 4.5347 | 1001 | 83.680 | 2278 | 229.517 |
| 126 | 71.036 | 5.0677 | 1032 | 89.638 | 2436 | 249.266 |
| 133 | 78.104 | 5.3095 | 1052 | 93.166 | 2568 | 265.534 |
| 140 | 83.703 | 4.6349 | 1042 | 84.465 | 2617 | 232.767 |

Treatment 24: B*=3% Pmat=10% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.038 | 0.8661 | 293 | 24.394 | 340 | 37.322 |
| 42 | 10.208 | 1.0406 | 351 | 27.602 | 438 | 46.746 |
| 49 | 12.838 | 1.1994 | 412 | 31.019 | 549 | 61.757 |
| 56 | 15.936 | 1.4071 | 476 | 34.709 | 681 | 74.737 |
| 63 | 19.428 | 1.6499 | 543 | 38.734 | 827 | 91.651 |
| 70 | 23.450 | 1.8661 | 610 | 43.158 | 990 | 108.599 |
| 77 | 27.922 | 2.1487 | 676 | 48.069 | 1163 | 128.481 |
| 84 | 32.852 | 2.4392 | 741 | 53.458 | 1345 | 148.800 |
| 91 | 38.244 | 2.7691 | 803 | 59.382 | 1533 | 171.789 |
| 98 | 44.012 | 3.1508 | 860 | 65.771 | 1722 | 194.283 |
| 105 | 50.188 | 3.5312 | 912 | 72.585 | 1909 | 219.257 |
| 112 | 56.726 | 3.9661 | 958 | 79.673 | 2091 | 241.108 |
| 119 | 63.556 | 4.4473 | 996 | 86.908 | 2262 | 266.395 |
| 126 | 70.636 | 4.9792 | 1028 | 94.116 | 2427 | 282.177 |
| 133 | 77.837 | 5.4897 | 1051 | 100.015 | 2570 | 302.432 |
| 140 | 83.300 | 4.7278 | 1037 | 88.834 | 2599 | 283.466 |

Treatment 25: B* = 3% Pmat = 15% LPmat = 10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.092 | 0.8793 | 296 | 23.732 | 353 | 36.232 |
| 42 | 10.266 | 1.0106 | 353 | 26.679 | 444 | 47.695 |
| 49 | 12.908 | 1.1859 | 415 | 29.838 | 561 | 56.978 |
| 56 | 16.020 | 1.3694 | 480 | 33.269 | 691 | 71.015 |
| 63 | 19.578 | 1.5840 | 546 | 37.064 | 840 | 81.207 |
| 70 | 23.612 | 1.8155 | 614 | 41.388 | 1003 | 93.514 |
| 77 | 28.086 | 2.0754 | 680 | 46.277 | 1178 | 104.099 |
| 84 | 33.048 | 2.3394 | 745 | 51.913 | 1361 | 115.560 |
| 91 | 38.468 | 2.6524 | 806 | 58.247 | 1549 | 126.891 |
| 98 | 44.272 | 3.0273 | 863 | 65.363 | 1737 | 139.456 |
| 105 | 50.476 | 3.4294 | 914 | 73.106 | 1924 | 152.473 |
| 112 | 57.024 | 3.8352 | 959 | 81.410 | 2103 | 167.981 |
| 119 | 63.826 | 4.3175 | 997 | 90.077 | 2275 | 181.429 |
| 126 | 70.922 | 4.8493 | 1028 | 98.924 | 2432 | 200.333 |
| 133 | 78.141 | 5.3984 | 1050 | 107.092 | 2571 | 222.108 |
| 140 | 83.796 | 5.0560 | 1038 | 104.264 | 2636 | 214.897 |
| 147 | 85.899 | 4.3803 | 963 | 95.698 | 2548 | 182.569 |
| 154 | 86.556 | 4.1421 | 869 | 105.079 | 2420 | 200.093 |

Treatment 26: B* = 3% Pmat = 15% LPmat = 15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.024 | 0.8419 | 296 | 24.926 | 344 | 40.789 |
| 42 | 10.264 | 1.0337 | 353 | 28.384 | 443 | 51.078 |
| 49 | 12.890 | 1.1835 | 415 | 32.115 | 556 | 66.671 |
| 56 | 15.988 | 1.4184 | 480 | 36.151 | 690 | 79.442 |
| 63 | 19.584 | 1.6421 | 547 | 40.652 | 839 | 95.269 |
| 70 | 23.616 | 1.9120 | 615 | 45.606 | 1003 | 110.285 |
| 77 | 28.100 | 2.2036 | 682 | 51.192 | 1178 | 127.105 |
| 84 | 33.048 | 2.5287 | 747 | 57.389 | 1362 | 143.665 |
| 91 | 38.480 | 2.8883 | 809 | 64.355 | 1551 | 161.831 |
| 98 | 44.314 | 3.2841 | 866 | 71.989 | 1741 | 180.127 |
| 105 | 50.536 | 3.7073 | 918 | 80.261 | 1928 | 200.203 |
| 112 | 57.086 | 4.2045 | 963 | 88.983 | 2109 | 219.417 |
| 119 | 63.970 | 4.7618 | 1002 | 98.025 | 2280 | 241.614 |
| 126 | 71.082 | 5.3476 | 1033 | 107.222 | 2443 | 257.685 |
| 133 | 78.162 | 5.7274 | 1052 | 112.572 | 2577 | 269.107 |
| 140 | 83.271 | 5.0197 | 1032 | 106.071 | 2605 | 246.948 |
| 147 | 85.776 | 3.8584 | 964 | 97.318 | 2520 | 213.585 |

Treatment 27: B*=3% Pmat=15% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.044 | 0.9076 | 294 | 25.235 | 341 | 38.604 |
| 42 | 10.182 | 1.0465 | 351 | 28.769 | 440 | 48.270 |
| 49 | 12.850 | 1.2516 | 413 | 32.614 | 551 | 63.424 |
| 56 | 15.924 | 1.4431 | 477 | 36.909 | 684 | 76.335 |
| 63 | 19.448 | 1.6784 | 544 | 41.762 | 832 | 92.986 |
| 70 | 23.470 | 1.9761 | 611 | 47.197 | 995 | 109.519 |
| 77 | 27.946 | 2.2559 | 678 | 53.477 | 1169 | 128.703 |
| 84 | 32.890 | 2.5837 | 743 | 60.501 | 1352 | 148.900 |
| 91 | 38.252 | 2.9648 | 805 | 68.359 | 1541 | 171.433 |
| 98 | 44.096 | 3.3719 | 862 | 76.963 | 1731 | 194.615 |
| 105 | 50.288 | 3.8693 | 914 | 86.174 | 1918 | 220.311 |
| 112 | 56.814 | 4.3738 | 960 | 95.808 | 2100 | 244.254 |
| 119 | 63.688 | 5.0001 | 999 | 105.742 | 2272 | 271.873 |
| 126 | 70.764 | 5.6413 | 1031 | 115.729 | 2437 | 292.086 |
| 133 | 77.720 | 6.0372 | 1050 | 122.549 | 2570 | 308.017 |
| 140 | 83.101 | 5.5999 | 1033 | 114.669 | 2601 | 290.979 |

Treatment 28: B*=6% Pmat=5% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 6.062 | 0.6535 | 248 | 24.599 | 266 | 25.711 |
| 42 | 7.914 | 0.7771 | 304 | 30.822 | 350 | 34.914 |
| 49 | 10.242 | 0.9927 | 366 | 38.011 | 445 | 51.017 |
| 56 | 12.998 | 1.2365 | 431 | 45.837 | 565 | 66.254 |
| 63 | 16.212 | 1.5335 | 499 | 53.895 | 698 | 87.846 |
| 70 | 19.894 | 1.8873 | 569 | 61.838 | 849 | 107.437 |
| 77 | 24.102 | 2.2764 | 637 | 69.297 | 1011 | 131.047 |
| 84 | 28.744 | 2.7425 | 704 | 75.973 | 1184 | 151.934 |
| 91 | 33.882 | 3.2510 | 766 | 81.564 | 1360 | 174.880 |
| 98 | 39.426 | 3.8107 | 824 | 85.877 | 1540 | 192.949 |
| 105 | 45.358 | 4.3713 | 876 | 88.829 | 1716 | 212.083 |
| 112 | 51.602 | 4.9728 | 920 | 90.371 | 1888 | 223.250 |
| 119 | 58.158 | 5.5312 | 957 | 90.590 | 2047 | 236.213 |
| 126 | 64.968 | 6.1611 | 985 | 89.573 | 2201 | 235.790 |
| 133 | 71.888 | 6.6646 | 1005 | 87.444 | 2332 | 240.344 |
| 140 | 78.254 | 6.5756 | 1009 | 79.378 | 2416 | 234.715 |
| 147 | 82.867 | 5.6900 | 992 | 66.531 | 2443 | 199.416 |
| 154 | 85.063 | 4.8129 | 951 | 56.386 | 2387 | 162.206 |
| 161 | 85.641 | 3.9975 | 900 | 46.977 | 2304 | 144.687 |
| 168 | 87.087 | 2.6613 | 858 | 32.840 | 2230 | 98.640 |
| 175 | 89.000 | 1.7889 | 832 | 32.510 | 2195 | 115.278 |

Treatment 29: B*=6% Pmat=5% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.052 | 0.8430 | 299 | 29.401 | 347 | 39.343 |
| 42 | 10.256 | 1.0122 | 358 | 35.917 | 448 | 51.772 |
| 49 | 12.992 | 1.2308 | 422 | 43.210 | 564 | 70.710 |
| 56 | 16.130 | 1.4891 | 489 | 51.039 | 701 | 89.343 |
| 63 | 19.762 | 1.8199 | 558 | 59.277 | 852 | 113.481 |
| 70 | 23.902 | 2.2132 | 627 | 67.356 | 1020 | 137.122 |
| 77 | 28.470 | 2.6667 | 696 | 75.192 | 1198 | 163.829 |
| 84 | 33.572 | 3.1605 | 763 | 82.601 | 1386 | 190.535 |
| 91 | 39.072 | 3.7071 | 826 | 89.034 | 1577 | 217.600 |
| 98 | 45.048 | 4.3103 | 885 | 94.558 | 1770 | 242.191 |
| 105 | 51.400 | 4.9563 | 937 | 99.039 | 1970 | 253.468 |
| 112 | 58.094 | 5.5925 | 983 | 102.371 | 2143 | 285.985 |
| 119 | 65.108 | 6.2529 | 1022 | 104.540 | 2315 | 305.362 |
| 126 | 72.251 | 6.8372 | 1051 | 104.399 | 2474 | 308.621 |
| 133 | 78.408 | 6.3678 | 1057 | 89.611 | 2563 | 271.112 |
| 140 | 82.879 | 5.4030 | 1039 | 74.948 | 2575 | 238.859 |
| 147 | 85.775 | 4.5675 | 1002 | 63.653 | 2529 | 202.652 |
| 154 | 86.085 | 3.6880 | 949 | 55.235 | 2422 | 161.476 |
| 161 | 88.400 | 2.5578 | 916 | 52.882 | 2389 | 155.134 |

Treatment 30: B*=6% Pmat=5% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.098 | 0.8233 | 297 | 27.399 | 345 | 36.802 |
| 42 | 10.270 | 0.9813 | 356 | 33.555 | 445 | 48.418 |
| 49 | 12.952 | 1.1578 | 418 | 40.576 | 559 | 67.160 |
| 56 | 16.056 | 1.3960 | 484 | 48.270 | 694 | 85.516 |
| 63 | 19.636 | 1.6939 | 552 | 56.384 | 843 | 110.021 |
| 70 | 23.726 | 2.0812 | 621 | 64.551 | 1008 | 134.504 |
| 77 | 28.266 | 2.4713 | 689 | 72.644 | 1183 | 163.180 |
| 84 | 33.300 | 2.9624 | 755 | 80.221 | 1368 | 190.955 |
| 91 | 38.800 | 3.5004 | 817 | 87.104 | 1557 | 220.609 |
| 98 | 44.700 | 4.0816 | 875 | 93.102 | 1748 | 247.233 |
| 105 | 50.982 | 4.6743 | 927 | 98.286 | 1948 | 258.989 |
| 112 | 57.572 | 5.3402 | 973 | 102.444 | 2117 | 297.041 |
| 119 | 64.504 | 6.0112 | 1011 | 105.640 | 2287 | 320.717 |
| 126 | 71.710 | 6.6933 | 1042 | 107.882 | 2451 | 331.363 |
| 133 | 78.298 | 6.6430 | 1054 | 99.934 | 2559 | 315.703 |
| 140 | 82.462 | 5.3603 | 1029 | 77.201 | 2543 | 264.494 |
| 147 | 85.221 | 4.3977 | 989 | 66.014 | 2476 | 228.477 |
| 154 | 86.785 | 2.9128 | 951 | 70.491 | 2419 | 240.539 |
| 161 | 88.417 | 2.4665 | 881 | 89.732 | 2266 | 295.825 |

Treatment 31: B*=6% Pmat=10% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 6.048 | 0.6947 | 248 | 24.640 | 265 | 27.094 |
| 42 | 7.908 | 0.8420 | 304 | 30.415 | 349 | 36.335 |
| 49 | 10.196 | 0.9836 | 365 | 37.228 | 444 | 52.152 |
| 56 | 12.944 | 1.2263 | 431 | 44.650 | 564 | 67.010 |
| 63 | 16.178 | 1.5528 | 499 | 52.483 | 697 | 88.129 |
| 70 | 19.864 | 1.8645 | 568 | 60.384 | 848 | 107.133 |
| 77 | 24.068 | 2.2675 | 637 | 68.075 | 1009 | 130.356 |
| 84 | 28.702 | 2.7269 | 704 | 75.244 | 1182 | 151.001 |
| 91 | 33.818 | 3.2363 | 766 | 81.779 | 1359 | 173.564 |
| 98 | 39.376 | 3.7767 | 824 | 87.423 | 1538 | 192.637 |
| 105 | 45.304 | 4.3485 | 876 | 92.303 | 1714 | 212.758 |
| 112 | 51.588 | 4.9775 | 920 | 95.990 | 1886 | 225.904 |
| 119 | 58.122 | 5.5671 | 957 | 98.984 | 2045 | 241.304 |
| 126 | 64.918 | 6.1991 | 985 | 101.171 | 2200 | 243.718 |
| 133 | 71.838 | 6.7473 | 1005 | 101.348 | 2329 | 248.744 |
| 140 | 78.036 | 6.6054 | 1006 | 94.844 | 2408 | 243.520 |
| 147 | 82.595 | 5.6885 | 983 | 82.533 | 2424 | 200.527 |
| 154 | 84.941 | 4.5322 | 936 | 69.994 | 2373 | 152.775 |
| 161 | 86.634 | 3.6464 | 888 | 74.522 | 2316 | 137.449 |
| 168 | 87.963 | 2.6960 | 823 | 59.248 | 2242 | 116.254 |
| 175 | 89.000 | 1.2649 | 780 | 54.312 | 2204 | 85.113 |

Treatment 32: B*=6% Pmat=10% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.051 | 0.8531 | 294 | 29.180 | 342 | 38.471 |
| 42 | 10.244 | 1.0283 | 352 | 35.643 | 441 | 50.191 |
| 49 | 12.867 | 1.2359 | 414 | 42.976 | 553 | 69.401 |
| 56 | 15.986 | 1.4830 | 479 | 50.873 | 686 | 86.994 |
| 63 | 19.497 | 1.8188 | 545 | 59.374 | 834 | 111.161 |
| 70 | 23.550 | 2.2029 | 613 | 67.680 | 997 | 133.510 |
| 77 | 28.027 | 2.6413 | 680 | 76.223 | 1171 | 160.853 |
| 84 | 32.975 | 3.1295 | 745 | 84.130 | 1355 | 185.960 |
| 91 | 38.378 | 3.6964 | 806 | 91.853 | 1543 | 214.489 |
| 98 | 44.216 | 4.2876 | 863 | 98.575 | 1732 | 238.893 |
| 105 | 50.382 | 4.9680 | 914 | 104.767 | 1918 | 265.196 |
| 112 | 56.930 | 5.6604 | 960 | 110.100 | 2099 | 285.707 |
| 119 | 63.778 | 6.3567 | 998 | 114.658 | 2269 | 308.187 |
| 126 | 70.700 | 6.8867 | 1026 | 114.949 | 2425 | 307.867 |
| 133 | 77.254 | 6.9776 | 1038 | 107.174 | 2536 | 290.973 |
| 140 | 81.921 | 6.0354 | 1021 | 93.641 | 2556 | 256.804 |
| 147 | 84.500 | 4.9275 | 975 | 77.257 | 2509 | 212.539 |
| 154 | 86.411 | 4.0886 | 927 | 68.866 | 2451 | 187.019 |
| 161 | 87.250 | 3.5661 | 877 | 60.850 | 2376 | 164.652 |
| 168 | 87.833 | 1.3290 | 867 | 57.214 | 2332 | 127.045 |

Treatment 33: B*=6% Pmat=10% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.086 | 0.8603 | 298 | 29.022 | 348 | 41.107 |
| 42 | 10.308 | 1.0233 | 357 | 35.282 | 449 | 54.067 |
| 49 | 12.962 | 1.2376 | 420 | 42.498 | 563 | 74.158 |
| 56 | 16.128 | 1.5060 | 487 | 50.371 | 699 | 94.121 |
| 63 | 19.738 | 1.8298 | 555 | 58.885 | 850 | 119.958 |
| 70 | 23.828 | 2.2100 | 624 | 67.440 | 1016 | 145.524 |
| 77 | 28.406 | 2.6403 | 692 | 76.332 | 1193 | 176.258 |
| 84 | 33.438 | 3.1147 | 758 | 84.833 | 1379 | 205.376 |
| 91 | 38.958 | 3.6758 | 821 | 93.293 | 1569 | 238.397 |
| 98 | 44.860 | 4.3167 | 879 | 100.898 | 1761 | 266.937 |
| 105 | 51.176 | 4.9774 | 931 | 108.119 | 1963 | 280.975 |
| 112 | 57.812 | 5.6665 | 977 | 114.667 | 2133 | 322.825 |
| 119 | 64.768 | 6.4431 | 1015 | 120.525 | 2303 | 350.464 |
| 126 | 71.883 | 7.0375 | 1044 | 123.404 | 2463 | 357.624 |
| 133 | 78.175 | 6.9954 | 1051 | 116.235 | 2557 | 341.621 |
| 140 | 82.092 | 5.8356 | 1018 | 99.331 | 2520 | 303.995 |
| 147 | 84.733 | 4.5753 | 966 | 83.299 | 2435 | 249.556 |
| 154 | 86.493 | 3.6664 | 916 | 75.896 | 2350 | 221.578 |
| 161 | 87.957 | 3.0374 | 858 | 73.806 | 2224 | 204.723 |

Treatment 34: B*=6% Pmat=15% LPmat=10%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.004 | 0.9020 | 294 | 30.907 | 342 | 42.951 |
| 42 | 10.206 | 1.0890 | 352 | 37.301 | 442 | 55.417 |
| 49 | 12.812 | 1.3267 | 413 | 44.562 | 554 | 74.669 |
| 56 | 15.902 | 1.6105 | 478 | 52.340 | 688 | 91.997 |
| 63 | 19.456 | 1.9483 | 546 | 60.437 | 836 | 114.165 |
| 70 | 23.464 | 2.3176 | 613 | 68.868 | 1000 | 135.276 |
| 77 | 27.964 | 2.7954 | 680 | 77.240 | 1175 | 159.008 |
| 84 | 32.954 | 3.2731 | 746 | 85.508 | 1360 | 181.319 |
| 91 | 38.320 | 3.8339 | 808 | 93.505 | 1548 | 205.095 |
| 98 | 44.178 | 4.4603 | 865 | 101.245 | 1739 | 226.598 |
| 105 | 50.398 | 5.1303 | 917 | 108.422 | 1926 | 248.139 |
| 112 | 56.946 | 5.8281 | 962 | 115.349 | 2108 | 266.706 |
| 119 | 63.828 | 6.5767 | 1001 | 121.776 | 2278 | 285.965 |
| 126 | 70.789 | 7.2057 | 1031 | 126.077 | 2437 | 289.362 |
| 133 | 77.180 | 7.1225 | 1041 | 121.584 | 2547 | 277.239 |
| 140 | 81.622 | 6.3203 | 1018 | 111.451 | 2565 | 243.177 |
| 147 | 84.323 | 5.2799 | 968 | 101.461 | 2521 | 202.495 |
| 154 | 85.444 | 4.4422 | 897 | 99.569 | 2434 | 185.818 |
| 161 | 86.333 | 4.2127 | 817 | 100.854 | 2307 | 164.347 |
| 168 | 87.091 | 3.5342 | 735 | 105.902 | 2185 | 146.174 |

Treatment 35: B*=6% Pmat=15% LPmat=15%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.064 | 0.7881 | 297 | 27.467 | 348 | 37.958 |
| 42 | 10.244 | 0.9604 | 355 | 33.814 | 449 | 49.300 |
| 49 | 12.928 | 1.1478 | 418 | 41.059 | 563 | 66.980 |
| 56 | 16.022 | 1.3933 | 483 | 49.059 | 698 | 83.828 |
| 63 | 19.622 | 1.7044 | 551 | 57.760 | 848 | 106.224 |
| 70 | 23.682 | 2.0904 | 619 | 66.711 | 1012 | 127.503 |
| 77 | 28.226 | 2.5107 | 687 | 76.058 | 1188 | 153.088 |
| 84 | 33.230 | 3.0344 | 752 | 85.245 | 1372 | 177.241 |
| 91 | 38.666 | 3.5872 | 813 | 94.566 | 1560 | 204.017 |
| 98 | 44.552 | 4.2170 | 871 | 103.654 | 1749 | 229.283 |
| 105 | 50.780 | 4.8752 | 922 | 112.481 | 1946 | 241.663 |
| 112 | 57.380 | 5.6536 | 967 | 120.978 | 2115 | 279.146 |
| 119 | 64.280 | 6.4524 | 1005 | 129.107 | 2283 | 304.639 |
| 126 | 71.264 | 7.1019 | 1033 | 135.262 | 2440 | 314.834 |
| 133 | 77.518 | 7.0617 | 1039 | 128.604 | 2539 | 297.503 |
| 140 | 81.627 | 6.0355 | 1007 | 115.215 | 2534 | 267.964 |
| 147 | 84.213 | 4.9730 | 949 | 101.154 | 2467 | 216.526 |
| 154 | 85.767 | 3.9264 | 877 | 99.099 | 2376 | 198.182 |
| 161 | 86.700 | 3.5927 | 794 | 100.767 | 2245 | 187.093 |
| 168 | 87.333 | 3.2403 | 668 | 52.846 | 2068 | 109.096 |

Treatment 36: B*=6% Pmat=15% LPmat=20%

| Age (days) | Live Weight(kg) mean | s.d | ADG(g/d) mean | s.d | FI(g/d) mean | s.d |
|---|---|---|---|---|---|---|
| 35 | 8.090 | 0.9097 | 298 | 30.386 | 350 | 44.648 |
| 42 | 10.268 | 1.0801 | 356 | 36.798 | 450 | 57.872 |
| 49 | 12.946 | 1.3201 | 419 | 44.168 | 565 | 78.060 |
| 56 | 16.094 | 1.5601 | 484 | 52.209 | 700 | 97.266 |
| 63 | 19.688 | 1.9031 | 552 | 60.970 | 850 | 122.741 |
| 70 | 23.718 | 2.3050 | 620 | 69.948 | 1015 | 146.752 |
| 77 | 28.286 | 2.7538 | 688 | 79.323 | 1190 | 175.825 |
| 84 | 33.324 | 3.2527 | 753 | 88.572 | 1375 | 202.802 |
| 91 | 38.762 | 3.8636 | 815 | 97.831 | 1563 | 232.878 |
| 98 | 44.624 | 4.4912 | 872 | 106.978 | 1753 | 260.632 |
| 105 | 50.900 | 5.2223 | 923 | 115.772 | 1952 | 273.478 |
| 112 | 57.490 | 5.9522 | 968 | 124.229 | 2120 | 313.934 |
| 119 | 64.392 | 6.7802 | 1006 | 132.274 | 2288 | 341.350 |
| 126 | 71.412 | 7.4926 | 1035 | 137.436 | 2447 | 351.606 |
| 133 | 77.512 | 7.3192 | 1038 | 128.479 | 2535 | 328.325 |
| 140 | 81.564 | 6.3955 | 1006 | 115.296 | 2515 | 297.107 |
| 147 | 83.751 | 5.0257 | 950 | 106.573 | 2436 | 249.992 |
| 154 | 85.907 | 4.3110 | 882 | 103.448 | 2350 | 241.443 |
| 161 | 86.824 | 3.5544 | 813 | 102.464 | 2257 | 207.780 |
| 168 | 87.000 | 3.2404 | 708 | 115.563 | 2104 | 223.713 |

## APPENDIX 2

Summary of some of the results for pigs kept at 18°C in the experiment reported in Chapter 6.

| Protein Treatment | Starting weight (kg) | EBWT (kg) | Final weight (kg) | ADG (kg/d) | Food Intake (kg/d) | FCE | Body Protein (kg) | Body Lipid (kg) | Body Moisture (kg) | Body Ash (kg) | Protein Deposition (g/d) | Lipid Deposition (g/d) | Moisture Deposition (g/d) | Ash Deposition (g/d) | Total Heat loss (MJ/d) | ep | Avg¶ Protein (kg) | Avg¶ Lipid (kg) | Avg¶ Ebwt (kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P1 | 12.1 | 27.7 | 30.3 | 0.676 | 1.401 | 0.483 | 4.81 | 3.31 | 18.18 | 0.77 | 115.72 | 91.80 | 392.26 | 16.14 | 13.93 | 0.579 | 3.25 | 2.07 | 19.21 |
| | 12.5 | 26.9 | 29.9 | 0.791 | 1.396 | 0.567 | 4.35 | 2.94 | 18.48 | 0.84 | 118.31 | 94.72 | 481.86 | 22.33 | 13.68 | 0.589 | 3.05 | 1.90 | 19.00 |
| | 13.9 | 28.6 | 30.6 | 0.759 | 1.332 | 0.570 | 4.68 | 3.14 | 19.33 | 0.79 | 124.22 | 99.36 | 480.31 | 18.16 | 12.43 | 0.655 | 3.31 | 2.05 | 20.36 |
| | 13.3 | 27.9 | 30.6 | 0.723 | 1.422 | 0.508 | 4.55 | 3.52 | 18.38 | 0.81 | 112.36 | 108.69 | 418.00 | 18.30 | 12.34 | 0.55 | 3.20 | 2.22 | 19.89 |
| P2 | 12.3 | 27.8 | 30.4 | 0.787 | 1.461 | 0.539 | 4.39 | 3.56 | 18.44 | 0.73 | 115.90 | 117.96 | 464.88 | 16.82 | 13.60 | 0.636 | 3.05 | 2.20 | 19.35 |
| | 12.5 | 26.8 | 29.3 | 0.766 | 1.51 | 0.507 | 4.34 | 3.31 | 18.03 | 0.79 | 117.95 | 111.34 | 462.79 | 20.18 | 14.52 | 0.624 | 3.04 | 2.08 | 18.92 |
| | 14.3 | 26.9 | 29.3 | 0.75 | 1.3 | 0.577 | 4.37 | 2.99 | 18.31 | 0.75 | 118.51 | 100.32 | 465.10 | 17.73 | 11.92 | 0.72 | 3.19 | 1.99 | 19.84 |
| | 13.6 | 27.1 | 29.5 | 0.795 | 1.295 | 0.614 | 4.29 | 2.95 | 18.53 | 0.77 | 119.21 | 100.71 | 498.07 | 19.69 | 11.82 | 0.673 | 3.09 | 1.94 | 19.60 |
| P3 | 12.5 | 28.5 | 30.7 | 0.767 | 1.521 | 0.504 | 4.62 | 3.92 | 18.46 | 0.83 | 121.49 | 131.46 | 445.13 | 20.15 | 14.03 | 0.734 | 3.22 | 2.41 | 20.05 |
| | 11.8 | 28.9 | 31.3 | 0.672 | 1.389 | 0.484 | 4.88 | 4.25 | 18.54 | 0.85 | 111.32 | 118.66 | 382.81 | 17.84 | 12.86 | 0.749 | 3.26 | 2.53 | 19.74 |
| | 12.8 | 28.4 | 30.2 | 0.725 | 1.233 | 0.588 | 4.63 | 3.10 | 19.38 | 0.89 | 118.15 | 92.28 | 471.41 | 22.32 | 11.47 | 0.904 | 3.21 | 1.99 | 19.89 |
| | 11.6 | 27.1 | 29.1 | 0.761 | 1.334 | 0.570 | 4.18 | 3.22 | 18.57 | 0.84 | 111.10 | 105.10 | 489.74 | 22.58 | 12.60 | 0.768 | 2.90 | 2.01 | 18.73 |
| P4 | 14.3 | 29.1 | 30.5 | 0.63 | 1.434 | 0.439 | 4.80 | 4.79 | 18.47 | 0.76 | 105.80 | 132.91 | 371.91 | 14.58 | 13.33 | 0.826 | 3.21 | 2.79 | 19.66 |
| | 12.8 | 27.8 | 30.5 | 0.736 | 1.5 | 0.491 | 4.47 | 3.80 | 18.15 | 0.94 | 112.46 | 128.13 | 415.45 | 24.76 | 14.33 | 0.826 | 3.24 | 2.39 | 20.28 |
| | 11.7 | 28.8 | 30.9 | 0.711 | 1.396 | 0.509 | 4.58 | 4.56 | 18.07 | 0.82 | 108.99 | 139.24 | 396.10 | 18.33 | 12.44 | 0.872 | 3.11 | 2.69 | 19.62 |
| | 12.1 | 28.6 | 30.4 | 0.572 | 1.3 | 0.440 | 5.14 | 4.11 | 18.50 | 0.97 | 107.65 | 102.48 | 339.89 | 19.68 | 12.52 | 0.953 | 3.41 | 2.47 | 19.80 |
| P5 | 13.6 | 27.2 | 29.4 | 0.559 | 1.142 | 0.489 | 4.05 | 5.41 | 16.67 | 0.83 | 76.34 | 144.33 | 294.37 | 15.82 | 9.25 | 0.944 | 2.83 | 3.10 | 18.70 |
| | 11.6 | 28.4 | 30.4 | 0.726 | 1.67 | 0.435 | 4.41 | 5.44 | 17.32 | 0.79 | 107.44 | 173.92 | 389.22 | 18.25 | 15.10 | 0.864 | 2.96 | 3.09 | 19.02 |
| | 12.1 | 27.8 | 30.7 | 0.686 | 1.682 | 0.408 | 4.56 | 5.27 | 16.89 | 0.83 | 105.42 | 159.90 | 344.42 | 18.13 | 15.88 | 0.845 | 3.08 | 3.03 | 19.00 |
| | 14.2 | 28.1 | 29.2 | 0.627 | 1.49 | 0.421 | 4.24 | 4.98 | 17.88 | 0.80 | 94.24 | 166.72 | 373.49 | 16.92 | 13.06 | 0.859 | 3.11 | 2.97 | 20.35 |
| P6 | 11.8 | 27.8 | 29.3 | 0.516 | 1.351 | 0.382 | 3.64 | 6.35 | 16.30 | 0.71 | 58.66 | 162.89 | 261.64 | 11.34 | 12.27 | 0.828 | 2.64 | 3.58 | 19.12 |
| | 11.5 | 29.1 | 31.1 | 0.576 | 1.487 | 0.387 | 3.88 | 6.67 | 17.43 | 0.77 | 66.89 | 172.95 | 299.53 | 13.27 | 13.70 | 0.852 | 2.75 | 3.73 | 19.65 |
| | 12.4 | 24.6 | 26.4 | 0.468 | 1.211 | 0.386 | 3.25 | 5.74 | 14.42 | 0.65 | 50.74 | 162.84 | 221.17 | 10.24 | 10.37 | 0.798 | 2.49 | 3.29 | 17.80 |
| | 12.7 | 28.6 | 30.1 | 0.47 | 1.221 | 0.385 | 3.80 | 6.65 | 16.45 | 0.89 | 54.74 | 155.98 | 228.29 | 14.48 | 10.70 | 0.883 | 2.79 | 3.76 | 19.95 |

¶ Average values between Starting weight and Finishing weight.

Summary of some of the results for pigs kept at 22°C in the experiment reported in Chapter 6.

| Protein Treatment | Starting Weight (kg) | EBWT (kg) | Final Weight (kg) | ADG (kg/d) | Food Intake (kg/d) | FCE | Body Protein (kg) | Body Lipid (kg) | Body Moisture (kg) | Body Ash (kg) | Protein Deposition (g/d) | Lipid Deposition (g/d) | Moisture Deposition (g/d) | Ash Deposition (g/d) | Total Heat loss (MJ/d) | ep | Avg¶ Protein (kg) | Avg¶ Lipid (kg) | Avg¶ Ebwt (kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P1 | 12.7 | 28.6 | 30.8 | 0.787 | 1.369 | 0.575 | 4.42 | 3.13 | 20.01 | 0.83 | 114.84 | 97.91 | 521.89 | 20.81 | 13.23 | 0.574 | 3.10 | 2.00 | 19.95 |
| | 14.0 | 27.2 | 30.1 | 0.805 | 1.332 | 0.604 | 4.39 | 2.88 | 18.78 | 0.78 | 121.46 | 95.67 | 497.90 | 19.55 | 12.62 | 0.625 | 3.17 | 1.92 | 19.81 |
| | 13.4 | 26.9 | 29.4 | 0.800 | 1.245 | 0.643 | 4.34 | 2.83 | 18.78 | 0.75 | 123.13 | 95.53 | 516.69 | 19.00 | 11.33 | 0.681 | 3.11 | 1.88 | 19.42 |
| | 15.4 | 28.7 | 29.5 | 0.742 | 1.182 | 0.628 | 4.40 | 2.89 | 20.28 | 0.82 | 118.20 | 96.30 | 556.78 | 20.79 | 10.50 | 0.693 | 3.28 | 1.97 | 21.19 |
| P2 | 14.3 | 29.3 | 31.4 | 0.743 | 1.262 | 0.589 | 4.81 | 3.78 | 19.40 | 0.83 | 122.35 | 121.42 | 451.81 | 18.72 | 10.42 | 0.764 | 3.41 | 2.38 | 21.04 |
| | 11.5 | 27.8 | 29.8 | 0.732 | 1.454 | 0.503 | 4.38 | 3.64 | 18.60 | 0.71 | 111.00 | 114.04 | 453.93 | 15.59 | 13.74 | 0.587 | 3.00 | 2.22 | 19.01 |
| | 14.3 | 27.7 | 30.4 | 0.808 | 1.266 | 0.638 | 4.44 | 3.01 | 19.00 | 0.90 | 122.40 | 101.33 | 500.92 | 25.28 | 10.97 | 0.755 | 3.22 | 1.99 | 20.18 |
| | 11.9 | 28.7 | 31.3 | 0.774 | 1.181 | 0.655 | 4.63 | 3.33 | 19.51 | 0.76 | 118.43 | 100.37 | 479.13 | 17.10 | 10.18 | 0.793 | 3.15 | 2.08 | 19.68 |
| P3 | 12.5 | 28.2 | 29.7 | 0.717 | 1.339 | 0.535 | 4.47 | 3.90 | 18.81 | 0.69 | 113.29 | 126.45 | 455.38 | 14.25 | 11.74 | 0.748 | 3.11 | 2.38 | 19.66 |
| | 10.6 | 27.6 | 29.4 | 0.752 | 1.259 | 0.597 | 4.54 | 3.51 | 18.42 | 0.84 | 122.10 | 111.23 | 469.67 | 21.99 | 10.97 | 0.865 | 3.01 | 2.12 | 18.49 |
| | 10.8 | 29.4 | 31.8 | 0.700 | 1.265 | 0.553 | 4.98 | 3.91 | 19.44 | 0.97 | 115.51 | 105.49 | 421.06 | 22.20 | 11.45 | 0.825 | 3.24 | 2.33 | 19.49 |
| | 13.0 | 26.8 | 30.2 | 0.717 | 1.274 | 0.563 | 4.49 | 3.54 | 17.92 | 0.84 | 111.34 | 110.08 | 405.18 | 19.93 | 11.49 | 0.778 | 3.15 | 2.22 | 19.20 |
| P4 | 11.9 | 29.4 | 31.6 | 0.637 | 1.389 | 0.459 | 4.79 | 4.38 | 18.93 | 0.95 | 101.07 | 114.90 | 369.61 | 20.06 | 13.34 | 0.789 | 3.22 | 2.60 | 19.96 |
| | 15.6 | 28.4 | 30.0 | 0.720 | 1.520 | 0.474 | 4.45 | 4.11 | 18.54 | 0.90 | 113.18 | 151.85 | 435.44 | 23.05 | 13.50 | 0.790 | 3.31 | 2.59 | 21.13 |
| | 13.3 | 27.8 | 29.7 | 0.631 | 1.281 | 0.493 | 4.37 | 3.92 | 18.27 | 0.79 | 96.38 | 115.58 | 380.47 | 16.02 | 11.84 | 0.814 | 3.11 | 2.42 | 19.80 |
| | 12.3 | 26.5 | 29.2 | 0.704 | 1.334 | 0.528 | 4.15 | 3.63 | 17.58 | 0.89 | 101.12 | 116.03 | 409.36 | 22.77 | 12.49 | 0.810 | 2.93 | 2.24 | 18.73 |
| P5 | 11.3 | 28.2 | 30.2 | 0.540 | 1.230 | 0.439 | 4.10 | 5.39 | 17.54 | 0.79 | 72.09 | 131.91 | 297.64 | 13.50 | 11.12 | 0.787 | 2.84 | 3.09 | 19.12 |
| | 12.4 | 28.7 | 30.4 | 0.582 | 1.425 | 0.408 | 4.36 | 5.19 | 17.97 | 0.79 | 84.81 | 140.11 | 328.56 | 14.25 | 13.36 | 0.787 | 3.04 | 3.02 | 19.84 |
| | 12.6 | 21.7 | 23.5 | 0.583 | 1.400 | 0.416 | 4.30 | 4.79 | 16.71 | 1.11 | 87.34 | 135.15 | 302.35 | 26.32 | 13.13 | 0.825 | 3.03 | 2.83 | 19.18 |
| | 13.7 | 27.6 | 29.4 | 0.581 | 1.439 | 0.404 | 4.47 | 4.66 | 17.35 | 0.92 | 94.69 | 137.61 | 322.67 | 19.79 | 13.43 | 0.872 | 3.19 | 2.80 | 19.88 |
| P6 | 11.8 | 20.8 | 22.2 | 0.478 | 1.263 | 0.378 | 3.88 | 5.74 | 16.82 | 0.99 | 61.88 | 136.80 | 260.68 | 18.35 | 11.90 | 0.904 | 2.76 | 3.27 | 19.10 |
| | 15.4 | 29.1 | 30.8 | 0.616 | 1.385 | 0.445 | 3.85 | 5.88 | 18.11 | 0.77 | 67.86 | 192.84 | 336.37 | 13.67 | 11.35 | 0.885 | 3.00 | 3.47 | 21.40 |
| | 12.3 | 28.0 | 29.7 | 0.497 | 1.252 | 0.397 | 3.85 | 5.74 | 16.99 | 0.92 | 60.73 | 139.80 | 263.87 | 16.48 | 11.64 | 0.895 | 2.78 | 3.29 | 19.47 |
| | 13.0 | 28.8 | 30.4 | 0.483 | 1.250 | 0.386 | 3.95 | 6.19 | 17.36 | 0.85 | 59.34 | 147.00 | 254.63 | 13.50 | 10.35 | 0.882 | 2.89 | 3.54 | 20.19 |

¶ Average values between Starting weight and Finishing weight.

Summary of some of the results for pigs kept at 26°C in the experiment reported in Chapter 6.

| Protein Treatment | Starting Weight (kg) | EBWT (kg) | Final Weight (kg) | ADG (kg/d) | Food Intake (kg/d) | FCE | Body Protein (kg) | Body Lipid (kg) | Body Moisture (kg) | Body Ash (kg) | Protein Deposition (g/d) | Lipid Deposition (g/d) | Moisture Deposition (g/d) | Ash Deposition (g/d) | Total Heat loss (MJ/d) | ep | Avg¶ Protein (kg) | Avg¶ Lipid (kg) | Avg¶ EBWT (kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P1 | 12.1 | 28.1 | 30.1 | 0.721 | 1.056 | 0.683 | 4.63 | 2.62 | 19.80 | 0.85 | 117.43 | 71.69 | 487.01 | 20.55 | 9.66 | 0.779 | 3.16 | 1.73 | 19.46 |
| | 12.6 | 29.0 | 31.0 | 0.682 | 1.085 | 0.629 | 5.01 | 3.11 | 19.54 | 1.06 | 120.24 | 83.01 | 429.94 | 26.10 | 9.57 | 0.782 | 3.38 | 1.99 | 20.11 |
| | 11.7 | 28.7 | 30.9 | 0.769 | 1.044 | 0.737 | 4.57 | 2.80 | 20.08 | 0.95 | 117.15 | 79.83 | 508.20 | 24.96 | 9.17 | 0.786 | 3.10 | 1.80 | 19.56 |
| | 11.6 | 27.7 | 29.3 | 0.710 | 1.104 | 0.643 | 4.51 | 2.70 | 19.24 | 0.87 | 115.81 | 76.19 | 477.56 | 21.86 | 10.22 | 0.729 | 3.07 | 1.75 | 18.99 |
| P2 | 14.7 | 28.2 | 30.1 | 0.704 | 1.203 | 0.585 | 4.45 | 3.47 | 19.04 | 0.87 | 109.06 | 111.74 | 445.98 | 21.02 | 10.49 | 0.712 | 3.25 | 2.24 | 20.63 |
| | 11.0 | 27.7 | 29.9 | 0.727 | 1.058 | 0.687 | 4.57 | 3.09 | 18.80 | 0.81 | 116.53 | 89.65 | 450.78 | 19.35 | 9.07 | 0.883 | 3.05 | 1.92 | 18.74 |
| | 10.9 | 28.4 | 30.6 | 0.731 | 1.088 | 0.672 | 4.72 | 3.04 | 19.30 | 0.94 | 118.49 | 84.80 | 460.47 | 23.52 | 9.66 | 0.873 | 3.12 | 1.89 | 19.03 |
| | 12.2 | 28.8 | 30.3 | 0.725 | 1.023 | 0.709 | 4.66 | 3.10 | 19.62 | 0.99 | 118.31 | 90.45 | 477.28 | 26.17 | 8.49 | 0.934 | 3.19 | 1.97 | 19.83 |
| P3 | 13.4 | 28.3 | 29.7 | 0.739 | 1.263 | 0.585 | 4.48 | 3.91 | 18.59 | 0.93 | 118.29 | 135.58 | 460.01 | 25.17 | 10.43 | 0.880 | 3.18 | 2.42 | 20.12 |
| | 11.0 | 28.1 | 31.9 | 0.721 | 1.164 | 0.625 | 4.74 | 3.83 | 18.39 | 1.01 | 106.37 | 103.91 | 377.79 | 23.50 | 10.37 | 0.885 | 3.19 | 2.32 | 19.29 |
| | 13.5 | 30.2 | 31.8 | 0.654 | 1.123 | 0.582 | 4.97 | 4.13 | 19.93 | 0.98 | 110.02 | 114.16 | 407.84 | 21.54 | 9.42 | 0.952 | 3.43 | 2.53 | 21.13 |
| | 13.7 | 28.8 | 30.2 | 0.750 | 1.333 | 0.563 | 4.56 | 3.86 | 19.18 | 0.87 | 120.27 | 132.67 | 479.45 | 21.99 | 11.53 | 0.844 | 3.24 | 2.40 | 20.49 |
| P4 | 13.8 | 28.5 | 29.4 | 0.622 | 1.381 | 0.450 | 4.34 | 4.56 | 18.39 | 0.85 | 96.31 | 144.45 | 387.73 | 18.65 | 12.44 | 0.764 | 3.13 | 2.76 | 20.38 |
| | 11.5 | 31.3 | 33.1 | 0.802 | 1.469 | 0.546 | 4.53 | 5.27 | 20.13 | 0.91 | 108.47 | 165.88 | 477.73 | 21.76 | 12.61 | 0.807 | 3.07 | 3.03 | 20.74 |
| | 14.5 | 27.6 | 29.4 | 0.675 | 1.271 | 0.531 | 4.33 | 4.20 | 17.75 | 0.87 | 104.47 | 145.24 | 390.36 | 21.15 | 10.59 | 0.911 | 3.18 | 2.60 | 20.28 |
| | 13.7 | 29.2 | 31.2 | 0.796 | 1.440 | 0.553 | 4.32 | 4.82 | 18.38 | 0.83 | 109.67 | 176.22 | 444.08 | 20.57 | 11.74 | 0.829 | 3.12 | 2.88 | 20.48 |
| P5 | 11.6 | 28.9 | 29.6 | 0.732 | 1.345 | 0.544 | 4.29 | 5.31 | 18.05 | 0.89 | 91.82 | 155.59 | 370.20 | 19.70 | 11.54 | 0.918 | 2.95 | 3.05 | 19.59 |
| | 11.4 | 28.0 | 30.4 | 0.637 | 1.450 | 0.439 | 4.08 | 4.99 | 17.55 | 0.97 | 95.43 | 161.90 | 398.70 | 25.19 | 12.76 | 0.868 | 2.84 | 2.89 | 19.08 |
| | 11.7 | 28.4 | 30.2 | 0.657 | 1.238 | 0.531 | 4.10 | 5.20 | 18.09 | 0.94 | 84.88 | 151.69 | 369.52 | 21.03 | 10.28 | 0.928 | 2.87 | 3.00 | 19.42 |
| | 15.0 | 31.8 | 33.4 | 0.504 | 1.500 | 0.336 | 4.66 | 6.25 | 19.56 | 1.00 | 91.70 | 186.44 | 361.29 | 20.86 | 12.61 | 0.819 | 3.38 | 3.64 | 22.55 |
| P6 | 12.8 | 27.9 | 29.2 | 0.504 | 1.132 | 0.445 | 3.68 | 6.23 | 16.68 | 0.84 | 49.70 | 140.67 | 226.12 | 12.67 | 10.08 | 0.810 | 2.74 | 3.56 | 19.64 |
| | 13.4 | 28.2 | 30.4 | 0.576 | 1.344 | 0.429 | 3.93 | 7.12 | 15.91 | 0.82 | 62.38 | 187.74 | 226.31 | 13.42 | 11.07 | 0.836 | 2.90 | 4.02 | 20.05 |
| | 14.1 | 28.0 | 29.3 | 0.561 | 1.343 | 0.418 | 3.82 | 6.86 | 16.05 | 0.87 | 68.30 | 218.01 | 264.30 | 17.58 | 9.71 | 0.910 | 2.90 | 3.92 | 20.28 |
| | 13.2 | 28.8 | 30.8 | 0.651 | 1.456 | 0.447 | 3.83 | 7.01 | 16.69 | 0.87 | 73.63 | 225.95 | 310.03 | 18.50 | 10.95 | 0.892 | 2.84 | 3.96 | 20.30 |

¶ Average values between Starting weight and Finishing weight.

Summary of some of the results for pigs kept at 30°C in the experiment reported in Chapter 6.

| Protein Treatment | Starting Weight (kg) | EBWT (kg) | Final Weight (kg) | ADG (kg/d) | Food Intake (kg/d) | FCE | Body Protein (kg) | Body Lipid (kg) | Body Moisture (kg) | Body Ash (kg) | Protein Deposition (g/d) | Lipid Deposition (g/d) | Moisture Deposition (g/d) | Ash Deposition (g/d) | Total Heat loss (MJ/d) | ep | Avg¶ Protein (kg) | Avg¶ Lipid (kg) | Avg¶ EBWT (kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P1 | 12.0 | 29.1 | 31.3 | 0.691 | 0.915 | 0.755 | 5.07 | 2.45 | 20.57 | 0.92 | 120.99 | 57.93 | 464.72 | 21.06 | 8.08 | 0.958 | 3.37 | 1.64 | 19.90 |
| | 13.4 | 29.1 | 31.0 | 0.626 | 1.086 | 0.576 | 5.09 | 2.72 | 20.25 | 0.85 | 114.70 | 64.03 | 420.80 | 16.98 | 10.47 | 0.747 | 3.49 | 1.82 | 20.53 |
| | 11.8 | 28.8 | 30.6 | 0.679 | 0.956 | 0.710 | 4.85 | 2.38 | 20.51 | 0.93 | 115.31 | 56.41 | 471.00 | 21.78 | 8.87 | 0.862 | 3.24 | 1.59 | 19.59 |
| | 12.8 | 28.0 | 29.9 | 0.656 | 1.149 | 0.571 | 4.78 | 3.88 | 18.40 | 0.81 | 114.82 | 115.20 | 396.51 | 17.56 | 9.35 | 0.696 | 3.29 | 2.38 | 19.73 |
| P2 | 12.8 | 27.6 | 29.1 | 0.543 | 1.050 | 0.517 | 5.18 | 3.32 | 18.13 | 0.84 | 113.10 | 81.39 | 335.52 | 16.12 | 9.37 | 0.881 | 3.49 | 2.10 | 19.50 |
| | 12.1 | 31.5 | 34.1 | 0.734 | 1.272 | 0.577 | 5.27 | 4.42 | 20.62 | 1.00 | 119.48 | 119.49 | 433.48 | 22.25 | 10.94 | 0.749 | 3.48 | 2.62 | 21.11 |
| | 12.7 | 28.4 | 30.1 | 0.644 | 1.082 | 0.595 | 4.94 | 3.08 | 19.31 | 0.96 | 117.08 | 81.53 | 417.89 | 22.50 | 9.73 | 0.874 | 3.36 | 1.98 | 19.87 |
| | 12.6 | 28.7 | 30.0 | 0.644 | 0.968 | 0.665 | 4.74 | 3.67 | 19.05 | 0.96 | 110.09 | 103.70 | 411.14 | 22.45 | 7.36 | 0.929 | 3.25 | 2.27 | 19.97 |
| P3 | 10.4 | 27.1 | 29.2 | 0.671 | 1.158 | 0.579 | 4.30 | 3.84 | 17.79 | 0.88 | 101.38 | 111.34 | 400.45 | 21.19 | 10.25 | 0.828 | 2.88 | 2.28 | 18.21 |
| | 11.8 | 26.7 | 28.8 | 0.606 | 1.123 | 0.540 | 4.50 | 3.63 | 17.58 | 0.85 | 101.60 | 100.64 | 362.36 | 18.69 | 10.15 | 0.865 | 3.07 | 2.22 | 18.60 |
| | 12.2 | 27.0 | 29.5 | 0.619 | 1.131 | 0.547 | 4.55 | 3.42 | 17.95 | 0.91 | 101.87 | 92.17 | 367.52 | 20.48 | 10.60 | 0.862 | 3.13 | 2.13 | 18.94 |
| | 14.3 | 29.4 | 31.5 | 0.635 | 1.174 | 0.541 | 4.89 | 3.44 | 19.88 | 0.96 | 106.88 | 90.92 | 401.61 | 20.89 | 11.16 | 0.876 | 3.45 | 2.21 | 21.08 |
| P4 | 12.1 | 29.0 | 30.7 | 0.665 | 1.298 | 0.512 | 4.47 | 5.35 | 18.17 | 0.85 | 99.56 | 161.36 | 377.63 | 18.42 | 10.47 | 0.852 | 3.08 | 3.09 | 19.85 |
| | 11.7 | 29.7 | 30.7 | 0.655 | 1.307 | 0.501 | 4.52 | 5.29 | 18.70 | 0.93 | 99.34 | 154.63 | 389.73 | 20.82 | 10.87 | 0.845 | 3.08 | 3.05 | 20.08 |
| | 14.8 | 28.5 | 30.8 | 0.590 | 1.111 | 0.531 | 4.46 | 5.03 | 17.99 | 0.83 | 88.35 | 148.56 | 320.48 | 15.64 | 8.47 | 0.906 | 3.27 | 3.03 | 20.83 |
| | 10.8 | 28.1 | 30.0 | 0.640 | 1.118 | 0.572 | 4.18 | 4.81 | 18.14 | 0.85 | 88.78 | 135.37 | 377.01 | 18.30 | 9.09 | 0.893 | 2.85 | 2.78 | 18.88 |
| P5 | 12.3 | 28.9 | 30.7 | 0.656 | 1.270 | 0.517 | 4.04 | 5.52 | 18.32 | 0.91 | 82.80 | 167.03 | 377.76 | 20.41 | 10.19 | 0.876 | 2.88 | 3.18 | 19.89 |
| | 12.7 | 23.9 | 25.8 | 0.554 | 0.895 | 0.619 | 3.42 | 4.44 | 15.19 | 0.66 | 56.59 | 122.88 | 247.76 | 10.65 | 7.02 | 0.880 | 2.60 | 2.66 | 17.60 |
| | 13.3 | 27.5 | 29.3 | 0.433 | 0.950 | 0.456 | 4.01 | 5.33 | 17.17 | 0.85 | 57.98 | 119.27 | 237.49 | 12.94 | 7.94 | 0.869 | 2.93 | 3.12 | 19.67 |
| | 11.6 | 28.5 | 30.1 | 0.616 | 1.330 | 0.463 | 4.32 | 5.92 | 17.26 | 0.89 | 89.86 | 170.80 | 331.59 | 18.95 | 10.76 | 0.912 | 2.97 | 3.36 | 19.42 |
| P6 | 13.9 | 27.6 | 29.9 | 0.409 | 0.980 | 0.417 | 3.69 | 6.47 | 16.49 | 0.81 | 44.64 | 141.26 | 197.83 | 10.73 | 7.92 | 0.873 | 2.82 | 3.71 | 19.98 |
| | 13.5 | 27.2 | 28.1 | 0.356 | 1.145 | 0.311 | 4.04 | 6.98 | 15.35 | 0.69 | 52.54 | 147.68 | 167.14 | 7.57 | 9.93 | 0.863 | 2.96 | 3.96 | 19.62 |
| | 13.4 | 28.6 | 29.4 | 0.388 | 1.050 | 0.370 | 3.82 | 6.74 | 16.93 | 0.96 | 47.25 | 141.90 | 206.30 | 14.24 | 8.87 | 0.854 | 2.85 | 3.83 | 20.28 |
| | 13.1 | 28.1 | 29.9 | 0.420 | 0.975 | 0.431 | 3.71 | 6.66 | 16.72 | 0.91 | 47.13 | 143.92 | 212.03 | 13.64 | 7.68 | 0.929 | 2.77 | 3.78 | 19.88 |

¶ Average values between Starting weight and Finishing weight.

## APPENDIX 3

The following data were used in the multiple regression analysis to determine the maximum total heat loss of a pig growing between 12 and 30 kg.

| Temperature Treatment | Protein Treatment | 38-t | Body Protein (kg) | $EBWT^{0.67}$ (kg) | Total Heat Loss (MJ/d) |
|---|---|---|---|---|---|
| 18°C | 5 | 20 | 2.96 | 7.19 | 15.10 |
| | 5 | 20 | 3.08 | 7.19 | 15.88 |
| | 5 | 20 | 3.11 | 7.53 | 13.06 |
| | 6 | 20 | 2.64 | 7.22 | 12.26 |
| | 6 | 20 | 2.75 | 7.36 | 13.69 |
| | 6 | 20 | 2.49 | 6.88 | 10.37 |
| 22°C | 4 | 16 | 3.22 | 7.43 | 13.34 |
| | 4 | 16 | 3.31 | 7.72 | 13.50 |
| | 4 | 16 | 3.11 | 7.39 | 11.84 |
| | 4 | 16 | 2.93 | 7.12 | 12.49 |
| | 5 | 16 | 2.84 | 7.22 | 11.12 |
| | 5 | 16 | 3.04 | 7.40 | 13.36 |
| | 5 | 16 | 3.03 | 7.24 | 13.13 |
| | 5 | 16 | 3.19 | 7.41 | 13.43 |
| | 6 | 16 | 2.76 | 7.22 | 11.90 |
| | 6 | 16 | 3.00 | 7.79 | 11.35 |
| | 6 | 16 | 2.78 | 7.31 | 11.64 |
| | 6 | 16 | 2.89 | 7.49 | 10.35 |
| 26°C | 4 | 12 | 3.13 | 7.54 | 12.44 |
| | 4 | 12 | 3.07 | 7.63 | 12.61 |
| | 4 | 12 | 3.18 | 7.51 | 10.59 |
| | 4 | 12 | 3.12 | 7.56 | 11.74 |
| | 5 | 12 | 2.95 | 7.34 | 11.54 |
| | 5 | 12 | 2.87 | 7.30 | 10.28 |
| | 5 | 12 | 3.38 | 8.06 | 12.61 |
| | 6 | 12 | 2.74 | 7.35 | 10.08 |
| | 6 | 12 | 2.90 | 7.45 | 11.07 |
| | 6 | 12 | 2.90 | 7.51 | 9.71 |
| | 6 | 12 | 2.84 | 7.52 | 10.95 |
| 30°C | 3 | 8 | 2.88 | 6.99 | 10.25 |
| | 3 | 8 | 3.07 | 7.09 | 10.15 |
| | 3 | 8 | 3.13 | 7.17 | 10.60 |
| | 3 | 8 | 3.45 | 7.71 | 11.16 |
| | 4 | 8 | 3.08 | 7.40 | 10.47 |
| | 4 | 8 | 3.08 | 7.46 | 10.87 |
| | 4 | 8 | 2.85 | 7.16 | 9.09 |
| | 5 | 8 | 2.87 | 7.42 | 10.19 |
| | 5 | 8 | 2.60 | 6.83 | 7.02 |
| | 5 | 8 | 2.93 | 7.36 | 7.94 |
| | 5 | 8 | 2.97 | 7.30 | 10.76 |
| | 6 | 8 | 2.82 | 7.44 | 7.92 |
| | 6 | 8 | 2.96 | 7.34 | 9.93 |
| | 6 | 8 | 2.85 | 7.51 | 8.87 |
| | 6 | 8 | 2.77 | 7.41 | 7.68 |