

**THE EFFECT OF DIETARY PROTEIN AND ENERGY ON FEED INTAKE AND
PERFORMANCE OF LAYING HENS**

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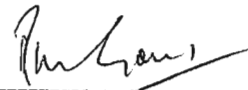
DECLARATION

I hereby declare that this thesis is the result of my own investigation. Where use of work of others has been made, it has been duly acknowledged in the text.



T. T. NKUKWANA

I hereby certify that this statement is correct



Prof. R. M. Gous (Supervisor)

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ACRONYMS

BDW	Change in Body Weight
Calc	Calculated
CP	Crude Protein
DCP	Dietary Crude Protein
CPI	Crude Protein Intake
Deter	Determined
EW	Egg Weight
EO	Egg Output
FCE	Feed Conversion Efficiency
FI	Feed Intake
HB	Hy-line Brown
HE	High Energy
HP	High Protein
LB	Lohmann Brown
LE	Low Energy
LP	Low Protein
LW	Lohmann White
ROL	Rate of Laying
⁰ C	Degrees Celsius
MEI	Metabolisable Energy Intake

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ABSTRACT

This study was designed to devise a method by which the optimum combination of dietary energy and protein could be found that maximises the margin over feeding cost in an egg production enterprise. It was necessary to be able to predict feeding costs and revenue associated with the use of a wide range of feeds varying in protein and energy.

To this end, two experiments were conducted using 256 Lohmann (128 White and 128 Brown) in the first, and 1296 Hy-line Brown laying birds in the second trial, that were 33 and 38 weeks old at the beginning of the two trials. Using the WinFeed 1.1 (1996) feed formulation programme, four basal (corner) feeds were formulated in both experiments, from which four protein and four energy contents (16 feeds) were produced in the first experiment, and six protein and three energy contents (18 feeds) were used in the second. Each feed was given to three replicates of 16 birds in the first trial, and to three replicates of 24 birds in the second. The trials each lasted ten weeks, and the data collected included food intake, change in body weight, egg weight and rate of laying.

Using the results from these two experiments and from previously published research, the effects of dietary protein and energy on food intake were predicted independently, and these predictions were then used to determine the cost of feeding. Similarly, egg weight and rate of lay were predicted independently for changes in dietary protein and energy, from which the revenue could be calculated over the range of energy and protein contents. It is understood that a more integrated approach would be more accurate for this purpose, but such an approach was beyond the scope of this investigation.

The use of contour plots based on regression analyses of the estimated income-minus-feeding cost on changes in dietary protein and energy enabled evaluations to be made of the effect on profitability of changes in egg price and maize price. And it was deduced that under conditions in which the maize price is high, maximum profitability is achieved with high energy and high protein content, irrespective of the price paid for eggs. When the maize price is reduced, the combination of protein and energy that yields the highest

return over feed cost changes to low protein and low energy feeds. This change is defensible on the grounds that the price of high-density feeds does not change as much as that of low-density feeds when the maize price is lowered, whereas production, and hence returns, remains the same, hence the low density feeds yield higher returns under such circumstances.

The method applied in this study appears to be a useful tool for decision-making by egg producers and nutritionists.

CHAPTER 1

GENERAL INTRODUCTION

Over the past three decades nutrition of the laying hen has been researched extensively. To a considerable extent, with the use of linear programming designed to meet certain nutritional requirements at minimal costs, nutritionists managed to come up with feeding and management programmes that were aimed at satisfying nutritional requirements of most present strains of laying hens, simultaneously taking into consideration the effects of many interacting factors that influence nutrient intake and the efficiency with which nutrients are partitioned to satisfy the needs for maintenance and egg production once in the hen's body.

However, geneticists have continued to improve laying performance of commercial laying strains and mean maximum egg output is now in excess of 60g/d whereas 10 years ago it was around 55g/d. As a result, the nutritional needs for egg production, and the optimum environment in which the hen performs these tasks, are clearly different from what they used to be ten years ago.

The concept of potential production is the main reason behind studying nutrition and for several years now feed intake has been realized as the most important determinant of performance in poultry feeding. Poultry, in general, primarily eat food to satisfy a need for essential nutrients, and as soon as this need is met, they stop eating. However, like any other biological process, the amount of food that a hen will eat is affected by several factors, including dietary constraints (food bulk or toxins), the environment, nutritional requirements, physiological state of the bird, genotype and the sensory system. In practical terms it is very difficult to separate feed intake from these factors, because they are a part of the hen's daily existence. Thus, despite adequate diet formulation, maintaining efficiency in daily feed intake of the hen is critical.

There is a common belief that a specific combination of energy and protein in the diet will maximize feed utilization efficiency and egg production (both egg numbers and egg mass). However, it is also realized that this combination may not be the same for both objectives.

Hence, there is a need for accurate decision-making in commercial nutrition, because as much as several theories have been developed to address nutrient specifications, collectively they still do not form a generalized theory. Also, the objective of any egg producer is to maximise profit, not necessarily egg production or food conversion efficiency.

To this date, there is still no suitable method for predicting the amount of a given food that a laying hen will consume each day when kept in a given environment, and until such a model is produced it is worth continuing to measure responses of hens to dietary protein and energy, as these data may assist modellers to produce sufficiently accurate models of food intake at a later date. And unless a complete review of feed and management practices is made, it will always be difficult to correct problems associated with poor feed intake. Hence, it is critical that geneticists and nutritionists work together to understand thoroughly how economics and environmental control can be integrated into feeding and management programs of the laying hen.

The work reported in this thesis was designed to contribute some new knowledge or put more emphasis on what has already been discovered about the nutrition of the laying hen. By making use of published theories and past research, a method was devised to determine the combination of dietary protein and energy that would maximise profitability in an egg-production enterprise, given information about the genotype, the cost of feed ingredients and the revenue derived from the sale of eggs. This method could then be applied generally as these above conditions were changed.

Two experiments were performed in this study, in which three strains of laying hens were used, and in which comparisons of food intake and laying performance were made of these hens when they were offered feeds varying in dietary energy and protein. The objectives were first to characterise these genotypes such that their responses to changes in dietary protein and energy could be applied in the method devised to determine the optimum combination of these two dietary attributes under current economic conditions, and then to make use of this information to predict how these optimum conditions would change with changes in the value of the eggs produced. This has practical implications especially for egg producers who produce their own feed, and are hence in a position to alter the composition of the feed when economic conditions warrant such a change.

CHAPTER 2

REVIEW OF FACTORS ASSOCIATED WITH THE FEED, THE ENVIRONMENT AND THE GENOTYPE THAT AFFECT FEED INTAKE AND PERFORMANCE IN LAYING HENS

2.1 INTRODUCTION

The egg is an important animal product by virtue of its contribution to human nutrition and its biochemical components await entrepreneurial development for both food and non-food use. Besides the controversy surrounding its cholesterol levels, its overall nutritional value as a source of energy, protein and other nutrients in many parts of the world, has brought about remarkable developments in the poultry industry. This in turn placed additional pressure on poultry producers to generate optimal solutions to a variety of factors that constrain feed intake and potential output of the hen, such as age, sex, genetic potential, environment and nutritional specifications.

Due to the influence of these factors birds provided with a balanced feed in a given environment may be unable to meet their nutritional needs. In flocks of birds over time there is a complex mixture of successive over- and underfeeding which is difficult to explain. This, results from failure to recognize the implications these constraining factors have on nutrition, which more than anything have hindered the actual approach to meeting nutritional requirements.

Defining the interdependence that exists among production parameters is a major objective in animal nutrition studies. Whilst it may be agreed that there is no fixed requirement for dietary energy or dietary amino acids, this approach requires a precise knowledge of the energy and protein requirements of the bird, and their control on food intake and the efficiency with which the stocks in use are capable of reaching the desired level of output.

Usually the nutritional consequences associated with genetic change can be predicted, from which consequent nutritional changes can be analyzed. The same route can be followed

where environmental issues are concerned. Of more importance, is that to maintain maximum production levels, nutritionists need to relate nutritional inputs to financial output to allow producers to alter the composition of the feed when economic conditions change.

2.2 DIETARY FACTORS INFLUENCING FEED INTAKE

The problem of describing requirements and expressing them quantitatively has always been a central one in nutrition. Interpreting the response of laying hens to diet composition with *ad libitum* feeding may be difficult if it is not clear whether energy or another nutrient in the diet is the first limiting resource (Fisher, 1994). To a considerable extent intake is driven by nutrient requirements, and an approximate estimate of how much food an animal will eat is normally calculated in relation to the ME content of the diet with all the other nutrients, including protein (and amino acids) expressed per unit of ME.

Birds have a genetically defined requirement for nutrients and they will attempt to consume a 'desired' amount of feed in order to meet their requirements for the first-limiting nutrient in the feed (Emmans, 1987). Laying hens, however, are also known to be very responsive to dietary influences on intake because, unlike meat-type poultry, they are not selected for body weight gain and over-consumption of energy might lead to excessive body fat accumulation, which may or may not increase egg production, depending on its source.

The sensory system is principally responsible for feed intake control through a series of negative feedback signals obtained by the brain from the digestive tract, liver and other organs, in response to dietary nutrient levels. After thorough analysis, the brain uses this information on nutritional composition of the feed as the basis for decision making as to which feed to eat, in the case of choice feeding. However, when only one feed is on offer the bird is left with only one choice, to eat the food. This is why there should be certainty of nutrient composition and bioavailability in feedstuffs, since this affects the extent of intake of a given diet.

Nutritional needs can only be quantified in terms of nutrient intakes or allowances and not nutritional requirements because a requirement is a measurement of the minimum requirement needed to maintain the bird in a healthy state for production and it only applies to the bird the measurement was made for. Hence asking for statements of requirements for energy and protein is somehow nonexistent (Morris, 1968).

Since the 1970's many trials directed towards adjusting levels of each nutrient so as to maximize profit margins rather than to achieve maximum levels of production have been performed - meaning that the idea of a "fixed" requirement for a nutrient should be abandoned and replaced with the data relating rates of output to input obtained from suitably designed feeding trials (Fisher and Morris, 1970).

It is very unlikely though that nutrients in the food on offer will be present in the same ratio as required by the hen: perhaps protein content is too low in relation to energy, which places a heavy nutritional burden on the hen. She must either increase her intake in order to satisfy her protein requirements, thereby taking in an excess of energy, or reduce her intake to avoid over- consumption of energy, in which case the quantity and/ or quality of eggs will be reduced due to lack of protein.

2.2.1 Dietary Amino Acid Requirements

It is difficult to define exactly what constitutes a valid determination of amino acid requirements, other than that the determined amino acid value is applicable over a wide range of practical conditions (Fisher and Morris, 1970) or is balanced enough to meet the daily requirements for maintenance and egg output of the bird. A model is available which will both interpret responses to amino acids in laying trials and give economically optimal estimates of amino acid inputs for practical feed formulation. Flocks coming into lay and flocks nearing the end of the pullet year have bimodal distributions of rates of lay, with the result that calculations of requirement based on mean output will underestimate the optimal amino acid input for the flock (Morris, 2004).

When protein supply is severely limiting, the major response is a reduction in rate of lay, whereas egg weight seldom falls below 0.90 of its maximum value until amino acid intake

is well below 0.5 of its optimum value (Morris and Gous, 1988). However, the relative magnitude of the responses in rate of lay and egg weight may vary between amino acids, while egg protein synthesis and voluntary food intake vary systematically, both within and between days, which to a certain extent determines the efficiency of amino acid utilization.

The Reading model optimizes the intake of individual amino acids providing that all the other amino acids, are not limiting- it is based on the premise that a laying hen has a requirement for maintenance proportional to her body weight, and that egg output will only be possible once this maintenance requirement is met (Fisher *et al.*, 1973). However, the maintenance concept of the response to amino acids in laying hens is neither well defined nor well established quantitatively (Fisher, 1994).

The most important factor affecting the efficiency of protein utilization for egg production is the balanced composition of amino acids in the diet. Food intake rather than dietary amino acid concentration accounts for much of the variation observed in production levels. In order to determine the extent to which food intake will differ between hens, several factors that constrain food intake need to be thoroughly reviewed. Quantitative descriptions of these responses might enable nutritionists to work out optimum feeding strategies and thus meet nutritional needs for each hen (Morris, 1968).

Predictions made using the Reading model show that a small proportion of a flock is capable of responding to inputs beyond the rates normally defined as the requirement, with the assumption that some birds have very high rates of egg output (Morris and Blackburn, 1982). In general, the optimum economic intake of the amino acid is reached when the marginal revenue for the eggs sold is no longer greater than the marginal cost of supplying additional amino acids for a population response deduced from individual responses (Fisher *et al.*, 1973).

2.2.1.1 *Essential amino acids*

Usually the bird is supplied with about 22 amino acids of which all are physiologically essential. Of these, methionine, lysine, threonine, leucine, valine, isoleucine, arginine, phenylalanine, histidine, and tryptophan are dietary essentials with cysteine and tyrosine being semi-essential. Mostly, essential amino acids are found to be limiting in most feedstuffs. Methionine is considered to be the first-limiting amino acid in reduced protein corn-soybean feeds for laying hens (Waldroup and Hellwig, 1995), with lysine accepted as the second-limiting amino acid, followed by tryptophan and/or threonine. This implies that synthetic essential amino acids have to be added during feed formulation to make them available to the hen to meet her protein requirements.

In as much as birds have specific dietary requirements for essential amino acids, they will not achieve their genetically determined potential if the dietary nitrogen is supplied exclusively in the form of essential amino acids, hence a combination of the non essential amino acids should also be provided to maximize production potential (D'Mello, 1994). Nonetheless, when conventional ingredients are included in feeds for laying hens, with the minimum usage of synthetic amino acids, it is not necessary to specify minimum concentrations of dietary protein that should be included in the diet, as the non-essential amino acids will be supplied in sufficient quantities from the ingredients used.

For instance, D'Mello (1994) found that when the proportion of essential to non-essential amino acids is fixed at 55:45, growth performance, efficiency of food utilization and total carcass protein of broilers are optimized. At the higher ratio of 65:35, the rate of deamination of the surplus essential amino acids is insufficient to satisfy the requirements for the synthesis of the non-essential amino acids. While at a lower ratio of 35:65 an excess of non-essential amino acids relative to essential amino acids results in both a deficiency of the latter amino acids and a need for additional energy for the excretion of surplus nitrogen.

2.2.1.2 *Amino acid imbalances*

An imbalanced diet is one that contains more of several essential amino acids than the other or that meets the entire requirements for all but the limiting amino acid (Harper *et al.*, 1970). However, it is important to distinguish between deficiencies and imbalances, between antagonism and imbalance, and an imbalance and toxicity (Harper *et al.*, 1970). A deficiency is related to the bird's response to an inadequate amount of amino acids, while an imbalance is about the effects of surpluses of essential amino acids, other than the one that is limiting, on production or maintenance. An imbalance differs from an antagonism in that the effects of the latter are not prevented by supplementing the imbalanced diet with small quantities of the limiting amino acid, but only by a supplement of an amino acid that is structurally similar to the one in surplus.

While toxicity is applied to conditions in which an adverse effect is due to a large surplus of an individual amino acid, quantities of amino acids added to create an imbalance may be greater than amino acid quantities causing toxicity. However, no one amino acid can be included in the diet in an amount that by itself would be considered toxic, but it can induce an apparent deficiency of another amino acid, for example a relatively small excess of leucine can cause an apparent deficiency of isoleucine (Harper, *et al.*, 1970; Buttery and D' Mello, 1994).

It is unlikely that a balanced mixture of dietary amino acids will exactly meet the requirements of each of the hen's tissues (Buttery and D'Mello, 1994). Thus the addition of a relatively small quantity of an amino acid to a low- protein diet, or to an incomplete mixture of amino acids (D'Mello, 1994), as well as amounts above the maintenance and below the minimum requirements for optimum production (Fisher *et al.*, 1960), may induce an imbalance.

The severity of the adverse effects that surpluses and imbalances have on the requirement and/ or utilization of the first limiting amino acid is not quite clear (D'Mello, 1988). But it is known that a deficiency of an amino acid is likely to cause a reduction in performance; excesses can also be deleterious, even small excesses. However, the severity of their effects varies with the nature and degree of the amino acid disproportion, the nutritional adequacy of the diet as a whole, and with the age and physiologic state of the bird. At the

same time, an animal will tolerate large surpluses or become adapted to diets containing excesses or having imbalances of amino acids well when they are provided in the form of a high protein diet and the degree of disproportion is not too great (Harper, *et al.*, 1970).

Fisher *et al.* (1960) noted that chicks manifest their sensitivity to a severe imbalance by a rapid and marked reduction in food intake, which consequently reduces intake of the limiting amino acid, and ultimately reduced growth. Whereas, in the laying hen food intake appears to be the main factor that mediates response to amino acid imbalance (Fisher, 1994). This implies that birds adjust feed intake on the basis of the requirement for that particular amino acid and its concentration in the diet, and that any change in amino acid balance would affect food intake rather than the efficiency of utilization of the limiting amino acid. Hence, this discounts the claim that dietary amino acid balance changes with every supplementation of the limiting amino acid, thereby affecting the response (D'Mello, 1994).

2.2.1.3 Phase feeding

Over time, as the hen progresses through her laying cycle, variations occur in voluntary feed intake and rate of laying, both of which affect the net efficiency of utilization of protein for egg production (Pilbrow and Morris, 1974; Wethli and Morris, 1978). As a result, some egg producers reduce protein and amino acid levels in the late-laying diet, with the hope of reducing both feed costs and egg size. This is known as phase feeding, but its validity and influence on feed intake is not quite clear. A prior investigation by Morris and Taylor (1967) showed that between days birds consumed 16.5% more feed on laying days than on a non-laying day. Thus, reducing dietary protein without compromising the performance of the laying hen is still controversial, especially with the major manipulations in genetics, nutrition and management of hens.

Consequently, Wethli and Morris (1978) conducted four experiments to determine the effect of age on the tryptophan requirements of laying hens using White Leghorn pullets that had been used for an assay of tryptophan requirement between 32 and 40 weeks of age. The same birds were used for similar determinations between 63 and 73 and, after a moult, from 97 to 106 weeks of age. They observed that at peak egg production, individual

egg outputs were normally distributed, but that later in lay, pausing, moulting and morbidity resulted in considerable skewness and an increase in non-laying birds. The relationship between egg output and tryptophan intake was the same in moulted hens as in young pullets, except that 63 to 73 weeks old hens yielded a different response curve, meaning that more tryptophan was needed for a given egg output.

Morris and Wethli (1978) suggest that changes in metabolic rate associated with ageing or compounding together the efficiencies of laying and non-laying pullets could be the reason for differences in productivity. A flock that has been brought into a highly productive state after moulting should be less efficient than a pullet flock if efficiency of protein utilization is a function of age. However, if efficiency is a function of rate of egg output, then hens at the peak of the second cycle of egg production may be as efficient as young pullets.

Waldroup and Hellwig (1995) found evidence indicating that methionine and TSAA requirements for maximum egg production, egg weight, and egg output do not diminish with age and stage of production. Requirements were found to be greater for the middle and final quarters of production than for the initial quarter, with peak daily requirements of 340, 380, and 402 mg/day for rate of lay, egg weight, and egg output, respectively.

Pilbrow and Morris (1974) argue that the theoretical argument behind phase feeding does not make sense, as it is based on the assumption that the amount of protein required per unit of egg output remains constant. This is in contrast with their findings that the relationship between requirement and output decreases as hens age. Generally, any other nutrient, which is not related to amino acid availability or deficiency, could be responsible for this effect. Hence, it is always suggested that adjustment should rather be done to compensate for changes in daily feed intake as influenced by environmental changes, feather covering, or other factors in order to maintain constant amino acid intake (Waldroup and Hellwig, 1995).

2.2.2 Dietary Energy Requirement of the Laying Hen

Metabolisable energy (ME) is frequently believed to be a property of a feed, while it is actually a characteristic of the animal that is being fed, together with the kind of environment in which the hen is kept, and is a useful currency for defining mass conversion of the components of the food in the bird. The economic importance of energy in the formulation of least-cost diets for poultry and the decreasing profitability of commercial poultry production are sustaining interest in the metabolisable energy (ME) values of diets and constituent raw materials.

When formulating least-cost poultry diets, ME concentration should be optimised by an iterative procedure, not entered as a fixed value. This iteration must calculate profit margins by taking into account the way in which feed intake and saleable outputs vary with ME concentration (Morris, 2004).

Energy requirements are based on the needs for maintenance, for egg production and for growth, and on the efficiencies with which dietary ME is converted to carcass and egg energy (Emmans, 1974). Thus, energy requirements for laying hens should be accurately partitioned into maintenance and production at all times.

2.2.2.1 Regulatory effect of dietary energy level on feed intake

When all essential nutrients are in adequate supply in the feed the energy concentration of the feed is the main dietary factor that controls voluntary feed intake (Emmans, 1981; Cheeke, 1999). Consequently, feed conversion efficiency of different feeds is largely dependent on the energy content of the feed and is independent of the level of feeding.

Emmans and Fisher (1986) suggested that a bird will attempt to consume sufficient food to meet its requirements for maintenance and growth, the so-called desired feed intake (DFI). As the digestibility of the feed or the nutrient density is reduced, intake will therefore increase until this is constrained by feed bulk or gut capacity; at which point food intake is reduced, as shown in Figure 2.1 (Cheeke, 1999).

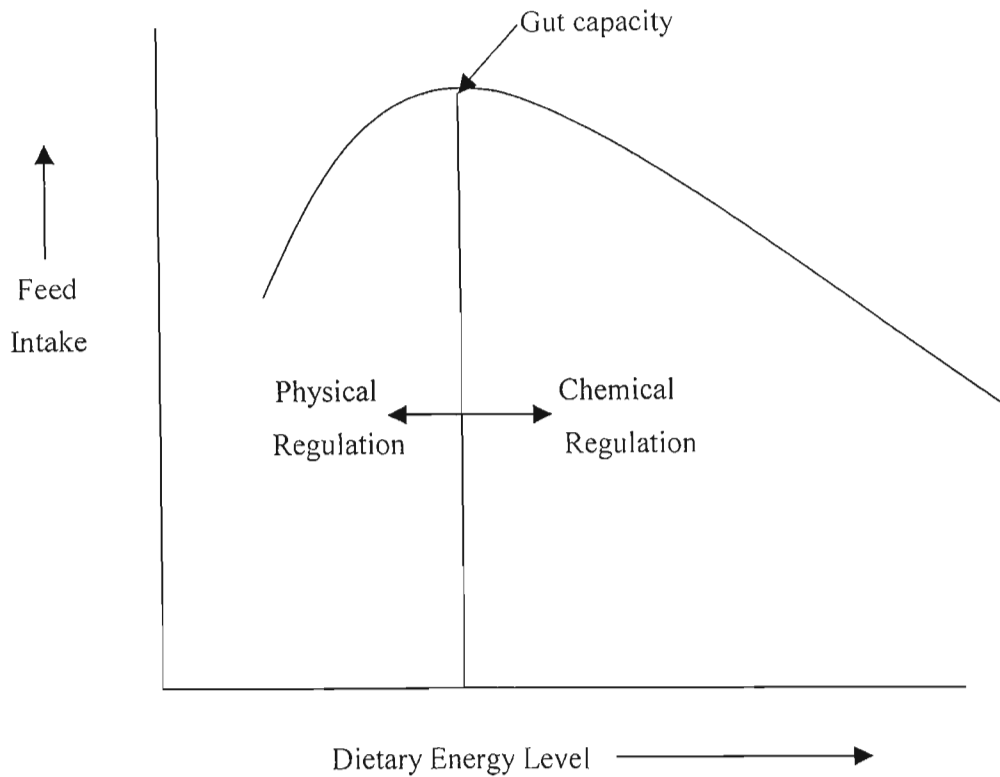


Figure 2.1 *The relationship between feed intake and dietary energy level (Cheeke, 1999).*

Laying hens do not adjust their food intake accurately to satisfy their energy requirements when they are subjected to changing dietary energy concentrations (Morris, 1968; Forbes, 1995). Similar findings by Cherry (1979) show that hens that were given a high ME diet (12.5 MJ/ kg) gained more weight than similar birds given a low ME diet (11.5 MJ/ kg) for 112 days, implying that they consumed more energy on the high than on the low energy feed.

De Groote (1972) reported that mortality and rate of laying (hen-days) were not affected by energy levels ranging from 10.5 to 13.4 MJ/ kg, thereby confirming the conclusions made by Morris (1968), that the laying rate of White Leghorn hens is not influenced by nutrient density, at least within the range energy levels tested. De Groote (1972) noted that, with every increment in the ME content, only partial compensation occurred in feed intake, egg weight and body weight.

2.2.2.2 *Energy requirements for egg production*

The energy requirements for egg production are more difficult to define than those for growth, mainly because trials with laying hens are of longer duration than growth trials, and birds undergo many stages in their productive life; hatching, maturity, egg production, moulting, etc. However, if the effects of these stages and of the environmental factors influencing egg production are described empirically by their effects on the rate of egg production in normal cycles, some progress may be made which will allow the description of nutritional response during lay. This implies that the choice of optimal nutritional inputs would involve simultaneous consideration of all these stages (Emmans and Fisher, 1986).

In response to nutrient requirements for egg production, laying hens eat more on egg-forming days than on non-egg-forming days. Thus energy needs for egg formation processes exceed that for maintenance. Energy does not affect egg output directly; however, it exerts its effects indirectly through food intake and amino acid intake (Morris, 1968; Gous *et al.*, 1987; Sloan *et al.*, 1999; Harms *et al.*, 2000).

It is possible to estimate the energy requirement for egg production by assuming that the ME contribution to egg formation is constant per unit of egg size, excluding the change in body weight (Balnave *et al.*, 1978). An egg contains between 270 and 480kJ of energy, depending upon its size. Thus, since the energy efficiency during digestion and metabolism is about 70%, each egg of average size will require about 506kJ of dietary energy (North, 1984).

Eggs contain 6.7 kJ energy/g. For each g egg the hen would require between 7.8 and 11.2 kJ ME (corresponding to efficiencies of utilization of 85 and 60%). On average the efficiency is 80%, therefore the requirement for egg production is 8.4 kJ/g egg output (Emmans, 1974).

Similarly, and bearing in mind that any growth during the laying period is likely to be fat deposition, i.e. efficiency of utilization of ME for growth is likely to be between 75 and 85%, the ME requirement for 1g body weight gain (17 kJ/g) would be approximately 20.9 kJ/g (Emmans, 1974).

The ME required for production was therefore estimated by Emmans (1974) to be:

$$\text{ME (kJ/ day)} = 8.4 E + 20.9 \text{ dW kJME/ bird d}$$

Where E= egg output (g/ bird d)
 dW= change in body weight (g/ bird d).

2.3 INTERACTION BETWEEN THE GENOTYPE AND FEED INTAKE

There is a remarkable amount of uniformity among and within laying birds as to their requirements for nutrients. Consequently, across genotypes, widely different intake requirements may be met on a single feed because of correlated differences in food intake (Fisher, 1994). Within this framework of uniformity, however, there are some genetic variations in the nutrient requirements of different strains, as well as in their characteristic food intake (Nesheim, 1966; Emmans, 1974).

Whilst in many cases the nutrient requirements of different strains are related to their body weight (maintenance) and egg output, in some instances there are strain differences in energy requirements, and this results in interactions between the strain and the amount of food that is consumed (Emmans, 1974). Thus, hens showing equal production levels and body weight may vary in food consumption and conversion efficiency.

Genetic variations that exist among individual strains are more quantitative than qualitative, with a relatively small degree of variation, thus allowing very little probing into the differences in nutrient metabolism between and among strains. For instance in the past, brown egg producing stocks were usually assumed to be heavier and eat more feed than white egg producing hens, with added advantage of producing a high egg mass, coupled with a good feed conversion compared to white egg producing stocks. However, Leeson (1986) discovered that Leghorn pullets, which are white egg producers, could adjust feed intake to meet their energy needs better than do brown egg layers, confirming the analysis done by Morris (1968).

2.3.1 Strain variation in response to amino acid utilization

Across animal genotypes and across groups treated in multi-faceted ways there will be a strong correlation between intake requirements for amino acids and food intake under *ad libitum* feeding (Fisher, 1994). The shape of the response curve (the Reading model) assumes that body weight and egg output vary amongst individuals of the flock and that all hens have the same efficiencies of utilization of amino acids for tissue maintenance and for egg synthesis, and that the correlation between body weight and potential egg output has a defined value (Morris and Blackburn, 1982).

The efficiency of utilization of protein or energy in a diet depends on many metabolic pathways which involve a large number of enzyme- controlled reactions, each of which is under some genetic control, which makes selection for better protein utilization seem like a too general objective while selection for a specific amino acid may have more greater success (Nesheim, 1966).

Pilbrow and Morris (1974) studied the response of eight commercial strains of laying hens to lysine. From the results in Table 2.1 below, showing the estimated lysine requirements from each stock for a mean body mass of 2 kg and a mean daily egg output of 44 g, it is clear that there were differences between the percentages of lysine in the diet required by each stock for maximum output. They speculated that genetic differences in daily protein requirement may be the result of the potential variation among strains, in the efficiency with which they digest and utilize component amino acids for egg production and maintenance, with the result that one strain may require more dietary protein than another for each unit of egg protein synthesized or unit of body weight maintained. Subsequent analysis (R.M Gous, Personal Communication) has shown that the differences in efficiency measured in this trial were the consequence of inaccurate curve-fitting procedures and not of differences in efficiency between strains. When a more accurate curve-fitting procedure was used, the efficiencies of utilisation of lysine were the same in all stocks used.

Table 2.1 *Estimates of the coefficients of lysine utilization per egg produced a, per kg body mass maintained b, and for all stocks combined (Pilbrow and Morris, 1974)*

Stock	a (mg/ gE)	b (mg/ kg W)	Estimate of lysine required (mg /d) for a 2kg bird producing 44g egg/d
Thorner 606	10.2	73	595
Hyline 934	5.0	190	600
Shaver 288	8.5	120	614
Babcock B300	7.3	140	599
Thorner 404	9.1	95	590
Skyes H4	10.0	70	584
Harco Sex Link	8.3	105	573
Alexander and Angell 3	7.0	120	548
All stocks combined	9.5	90	598

Wethli and Morris (1978) found that the Arbor Acres stock had higher maintenance requirements for tryptophan (per unit weight) and lower requirements per unit of egg output as compared to the Shaver 288 hens. However, these apparent differences among strains disappeared when the Reading model was fitted to the data from all strains simultaneously.

The amount of lysine, methionine or tryptophan needed per gram of egg output or per kilogram bodymass does not differ to any measurable extent between stocks. And therefore, using the Reading model, the optimum dietary concentrations for these amino acids can be calculated for any existing (or future) stock for which the egg output, body mass and feed intake characteristics can be predicted.

2.3.2 Strain variation in response to energy utilization

Provided all other resources are non-limiting, it may be concluded that there are differences in the maintenance energy requirements between various strains of laying hens,

which may give the impression that some strains require less energy to produce a gram of egg content, as compared to others (Harms *et al.*, 2000) (Table 2.3). Emmans (1974) has shown that Rhode Island Reds are more efficient than White Leghorns in utilizing ME for maintenance, and even within strains of White Leghorns the efficiencies have been shown to vary from 64 to 85 percent. Brown-egg laying strains are more efficient than white-egg strains (maintenance requirements of 380 kJ/kg d vs 480 kJ/kg d respectively). Feather cover also affects energy required for maintenance - based on a range of feather loss from 1 to 6, maintenance increased by about 9% for each unit increase in feather loss score (Emmans, 1974).

Morris (1968) observed that birds fed higher energy diets tend to over-consume energy and increase weight more than do birds fed lower energy diets. This suggests that strains on the high plane of nutrition will adjust their feed intake less efficiently than birds on the low plane of nutrition, to compensate for varying dietary energy levels. The extent to which birds are capable of adjusting their intake of nutrients, is determined by the characteristic energy intake of that particular strain, $r = 0.667$ (Morris, 1968). Using the following equation: $y = y_{11.3} + (0.0005465 y_{11.3} - 0.1466) (x - 11.3)$, Morris (1968) predicted the energy intake of various strains of birds at increasing levels of energy (Table 2.2).

Table 2.2 *The predicted energy intake of strains of birds at different levels of energy (Morris, 1968).*

Dietary energy x MJ ME/ kg	Characteristic energy intake ($y_{11.3}$), kJ ME /kg bird day					
	1172	1297	1423	1548	1674	1799
10.0	1163	1268	1372	1480	1582	1686
10.8	1167	1289	1406	1523	1644	1761
11.7	1176	1305	1439	1573	1703	1837
12.5	1180	1326	1473	1619	1766	1912
13.3	1184	1343	1506	1665	1824	1983

From Table 2.2 it is apparent that White Leghorns (low characteristic intake of about 1339 kJ ME/ bird d) would be expected to increase their energy intake by 2 or 3%, while heavier

strains (1674 kJ ME/ bird d) would increase their energy intake by 4 or 5%, for each 10% increase in dietary energy (Morris, 1968).

Harms *et al.* (2000) conducted an experiment to determine the response of Hy-Line Brown, Hy-Line W98, Hy-Line W36, and DeKalb White hens, to decreases or increases in dietary energy. The diets contained 10.5 (low), 11.7 (medium) and 12.9 (high) MJ ME/kg. They observed that hens fed the low energy diets consumed 8.5% more feed than did hens fed control diets, and hens fed high energy diets consumed 1.5% less feed than did hens fed the control diet, which means that hens were more sensitive to low energy than high energy diets. And Hy-Line W98 and the Hy-Line Brown hens were more sensitive to the change in energy than the Hy-Line W36 and DeKalb White hens.

Table 2.3 *Performance of four strains of commercial layers fed three levels of energy*

Dietary Energy (MJ/kg)	Egg Production (%)	Egg Weight (g)	Weight Gain (g)	Feed Intake g/bird day	Energy Intake MJ/bird d
Low (10.5)	91.5 ^a	62.0 ^b	65 ^c	118.6 ^a	1.245 ^b
Control (11.7)	91.7 ^a	61.5 ^b	82 ^b	109.3 ^b	1.274 ^b
High (12.9)	91.7 ^a	64.1 ^a	209 ^a	107.7 ^b	1.380 ^a

^{a-c} Means within columns with no common superscripts differ significantly ($p < 0.05$). Adapted from (Harms *et al.*, 2000).

2.3.3 Effect of nutrient composition on strain variation in egg mass and production

Some strains of layers produce large numbers of small eggs; others produce fewer but large eggs. Thus, the use of egg output (number x weight) rather than egg numbers will lead to better comparisons of flocks or strains of birds, along with feeding and management programs (North, 1984). He suggests that by taking egg weight and egg production into

focus as one index rather than two, the average daily egg output produced per hen on a hen-day basis could be a more efficient means of comparing various strains of birds.

Sharpe and Morris (1965) compared responses in a Rhode Island Red x Light Sussex strain and a small White Leghorn-type hybrid. These strains differed in egg output and also in body mass, and response curves drawn from the data were quite separate. They concluded that for an output of 35 g egg material per day the larger bird will need 4-5 g extra protein, part of which will be used to maintain extra body mass of 1.1 kg.

Shalev (1995) compared white and brown eggshell stocks for egg mass, body weight, feed conversion ratio and hen- housed egg production. He found that, over the years, there has been a body weight reduction in the brown egg stock, which has brought about a significant (0.5kg) increase in egg mass and a consistent improvement in the feed conversion ratio (kg feed to kg egg mass).

2.4 ENVIRONMENTAL FACTORS AFFECTING FEED INTAKE AND PERFORMANCE OF LAYING HENS

Environmental factors considered to influence the productivity of the laying hen include parameters such as ambient temperature, seasonal effects, lighting intensity, group size, unit floor area per bird and method of housing. All these factors are important to the hen, in order to survive and produce eggs. However, under poor management conditions each of these factors may exert a negative influence on the potential rate at which the bird produces eggs (egg weight and egg numbers) or even constrain the quantity of food that the hen consumes to an amount less than that required for the hen to achieve her potential performance.

2.4.1 Lighting

Lighting is an indispensable tool in the management and production of laying hens. The perception of light exerts an important influence on the performance and behavior of the

laying hen- it enables the hen to identify a subjective day and also controls ovulation and oviposition as well as maintenance activities (Lewis *et al.*, 1994).

Physical activity is considered the hen's response to light stimuli (Boshouwers and Nicaise, 1993) and is directly related to her energy requirement, because as light increases there is a concomitant increase in the hen's physical activity. However, this energy is not available for egg production, but is reflected in higher feed consumption, which results in poor food conversion efficiency. The inactive state of birds, however, has a positive effect on feed utilization efficiency; it reduces the amount of energy spent on maintenance, which increases production levels (Lewis *et al.*, 1994). Thus, a combination of a proper lighting program together with a correct feed specification may help egg producers partition energy and nutrient needs accurately in relation to the hen's activities in response to lighting.

2.4.1.1 Effect of lighting on feed intake and egg production

The hen has an internal cycle length (ICL), which affects her rate of lay in a given environment, which is defined by the external cycle length (EXCL). The value of EXCL is critical since it usually represents the length of the repeating light: dark cycle and estimates the value of ICL. When $ICL = EXCL$ the hen is expected to ovulate once in each environmental cycle, thus laying a total of six eggs per week. However, when $EXCL < ICL$, at each ovulation, the hen attains a lag which is accumulated until a clutch pattern is established, i.e. no ovulation occurs for a day (Emmans and Fisher, 1986).

The above theory suggests that lighting and reproductive traits are interlinked by many processes, through retinal and/ or extra-retinal light perception, neuro-endocrine processing, ovulation, egg formation and oviposition (Boshouwers and Nicaise, 1993). Egg mass of both broiler and layer strains increases, without a decrease in the rate of lay, when they are subjected to continuous light as compared to a conventional 14 hours light: 10 hours dark regime (Smith, 1978 a).

Increments in photoperiod at sexual maturity must coincide with increases in feed consumption (North, 1984) because for the first few weeks after the onset of lay, both egg production and body weight increase rapidly, thus increasing nutrient demand to satisfy

ovulation and shell calcification needs. This increase in feeding activity is presumably triggered by the bird's anticipation of darkness because they start filling their crops just before the night so that digestion and absorption of nutrients can take place during dark hours (Savory, 1980 cited by Lewis *et al.*, 1997).

Lewis *et al.* (1997) compared the subsequent performance of ISA Brown and Shaver 288 laying hens at first egg. They found that photoperiod significantly increased mean daily food intake during lay by 1.26g/ h. A ten-day retardation in age at first egg (AFE) led to a 1g/d reduction in food intake and significantly improved the efficiency of converting food into eggs. However, efficiency deteriorated according to the square of the photoperiod, and changed curvilinearly according to age at photo-stimulation.

2.4.1.2 *Light sources for laying hens*

There are two intermittent lighting systems for laying hens; the Biomittent system, using an asymmetric pattern of 0.25L:0.75D for 16 h followed by 8D, which entrains oviposition to 24 h cycles and, compared with standard lighting programmes, gives the same egg number and egg size but a smaller feed cost, and a symmetrical system (4[3L: 3D]) which allows intervals between ovipositions to stretch, giving bigger eggs with thicker shells, but yielding fewer eggs and achieving no saving in food intake (Morris and Butler, 1995).

Both ahemeral and intermittent lighting are particularly useful for increasing early egg size, advancing age at photo-stimulation, and reducing use of feed and electricity (Grimes and Siopes, 1999). Biomittent lighting on the other hand reduces voluntary energy intake, by approximately 6%, which in turn results in a small reduction in egg output if the amino acid intake drops below that needed for maximum yield (Midgely *et al.*, 1988; Peguri and Coon, 1993). Nevertheless, if inefficiency were caused by a variable rate of amino acid supply from the diet, then that would be accentuated by a short day and ameliorated in constant light (Smith, 1978a).

Rose *et al.* (1985) subjected laying hens to three lighting treatments, for which the bright and dim light of 28-h ahemeral light cycles was provided by incandescent (tungsten filament) lamps only or by combinations of tubular fluorescent or compact gas-discharge

lamps with incandescent lamps. They observed that there were no differences in entrainment (the proportion of eggs laid in 4, 6 or 8 h modal periods) between the three bright: dim treatments. They introduced a fourth ahemeral lighting treatment, in which the dim lights (bright: dim: dark) were extinguished except during a designated work period (09.00 h to 12.00 h daily). Hens given the bright: dim: dark treatment showed an increased entrainment compared with the three bright: dim light treatments, although there were no differences ($p > 0.05$) in egg numbers or mean egg weight between all 4 lighting treatments. Birds given the bright: dim: dark treatment tended to have a lower ($p > 0.05$) food intake compared to the three bright: dim treatments.

Recently, Morris and Butler (1995) devised a new system to combine the increased egg size and shell thickness, characteristic of symmetrical intermittent lighting programmes, with the reduction in food intake, which is a feature of programmes that reduce total activity time. The pattern tested was 24(0.25L: 0.75D). The results of 2 trials showed that this new system gives about 2% fewer eggs than conventional (Step Up) or Biomittent lighting with a 2% increase in mean egg size and a 3% improvement in shell thickness at the end of the laying year. Feed consumption with the new system was similar to that under Biomittent lighting and 6% lower than that recorded for Step Up lighting, mortality was also lower than with Step Up lighting, but not significantly so.

Lewis and Morris (1998) reported that egg production and egg weight of laying hens is unaffected by the type of lighting source used, although significant but inconsistently higher rate of lay was observed in White Leghorn hens during isolated months under fluorescent compared to under incandescent lighting. While food intake is usually not affected by light source, birds under fluorescent light may eat more to make up for the energy lost during physical activity. These results, however, may be a response to a change in photoperiod and/ or a different light wavelength rather than to the light source *per se* (Lewis and Morris, 1998).

2.4.2 Temperature

A number of factors influence the animals' response to heat stress. Among these are age (stage of production), breed (size and feather cover) and nutrient density in the feed. The overwhelming effect is to reduce food intake, but these factors influence the extent to which intake is reduced.

Birds can influence their heat loss by changing their behaviour. Birds subjected to cold environments can huddle together in a flock, or reduce their surface area by postural changes and reduce their activity; while those in hot environments can adopt panting to increase evaporative heat loss. This is the main advantage of homeothermy in birds, their ability to reach a balance between heat production and heat loss to maintain a constant body temperature, which enables them to function at their optimum potential (Balnave, 1998).

To the contrary, Peguri and Coon (1993) found that laying hens housed at high temperatures have difficulty dissipating heat. Respiratory evaporation is a more significant way of heat dissipation above 30°C, panting in itself is a heat producing mechanism, to a certain extent it increases heat loss, but it can also generate heat as a result of the panting activity. Furthermore, panting is less effective for layers housed in conditions of high humidity, because evaporation depends on the difference in vapor pressure between the environment and the surface from which evaporation is taking place.

However, because heat loss varies with the temperature of the environment, the environmental constraints on the rate of heat loss will exert the same effect on heat production. Since heat production is related to the rate of intake of a given feed the temperature of the environment sets an upper limit on the rate of feed intake. At temperatures in excess of an upper limit birds are unable to maintain a constant body temperature, as a result body temperature will either rise or fall, inevitably. This alters metabolisable energy intake and causes metabolic changes in the laying hen (Leeson, 1986), which prevent the hens from reaching their potential production levels.

2.4.2.1 Effect of temperature on nutrient requirements and performance of laying hens

Temperature normally exerts its influence on production indirectly through its influence on food and/ or nutrient intakes, of which a direct effect on egg mass output would result in a change in nutrient requirement. Since nutrient intake is influenced by food intake it is necessary that the nutrient density of diets at high temperatures be increased because an inability to consume sufficient nutrients at these temperatures poses major limitations to egg output (Scott and Balnave, 1988).

Throughout the whole range of environmental factors, however, it has been proven that there are physiological responses that affect the production and efficiency of feed utilization in poultry (Marsden and Morris, 1987). The hen will vary her intake of food in accordance with her requirements for energy in a particular environment. For instance, in cold environments more energy is required to maintain body temperature with a consequent increase in food intake. In a cold environment the consumption of all essential nutrients will also increase above levels needed to support optimal egg production unless adjustments are made to the composition of the feed. In hot temperatures appetite declines and only a minimum amount of energy is needed to maintain body temperature. This is one of the reasons for the reduction of food intake at high temperatures. Of more importance is that the hen must remain in thermal balance and she can do this only by reducing food intake, thereby reducing heat production. This may result in a reduction in the consumption of some of the critical nutrients required for egg production, and unless the diet is altered to provide more amino acids and nutrients, egg production will decline.

Energy required for maintenance is expected to decrease as the environmental temperature increases, and this decrease will depend on the strain of laying hen, i.e. by 9.2 kJ/kg d °C for white strains and 8.4 kJ/kg d °C for brown strains (Emmans, 1974). Emmans suggested that if the effect of temperature is to be considered, the following equation should be used:

$$ME = W (a + bT) + 8,4 E + 20,9 W$$

As the environmental temperature is not expected to influence the amount of energy required for egg production or growth, but only maintenance requirement, the effect of temperature is applied to the maintenance term only. He suggested the following:

a has values 711 for white strains, 648 for tinted strains and 586 for brown strains, whereas b has values -9,20 for white strains, -8,78 for tinted strains and -8,37 for brown strains.

T is the environmental temperature (°C).

Some studies have shown that sometimes, at extremely high temperatures an extreme efficiency in utilization of food can be obtained, equivalent to approximately 1.5 kg of food per dozen eggs throughout the laying year. It is an economic factor, however, that cannot be ignored, that high temperatures always exert a negative effect on egg mass, and this reduction is hardly compensated for by high food intake (Payne, 1966).

Subsequently, Scott and Balnave (1988) performed an experiment to evaluate the influence of dietary energy, nutrient density and environmental temperature on pullet performance in early lay when kept at the prevailing air (10° to 24°C), cold (6° to 16°C) or hot (25° to 35°C) temperatures. They found that in all three environments, reducing the dietary ME concentration from 12.5 to 11.0 MJ/ kg increased protein intakes by 5.9, 7.9 and 9.2% respectively, with a corresponding reduction of 7.5, 4.7 and 3.7% in ME intakes. At all combinations of nutrient density (ME: nutrient ratio) only hens kept at prevailing air and cold temperatures were able to meet their recommended daily protein intakes. Whilst at hot temperatures, only hens fed the most concentrated diets could meet the same recommendations. Nonetheless, the highest intakes of energy and protein achieved at hot temperatures could increase egg mass output.

In contrast, Marsden and Morris (1987) found that when energy is the factor limiting egg output at temperatures above 30°C, it would be unnecessary to increase amino acid supply, as the extra protein undergoes digestion and deamination, thereby increasing heat production by the hen. Adding dietary fat rather, would reduce the heat load due to its lower heat increment as compared to protein.

Mueller (1961) cited by Payne (1966) found that intakes of methionine and tryptophan by hens housed at 32 °C were only about three quarters of the hen's known requirements, which shows that the poor egg production can probably be attributed to deficiencies of specific nutrients rather than environmental temperature *per se*. Therefore, providing nutritional formulations are considerate of the level of voluntary feed intake that occurs at temperature as high as 30 °C, egg production would not suffer (Payne, 1966).

Similarly, Emmans (1974) observed that mass gain and egg output in birds fed equal amounts of nutrients are virtually unaffected by temperature over a wide range, of which it is also unlikely that egg composition and egg mass gain are affected, except for a relatively minor change in egg mass. In conclusion, the ability to quantify the cost of a higher maintenance requirement at low temperatures against the cost of keeping higher environmental temperature that results in lower energy intake might help maximize net profits in the laying hen house (Peguri and Coon, 1993).

2.4.3 Stocking Density

Providing feed to the birds is not completely at the mercy of population trends, since birds are normally fed *ad libitum*, to allow them free access to the feed. Nonetheless, the number of birds per house or per cage, to a certain extent, determines the feeding behavior and performance of laying hens. Battery cages, generally, allow birds few opportunities for activities other than feeding and deny certain birds the opportunity to feed at will (Hughes and Black, 1976), whilst a few aggressive birds in a flock end up over-consuming nutrients, thus becoming more productive than other birds which will probably eat less feed than required.

Laying hens may find forming a stable dominance hierarchy stressful when exposed to high stocking densities (Lindberg and Nicol, 1993) especially during the laying stages and whilst feeding. However, their ability to cope under such situations modifies their feeding activity and production rates. This is one of the major challenges that face producers, to determine behavioral patterns exhibited by layers during production stages that are symptomatic of large numbers of birds housed together, and devise means to eliminate them.

2.4.3.1 *Effect of stocking density on feed intake and performance of laying hens*

McBride (1964) and Craig and Toth (1969) reviewed the relationship between social dominance, aggression and laying rate when layer strains were housed under high stocking

densities. Results showed that the more aggressive hens in a flock fought their way to the feeder, which often resulted in mortality and egg breakages, whereas the less aggressive groups gave each other a chance and more birds had access to the feed. This resulted in the less aggressive birds being more productive in both egg production and feed utilization efficiency than the aggressive group, even though they still exhibited superior production with larger eggs and maximum rate of lay.

Hughes and Black (1976) observed an increase in feeding activity in birds housed in groups of four per cage, which they attributed to diurnal feeding patterns. However, they observed that even when feeding activity was greatest, it was unusual for all the birds to feed simultaneously - certain birds seemed unwilling to compete, even though there was an adequate amount of space for them to feed. Under normal *ad libitum* feeding, these birds actually spent more time in feeding activity than the time required for the ingestion of food - which implies that, if necessary, birds can ingest much more feed in a comparatively short time than they would do under normal circumstances.

Subsequently, Carew *et al.* (1980) conducted an experiment with White Leghorns housed at cage floor densities of 660, 440 or 330 cm² each with 2, 3, or 4 birds per cage. The birds were fed three levels of energy (Table 2.4). They reported that increasing hen density per cage resulted in a significant ($p < 0.05$) decline in egg production, body weight and feed utilization efficiency. Loss in final bodyweight was more pronounced with hens housed 4 per cage.

Increasing energy from 11.5 to 12.6 or 13.9 kJ/g decreased feed intake and consequently increased efficiency of feed utilization; however, increments in energy did not reverse the effects that hen density/ cage induced on production levels and energy (Table 2.4). They then concluded that the reduction in egg production accompanying higher hen density is not simply a result of competition for limited feeder space or feeding time, because if it were so the least competitive hens, that were not allowed enough feeding time by the other hens, would have been able to meet their nutritional needs more readily when offered the high energy diets at exactly the same amount of feeding time (Carew *et al.*, 1980).

The findings of Carew *et al.* (1980) agree with previous observations by Hughes (1977). He found that no relationship existed between egg production and dominance in caged

birds; hence, he concluded that overt harassment by dominant cage-mates is not an important source of variation in egg production among birds.

Table 2.4 *Performance characteristics at differing hen densities and dietary energy levels (Carew et al., 1980)*

Treatments							Mortality
Hens/ cage	Dietary energy (DE) levels	Hen-day egg prod. ^a	Feed intake/ day ^a	Energy intake/ day ^a	Feed/ egg ^a	Final body weight ^a	from traumatic events
	(MJ/ kg ^b)	(%)	(g)	(kJ)	(g)	(kg)	(%)
2	11.5	74.4	106	1219	142	1.913	0.0
2	12.6	73.7	99	1243	134	1.959	1.2
2	13.9	73.7	86	1192	116	1.891	2.5
3	11.5	72.0	107	1222	148	1.867	0.8
3	12.6	72.5	98	1230	135	1.850	1.7
3	13.9	71.7	88	1226	123	1.950	5.0
4	11.5	70.0	105	1205	147	1.754	0.6
4	12.6	71.4	100	1255	140	1.788	3.1
4	13.9	68.3	87	1213	128	1.797	5.0
Av. for hen density							
2		74.0	97	1213	131	1.921	1.2
3		72.0	98	1226	135	1.889	2.5
4		69.9	98	1226	138	1.780	2.9
Av. for DE							
	11.5 MJ/ kg	73.1	106	1213	146	1.827	0.5
	12.6 MJ/ kg	72.5	99	1243	136	1.846	2.0
	13.9 MJ/ kg	71.2	87	1209	122	1.868	4.2

^aValues represent averages/ hen from 21 to 73 weeks of age, ^bMetabolizable energy

2.5 DISCUSSION

The main emphasis in this review has been on describing factors that influence the productivity of the laying hen, with nutritional factors being the most important, particularly the response to dietary energy and protein. The definition of these nutrients

involves the study of nutrient inputs and outputs corresponding to nutrient requirements followed by an economic analysis of such responses in order to ascertain the optimum daily intake of each nutrient that will allow the hen to meet her daily nutrient requirements for maintenance, growth and egg production, when offered feed *ad libitum*.

The accurate prediction of feed intake, through the quantitative study of nutritional value of the feed on the basis of its nutrient composition, is an essential component in the formulation of feeds for poultry that will maximise the profitability of the enterprise. Essentially, the type of feed and the method of preparation used affect the quality and palatability of the diet. Whilst laying hens are normally fed *ad libitum*, to allow them uninhibited access to the feed, due to certain management practices, some birds fail to meet their desired feed intake, which is manifested in reduced egg production. Clearly, a more thorough understanding of feed intake and nutrient partitioning in the hen's body is the major objective in poultry feeding, but the problem may not be overtly nutritional.

For a number of years nutrient specifications have been stated as a percentage of the diet with constant modifications in nutrient requirements in relation to the change in eating patterns of laying hens, due to continuous genetic manipulations and in response to environmental temperatures. However, this method has been found wanting. For example, energy intake changes according to the temperature regime used, thereby affecting intake of other nutrients and subsequently egg production. It is also perceived that, experimentally, individually caged birds give near-to-perfect response estimates as compared to pen means. This is because competition for resources among birds is non-existent.

From a bio-economic point of view it was important to review all the factors that influence the overall efficiencies with which dietary energy and protein (amino acids) are utilized for productive purposes. Nonetheless, the advancement of poultry nutrition relies on the development of a model that will accurately predict the amount of feed that a hen will consume whilst attempting to meet her requirements for maintenance and egg production, taking account of all the nutritional interactions that might constrain her desired food intake. This would be a major breakthrough in the commercial layer industry.

CHAPTER 3

RESPONSE OF TWO STRAINS OF LOHMANN LAYING HENS TO DIETARY ENERGY AND PROTEIN

3.1 INTRODUCTION

For several years, the broader context of poultry research and development has focused on ascertaining dietary energy and protein (amino acid) needs for previous, present and future strains of poultry. Indeed, to this day, many of these specifications are still applicable, even though there are still certain aspects in poultry feeding that require research attention.

Recently, the enhancement of poultry nutrition has shifted towards putting the existing knowledge to good use, for the development of more elaborate nutritional models and response prediction, and optimisation of optimal feeding. In animal feeding, generally, feed intake is the main determinant of optimal performance, and its optimisation lies on the effective evaluation of the necessary dietary nutrient contents and the assessment of feed intake, in relation to environmental and genetic parameters constraining intake and performance.

From an economic point of view, the energy and protein (amino acid) content of a feed is very important, since it defines the nutrient intake and growth or reproductive performance of the birds being offered this food. In laying hens, these nutrients are used for maintenance and egg production: once maintenance requirements have been met, the rate at which egg production can continue is proportional to the remainder of the nutrients consumed, being limited at surplus intake of a particular nutrient by the bird's genetic potential (Clark, 1981). Fisher and Morris (1970) stated that in as much as there may be no validity in determination of amino acid requirements, the determined amino acid value or any nutrient for that matter should be applicable over a wide range of practical situations.

The main objective of the experiment reported here was to determine the extent to which dietary energy interacts with the protein content of the diet.

3.2 MATERIALS AND METHODS

3.2.1 Housing

Birds were individually caged in an open-sided house, on 14h light per day. The house contained two banks of cages, with each bank consisting of four rows of 32 cages, comprising two tiers in a pyramid structure. Each cage, measuring 43 x 41 x 29 cm in length, height and width respectively, is supplied with a nipple drinker and drip cup and an individual feeder, designed to carry up to 1.5kg of feed.

3.2.2 Layer strains

Two hundred and fifty six Lohmann laying hen of two strains, Brown and White, 35 weeks of age at the start of the trial, were randomly allocated to individual pens. Equal numbers of the two strains (128 per strain) were used.

3.2.3 Dietary treatments

Four 'corner' feeds (HE/LP, HE/HP, LE/LP and LE/HP, where L and H represent Low and High, and E and P represent Energy and Protein respectively) were formulated, from which 16 combinations of protein and energy were produced by appropriate blending. The WinFeed 1.1 (1996) feed formulation programme was used to formulate these four basal feeds (Tables 3.1 and 3.2), and the blending proportions are shown in Table 3.3.

Self-feeding troughs were used in the trial, with each bird being allocated sufficient feed for a week at the beginning of each week of the trial. Feed intake was calculated weekly by subtracting the amount of feed that remained in the trough at the end of each week from that allocated, divided by 7 (days).

Table 3.1 *Ingredient composition (g/kg) of the four basal feeds, as fed*

Ingredients	HE/LP	HE/HP	LE/LP	LE/HP
Maize	602.2	481.4	543.2	490.7
Wheat bran	100.5	40.9	324.3	397.2
Soybean full fat	40.1	208.5	-	-
Sunflower 37	150.0	150.0	-	-
Limestone	92.0	88.6	121.3	92.6
Fish meal 65	-	14.0	-	6.5
Monocalcium phosphate	8.2	8.9	3.4	2.5
Vit+min premix	2.5	2.5	2.5	2.5
Salt	2.4	2.1	2.4	1.5
Sodium bicarbonate	1.9	1.6	2.6	2.5
DL- Methionine	0.3	1.3	0.2	1.2
L- Lysine HCl	0.6	0.2	0.1	2.9

Table 3.2 *Nutrient composition (g/kg) of the four basal feeds*

Nutrient composition	HE/LP		HE/HP		LE/LP		LE/HP	
	Calc	Deter	Calc	Deter	Calc	Deter	Calc	Deter
CP	139.5	119.1	200.0	186.6	120.0	105.0	163.0	150.0
ME (MJ/kg)	13.0	12.1	13.0	11.8	10.0	9.4	10.0	9.5
Lysine	5.0	4.4	10.0	8.6	4.0	3.8	8.1	7.6
Methionine	2.0	3.0	4.0	2.9	1.6	3.3	3.2	3.9
Tryptophan	1.2	-	2.4	-	0.9	-	1.9	-
Isoleucine	3.4	3.9	6.8	7.9	2.3	3.3	5.5	5.6
Leucine	4.6	11.0	9.2	16.4	3.7	8.6	7.4	12.0
Methionine + Cystine	4.3	-	8.5	-	3.4	-	6.8	-
Arginine	3.9	6.0	7.9	12.7	3.2	6.2	6.4	9.9
Threonine	2.7	3.6	5.4	8.0	2.2	3.3	4.4	5.2
Histidine	1.3	2.9	2.6	4.8	0.7	3.0	2.1	3.9
Valine	4.6	5.2	9.1	9.9	3.7	5.1	7.3	7.6
Phenyl. + Tyrosine	5.5	-	11.0	-	4.4	-	8.8	-
Calcium	35.0	-	35.0	-	35.0	-	35.0	-
Avail. Phosphorus	3.5	-	3.5	-	3.5	-	3.5	-
Sodium	1.8	-	1.8	-	1.8	-	1.8	-

Deter. =Obtained from lab analysis of four basal feeds, as fed

Table 3.3 *Blending proportions of the four basal feeds and resultant energy and protein compositions*

Diet	HE/LP	HE/HP	LE/LP	LE/HP	Theoretical		Actual ^a	
	(MJ.kg ⁻¹ :g/kg)	(MJ.kg ⁻¹ :g/kg)	(MJ.kg ⁻¹ :g/kg)	(MJ.kg ⁻¹ :g/kg)	ME	CP	ME	CP
Calc.	13.00/139.5	13.00/200.0	10.00/120.0	10.00/163.0				
Deter ^a .	12.10/119.1	11.80/186.6	9.40/105.0	9.50/150.0	(MJ/kg)	(g/kg)	(MJ/kg)	(g/kg)
1	100	-	-	-	13.00	139.5	12.10	119.1
2	67	33	-	-	13.00	159.5	12.00	141.4
3	33	67	-	-	13.00	180.0	11.90	164.3
4	-	100	-	-	13.00	200.0	11.80	186.6
5	67	-	33	-	12.01	133.1	11.21	114.4
6	45	22	22	11	12.01	151.1	11.15	134.2
7	22	45	11	22	12.01	169.8	11.10	154.7
8	-	67	-	33	12.01	187.8	11.04	174.5
9	33	-	67	-	10.99	126.4	10.29	109.7
10	22	11	45	22	10.99	142.6	10.28	127.0
11	11	22	22	45	10.99	159.1	10.27	144.8
12	-	33	-	67	10.99	175.2	10.26	162.1
13	-	-	100	-	10.00	120.0	9.40	105.0
14	-	-	67	33	10.00	134.2	9.43	119.9
15	-	-	33	67	10.00	148.8	9.47	135.2
16	-	-	-	100	10.00	163.0	9.50	150.0

^a Deter. = Obtained from laboratory analyses of the four basal feeds, as fed

3.2.4 Experimental design and analysis

The trial was designed as a 4 x 4 factorial (CP x ME) with two strains of Lohmann laying hens. The 16 dietary treatments x two strains (32 treatments) were each replicated eight times using 256 hens. Strains were alternated between cages, and four birds adjacent to one another (two of each strain) received a feeding treatment, thereby facilitating feed distribution. Four blocks, in which each of the 32 treatments was replicated twice, were distributed across the laying house. The experiment was conducted over a ten-week period, the hens being 35 weeks old at the start of the trial.

On analysing the feed once the trial had begun it was clear that the four corner feeds did not conform to the desired analyses (Table 3.2). As the contents of protein and energy varied considerably from the formulated values in each of the basal feeds a factorial design could not be used to analyse the experiment. Instead, a multiple regression analysis was used to determine the effects of protein and energy intake (not content) on reproductive performance using both the linear and quadratic terms for protein and energy intake, and their interaction. The effect of Strain was determined through the use of the 'Group' option (Multiple Regression with Groups) in Genstat Release 6.1 (2000).

The mean responses for the last 4 weeks of the experiment were calculated and used to reflect the mean performance of each bird, on the assumption that the birds would have reached a relatively steady state as a result of being on each dietary treatment for six weeks, considered to be an adequate period for a hen to acclimatise to its food (R.M. Gous, Personal Communication). The variables analysed by multiple regression, using protein and energy intake as the independent variables, were egg weight, rate of lay, egg output and change in body weight. Food intake was regressed against protein and energy contents to avoid multicollinearity (protein and energy intakes are calculated using food intake, which would be the dependent variable).

3.2.5 Data collection

Body weight was recorded at the start, after six weeks, and at the end of the experiment. From these measurements body weight change (g/bird d) was calculated. Feed intake was measured weekly. Egg weight was recorded on three consecutive days each week, from

which the mean egg weight per week was calculated for each hen. Egg numbers were recorded daily, from which the rate of lay per hen was calculated. Egg output was determined by multiplying the daily rate of lay during the week by mean egg weight for the week.

3.3 RESULTS

The mean responses in feed intake and change in body weight to dietary energy and protein content for Lohmann Brown and White hens over the last four weeks of the trial, are given in Table 3.4, and those for egg weight, rate of lay and egg output are given in Table 3.5.

Table 3.4 Mean response in feed intake and change in body weight of Lohmann Brown and White laying hens to protein and energy over the last four weeks of the trial

ME MJ/kg	CP g/kg	Food intake, g/bird. d			Change in BDW g/bird. d		
		LB	LW	Mean	LB	LW	Mean
12.10	119.1	99.7	108.2	104.0	0.08	-0.95	-0.44
12.00	141.4	105.0	105.3	105.1	0.44	0.11	0.28
11.90	164.3	98.5	101.5	100.0	0.21	0.44	0.33
11.80	186.6	98.0	96.9	97.5	1.34	0.76	1.05
11.21	114.4	119.9	118.9	119.4	-2.64	-0.84	-1.74
11.15	134.2	119.5	117.5	118.5	0.36	-0.75	-0.20
11.10	154.7	115.9	112.8	114.4	-0.60	-0.72	-0.66
11.04	174.5	111.4	112.0	111.7	0.02	1.00	0.51
10.29	109.7	124.6	127.5	126.0	-1.97	-3.24	-2.61
10.28	127.0	117.2	117.8	117.5	-1.83	-0.64	-1.24
10.27	144.8	117.7	110.9	114.3	-2.49	-1.19	-1.84
10.26	162.1	109.3	105.6	107.5	-0.35	0.05	-0.15
9.40	105.0	125.5	122.6	124.1	-7.44	-6.91	-7.18
9.43	119.9	117.8	120.1	118.9	-4.20	-3.86	-4.03
9.47	135.2	114.6	114.9	114.8	-4.82	-3.89	-4.36
9.50	150.0	114.8	111.3	113.0	-4.23	-3.94	-4.09

3.3.1 Feed intake

Dietary energy and protein concentrations both significantly ($P < 0.0001$) influenced feed intake, but the responses did not differ between strains. The effect of energy content was curvilinear while that for protein was linear, the best fitting equation being:

$$\text{Food intake} = -308(\pm 110) + 88.1(\pm 20.6)\text{ME} - 4.275(\pm 0.956)\text{ME}^2 - 1.987(\pm 0.325)\text{CP}$$

(Equation 3.1)

Where food intake is in g/bird d

ME is the ME content of the feed, MJ/kg

CP is the crude protein content of the feed, g/kg

The R^2 value for the above multiple regression equation was 30.8% with the standard error for each observation being 11.2 g/bird d.

When the squared term for ME was dropped from the regression the coefficient for CP remained almost constant, at -1.902 ± 0.336 , but the coefficient for ME changed from positive to negative (-3.982 ± 0.845). The R^2 value dropped to 25.3% with the standard error for each observation being 11.7 g/bird d.

3.3.2 Change in body weight

The two strains used in the trial responded in the same way in body weight change to dietary energy and crude protein, i.e. there was no significant strain effect. Both CP intake and ME intake influenced the change in weight, but only ME intake had significant effect ($P = 0.032$). The regression equation that best fitted the data was as follows:

$$dW = -25.1(\pm 10.73) - 0.567(\pm 0.710)\text{CPI} - 0.0272(\pm 0.0223)\text{CPI}^2 + 0.0410(\pm 0.0167)\text{MEI} - 0.0000163(\pm 0.00000679)\text{MEI}^2$$

(Equation 3.2)

Where dW = change in body weight, g/d

CPin = crude protein intake, g/d

MEin = ME intake, kJ/d

The R^2 value for the above multiple regression equation was 9.7% with the standard error for each observation being 2.64 g/d.

Table 3.5 *Mean response in egg weight, rate of lay and egg output of Lohmann Brown and White laying hens to dietary protein and energy over the last four weeks of the trial*

ME MJ/kg	CP g/kg	Egg weight g/bird d			Rate of lay %			Egg output g/bird d		
		LB	LW	Mean	LB	LE	Mean	LB	LW	Mean
12.10	119.1	57.4	56.5	56.9	92.0	96.3	94.1	52.6	54.5	53.5
12.00	141.4	58.0	54.0	56.0	93.8	96.3	95.0	54.4	52.1	53.2
11.90	164.3	58.0	55.9	56.9	97.3	95.9	96.6	56.5	53.5	55.0
11.80	186.6	60.5	61.1	60.8	95.4	100.0	97.7	57.8	61.1	59.5
11.21	114.4	55.1	54.6	54.9	92.9	96.9	94.9	51.1	52.8	52.0
11.15	134.2	57.8	55.3	56.5	94.0	95.0	94.5	54.3	52.6	53.5
11.10	154.7	59.0	55.3	57.1	98.6	94.1	96.4	58.1	53.0	55.5
11.04	174.5	61.9	54.9	58.4	97.4	96.4	96.9	60.2	52.9	56.6
10.29	109.7	54.3	53.0	53.7	85.2	85.3	85.2	46.3	45.9	46.1
10.28	127.0	55.7	52.5	54.1	88.7	88.3	88.5	49.4	46.2	47.8
10.27	144.8	56.8	53.0	54.9	90.5	94.0	92.3	51.4	49.8	50.6
10.26	162.1	56.2	55.5	55.8	89.8	96.3	93.0	51.0	53.4	52.2
9.40	105.0	50.3	49.7	50.0	69.1	70.9	70.0	34.9	35.3	35.1
9.43	119.9	50.2	49.3	49.8	68.7	77.4	73.1	34.5	38.3	36.4
9.47	135.2	51.1	49.5	50.3	73.6	78.4	76.0	37.7	39.1	38.4
9.50	150.0	56.5	50.8	53.6	74.8	76.4	75.6	42.6	38.6	40.6

3.3.3 Egg weight

Mean egg weight differed significantly between strains, with the Brown strain laying eggs, on average 2.136 (\pm 0.493)g heavier than the White strain. When egg weight was regressed on the intakes of protein and energy, no significant effects were measured when all terms were included in the model. Where CPI and CPI² were the only two terms fitted, they both influenced the egg weight significantly ($P=0.015$; $P=0.006$, respectively). The R^2 value for the restricted model was 9.7% with the standard error of 4.5 g/d.

3.3.4 Rate of lay

As with egg weight, the strains differed significantly in their mean rates of lay over the four-week period, with the White strain laying at a rate $2.45 \pm 1.15\%$ higher than the Brown

strain. However, unlike the response in egg weight, rate of lay was influenced significantly by the intakes of both protein and energy, the multiple regression equation for the Brown strain being as follows:

$$\text{ROL} = 174.0(\pm 43.2) + 3.15(\pm 2.42)\text{CPI} - 0.19(\pm 0.051)\text{CPI}^2 - 0.193(\pm 0.054)\text{MEI} + 0.000042(\pm 0.00002)\text{MEI}^2 + 0.00429(\pm 0.00154)\text{CPI.MEI}$$

(Equation 3.3)

A significant interaction existed between the intakes of protein and ME. The R^2 value for the above equation was 41.2, and the standard error for each observation was 8.76%. The rate of lay for the White strain may be calculated by adding 2.45g to the constant term in the equation above. The response to protein and energy intakes was the same in both strains.

3.3.5 Egg output

There were no significant strain differences in the response in egg output to protein and energy intakes, with both protein and energy intakes significantly influencing rate of lay to the same extent in both strains. As with rate of laying, a significant interaction was found to exist between the intakes of protein and energy ($P=0.023$). The regression equation describing the response to the intakes of these two dietary factors is given below:

$$\text{EO} = 102.0 (\pm 31.7) + 1.79(\pm 1.77)\text{CPI} - 0.091(\pm 0.038)\text{CPI}^2 - 0.1219(\pm 0.0399)\text{MEI} + 0.0000273(\pm 0.000015)\text{MEI}^2 + 0.00259(\pm 0.00113)\text{CPI.MEI}$$

(Equation 3.4)

The R^2 value for this equation was 48.0 with the standard error for a single observation being 6.45 g/bird d.

3.4 DISCUSSION

The main aim of the experiment reported here was to determine the extent to which dietary energy interacts with the protein content of the diet. However, interpreting the response of laying hens to diet composition, quantitatively, can be difficult in *ad libitum* feeding, especially when it is not clear whether energy or another nutrient in the diet is limiting intake (Fisher, 1994).

Food intake was influenced by both protein and energy content of the feed, reducing by 0.23g/bird d per g/kg increase in crude protein content. According to Emmans (1981) the desired feed intake is inversely related to the dietary concentration of the first limiting resource for a given bird at a given time, meaning that if the level of any resource in the feed is halved, birds will attempt to consume twice the amount they would have of a balanced feed in an attempt to meet the requirements for the first limiting nutrient. Hens in this trial appeared to follow this rule. In relation to dietary protein levels, therefore, these results are in agreement with previous findings, which indicated that birds that are fed protein-deficient diets will eat more feed than birds on adequate protein feeds (Fisher and Morris, 1967; Pilbrow and Morris, 1974; Morris and Blackburn, 1974; Griessel, 1980; Gous *et al.*, 1987). Usually, in the laying hen, food intake is the main factor mediating the response to protein deficiencies, which implies that at higher nutrient levels food intake will decline, as requirements are met at lower intakes (Fisher, 1994). And this was actually the case in this study, that diets were deficient in protein and that birds on lower protein feeds tried to adjust their intake further.

Energy content did not influence food intake to the same extent as did the protein content. This has been demonstrated previously (Gous *et al.*, 1987) when feeds varying in protein content and deficient in an amino acid were fed at various energy levels. The response to ME content was significantly curvilinear, the regression coefficients being positive for ME and negative for ME² implying that food intake increased with energy content at a decreasing rate, which is contrary to most previous observations of the effect of ME content on food intake. When the squared term was dropped, the linear coefficient changed to a negative sign, indicating that the food intake would have decreased as ME increased. The R² value for these equations was low, indicating that factors other than CP and ME also had an influence on food intake. One of these would undoubtedly be the rate

of laying of the birds: when the rate of lay decreases food intake declines also, as there is no need for nutrient intake to remain high. The question is whether the decline is due to a lower food intake or *vice versa*. There was no significant interaction between CP and ME in this trial, with food intake responding independently to the two dietary factors. But dietary ME was clearly less influential in manipulating food intake than was CP.

Even though food intake declined as the protein content of the feed increased, protein intake was positively related to the protein content of the feed, so the change in body weight would have been related to the dietary protein content through its relationship with protein intake. Body weight gain also increased with energy intake, with birds on the higher energy feeds gaining more weight than those on the lower energy feeds. These two effects acted independently on the change in body weight. Similar findings by Cherry (1979) showed that hens that were given a high ME diet of 12.5MJ/kg for 112 days, gained more weight than birds of the same strain, weight and age, given a low ME diet of 11.5MJ/kg for the same period of time, thus implying that birds on the high energy diets over-consumed energy than those on lower energy feeds.

It is not surprising that egg weight was unaffected by either protein or energy intake, as this is less sensitive to changes in nutrient intake than is rate of laying. Morris and Gous (1988) stated that as protein supply is reduced below that required for to maximise potential egg output, the decline in rate of lay would be much greater than the reduction in egg size. The lowest egg weight obtained was 48.7g while the highest was 61.8g, but these were not related to the dietary treatment imposed.

Egg weight and rate of lay are usually negatively correlated, and this was found to be the case in this trial, where egg weight was higher in the Brown than the White strain used, but rate of lay was lower in the Brown strain. Egg output was, as a result, not significantly different in the two strains. Rate of laying was improved with an increase in protein intake (3.15% per g protein) although this rate declined at higher intakes of protein, as would be expected as intake reached the upper limit required to meet the requirements of the most demanding individuals on the trial. Previously, Morris and Blackburn (1982) conducted experiments to test the hypothesis that, as dietary protein concentration is increased, increments of response gradually diminish as egg output reaches an asymptotic value. They observed that egg output continued to increase with increasing protein input up to a

rate of 22g/ bird d of well-balanced protein. The highest intake of protein in this trial was 23.9g/d.

Rate of lay declined as energy intake increased (-0.19% per kJ ME/d), although this was at a diminishing rate as intake increased to the highest amounts recorded. This is difficult to explain, as the expectation is that the hen would benefit from an increase in energy intake, but this was clearly not the case in this trial. The response is confounded by the significant quadratic coefficient for ME intake and the interaction between protein and energy intake, making interpretation of the regression equation more difficult.

Smith (1978b) reported that birds on low protein diets stop producing eggs due to their protein reserves from serum albumen being diminished to meet the daily egg protein that cannot be provided by the feed. As protein intake declines, and egg production diminishes, the effect on egg production is presumably made worse when energy intake is increased, causing the rate of lay to decline still further. The equation does suggest that energy intake is beneficial to rate of laying only where a concomitant increase in protein intake occurs. Clearly, when predicting the effect of protein and energy on rate of laying, it is necessary to consider both nutrients simultaneously, given this interaction.

Egg output is the combination of rate of lay and egg weight, and therefore factors that influence either of these measures of performance will also influence egg output. As mentioned, the differences in egg weight and rate of lay between the two strains used in this trial cancelled one another out, so egg output was unaffected by strain. But it was influenced, like rate of lay, by both protein and energy intake and the interaction between them. In this case egg output was increased by 1.79g/bird d for a 1g increase in dietary protein intake, and decreased by 0.12g for a kJ increase in ME intake, in both cases these changes levelling off as the intakes were increased further. The significant interaction suggests that egg output benefited more from an increase in protein intake when energy intake was also increased.

In conclusion, the results are of value in quantifying the effects of changes in protein and energy intake on food intake and reproductive performance of laying hens. Such information is useful when determining the optimum economic nutrient content of a laying feed, which is the subject of a forthcoming chapter in this thesis.

CHAPTER 4

RESPONSE OF HY-LINE BROWN LAYING HENS TO DIETARY ENERGY AND PROTEIN

4.1 INTRODUCTION

When a feed is formulated for a flock of laying hens it is unlikely that nutrients in the food on offer will be present in the same ratio as required by the hen: perhaps protein content is too low in relation to energy. This places a heavy nutritional burden on the hen, since she must either increase her intake in order to satisfy her protein requirements, thereby taking in an excess of energy, or reduce her intake to avoid over- consumption of energy, in which case the quantity and/ or quality of eggs will be reduced due to a lack of protein (Forbes, 2000).

Morris (1968), however, has shown that an increase in nutrient density of diets does not have any effect on the rate of lay in hens and that the egg weight increases only slightly with the increase in nutrient density. Thus, the ability of the hen to make adjustments to her food intake in order to maintain the same energy intake is imperfect because birds fed high energy diets tend to 'over- consume' energy and end up gaining more weight than birds fed lower energy diets. In defining the optimum economic nutrient density to feed a flock of laying hens the nutritionist must take account of the cost of the nutrients and the food intake by the hen, i.e. the feeding cost, as output is not affected. However, if protein and energy are varied independently, then the output by the hen is likely to vary, and the nutritionist must take account of the effect on performance if the optimum economic feed composition is to be specified.

This trial was designed to verify the responses obtained in the previous experiment, using a different strain of laying hen and feeding these hens in groups rather than individually. The objectives were the same as for the previous trial, that is, to provide information from which the optimal combination of protein and energy could be defined that would ensure optimal output from a given flock of laying hens.

4.2 MATERIALS AND METHODS

4.2.1 Housing

Birds were housed in an open sided, convection house providing 14h light per day. Each pen consisted of six 45.7 cm x 30.5 cm cages (3 cages on top and 3 at the bottom), supplied with nipple drinkers and a feeder designed to carry at least 3.5kg of feed.

4.2.2 Layer strain used

One-thousand two-hundred and ninety-six, Hy-Line brown laying hens at thirty-eight weeks of age, were randomly allocated to 54 pens, with six cages per pen. Four birds were housed per cage thus giving three replicates of 24 birds for each treatment. The birds were fed the experimental treatments *ad libitum* for a ten-week period.

4.2.3 Dietary treatments

Four 'corner' feeds (HE/LP, HE/HP, LE/LP and LE/HP, where L and H represent Low and High, and E and P represent Energy and Protein respectively) were formulated, from which 18 combinations of protein and energy were produced by appropriate blending. The WinFeed 1.1 (1996) feed formulation programme was used to formulate these four basal feeds (Tables 4.1 and 4.2), and the blending proportions are shown in Table 4.3.

4.2.4 Experimental design

The experiment was designed as a 6 x 3 factorial (see Table 4.3, blending proportions), consisting of six protein levels and three ME levels, thus giving a total of 18 dietary treatments. Each dietary treatment was replicated three times and these were allocated randomly to the 54 pens using a completely random design, i.e. no blocking was used.

On analysing the feed once the trial had begun, as with the previous trial, it was clear that the four corner feeds did not conform to the desired analyses (Table 4.2). As the contents of protein and energy varied considerably from the formulated values in each of the basal feeds a factorial design could not be used to analyse the results of the experiment. Instead,

a multiple regression analysis was used to determine the effects of protein and energy intake (not content) on reproductive performance using both the linear and quadratic terms for protein and energy intake, and their interaction. Genstat Release 6.1 (2000) was used to determine the means for each treatment, using GLM, and for the multiple regression analyses.

Table 4.1 *Ingredient composition (g/kg) of the four basal feeds, as fed*

Ingredients	HE/LP	HE/HP	LE/LP	LE/HP
Maize	713.43	492.74	570.98	506.70
Wheat Bran	32.91	-	232.44	48.61
Soybean Full Fat	145.74	300.00	90.86	65.22
Soybean 46	-	72.10	-	270.32
Limestone	90.82	87.06	-	89.81
Fishmeal 65	-	31.50	-	-
MonoCalcium Phosphate	10.29	8.06	6.19	9.74
Vit+min premix	1.50	1.50	1.50	1.50
Salt	2.79	2.13	2.61	2.57
Sodium Bicarbonate	2.12	1.88	2.12	2.17
DL-Methionine	0.40	3.02	0.48	3.37
L-Lysine HCl	-	-	0.43	-

The mean responses for the last 4 weeks of the experiment were calculated and used to reflect the mean performance of each bird, on the assumption that the birds would have reached a relatively steady state as a result of being on each dietary treatment for six weeks, considered to be an adequate period for a hen to acclimatise to its food (R.M. Gous, Personal Communication). The variables analysed by multiple regression, using protein and energy intake as the independent variables, were egg weight, rate of lay, egg output and change in body weight. Food intake was regressed against protein and energy contents to avoid multicollinearity (protein and energy intakes are calculated using food intake, which would be the dependent variable).

Table 4.2 Nutrient (g/kg) composition of the four basal feeds; as fed

Nutrients	HE/LP		HE/HP		LE/LP		LE/HP	
	Calc	Deter	Calc	Deter	Calc	Deter	Calc	Deter
CP	120.06	116.80	209.64	204.00	118.99	117.30	202.40	201.30
ME (MJ/kg)	12.00	11.87	12.00	11.70	10.5	9.50	10.50	9.80
Lysine	5.47	5.80	12.08	11.28	5.40	5.46	10.94	10.97
Methionine	2.50	1.81	6.40	4.95	2.50	1.94	6.36	4.78
Methionine + Cystine	5.12	-	9.90	-	5.11	-	9.90	-
Threonine	4.53	3.82	8.13	6.57	4.28	3.57	7.70	6.36
Tryptophan	1.20	-	2.40	-	1.29	-	2.40	-
Arginine	7.22	7.53	13.94	13.19	7.26	6.97	13.67	13.07
Isoleucine	4.86	4.60	9.43	8.64	4.50	4.27	9.06	7.96
Leucine	12.56	10.50	18.26	16.99	11.29	9.61	17.66	15.33
Histidine	3.48	3.45	5.73	5.33	3.47	3.21	5.52	5.37
Phenylalanine + Tyrosine	9.75	-	16.95	-	9.20	-	17.16	-
Valine	6.12	7.10	10.52	11.22	5.87	6.88	10.20	11.09
Calcium	35.00	-	35.00	-	35.00	-	35.00	-
Avail. Phosphorus	3.50	-	3.50	-	3.50	-	3.50	-
Sodium	1.80	-	1.80	-	1.80	-	1.80	-

Table 4.3 *Blending proportions for the four basal feeds and resultant energy and protein compositions.*

Diet	HE/LP	HE/HP	LE/LP	LE/HP	Theoretical		Actual	
	(MJ.kg ⁻¹ :g/kg)	(MJ.kg ⁻¹ :g/kg)	(MJ.kg ⁻¹ :g/kg)	(MJ.kg ⁻¹ :g/kg)	ME	CP	ME	CP
Calc.	12.01/120.0	12.00/209.6	10.50/119.0	10.50/202.4				
Deter.	11.87/116.8	11.70/204.0	9.50/117.3	9.80/201.3	(MJ/kg)	(%)	(MJ/kg)	(g/kg)
1	100	-	-	-	12.00	120.1	11.87	116.8
2	80	-	20	-	12.00	137.9	11.84	134.2
3	60	-	40	-	12.00	155.8	11.80	151.7
4	40	-	60	-	12.00	173.8	11.77	169.1
5	20	-	80	-	12.00	191.7	11.73	186.6
6	-	-	100	-	12.00	209.6	11.70	204.0
7	50	50	-	-	11.25	119.5	10.69	117.1
8	40	40	10	10	11.25	136.8	10.70	134.1
9	30	30	20	20	11.25	154.1	10.71	151.2
10	20	20	30	30	11.25	171.4	10.72	168.3
11	10	10	40	40	11.25	188.7	10.74	185.4
12	-	-	50	50	11.25	206.0	10.75	202.5
13	-	100	-	-	10.50	119.0	9.50	117.3
14	-	80	-	20	10.50	135.7	9.56	134.0
15	-	60	-	40	10.50	152.4	9.62	150.8
16	-	40	-	60	10.50	169.0	9.68	167.5
17	-	20	-	80	10.50	185.7	9.74	184.3
18	-	-	-	100	10.50	202.4	9.80	201.3

4.2.5 Data collection and analysis

Body weight was recorded at the start, after six weeks, and at the end of the experiment. From these measurements body weight change (g/bird d) was calculated. Feed intake was measured weekly. Egg weight was recorded on three consecutive days each week, from which the mean egg weight per week was calculated for each group of hens. Egg numbers were recorded daily, from which the rate of lay per pen was calculated. Egg output was determined by multiplying the daily rate of lay during the week by mean egg weight for the week.

A factorial analysis was performed on these data to calculate means for each of the 18 dietary treatments, for purposes of comparison only. Multiple regression analyses were used to determine the responses to dietary protein and energy content, as well as to dietary protein and energy intake. In each of these cases, the full model was fitted first, after which a second regression analysis was performed in which only the significant variables were included. The full model included protein and energy intakes, their squared terms, and the interaction between them. The regression coefficients were used to determine the effects of either protein or energy content, or intake, on performance.

4.3 RESULTS

The results presented in Table 4.4 represent the mean response of 24 birds per pen over the last four weeks of the trial. Feed intake, change in body weight, egg weight, rate of lay and egg output are given in the table.

4.3.1 Food intake

Food intake was unaffected by the protein content of the feed, but was almost significantly affected by the energy content, when all terms were included in the model. The regression coefficient of food intake on energy content (MEC) was $-105.6(\pm 58.7)$ and on MEC^2 it was $4.98(\pm 2.74)$, these coefficients having P values of 0.078 and 0.075 respectively. The constant term in the above equation was 687g/d. Where MEC and MEC^2 were the only two terms fitted (with a constant term), the coefficients were $-108.3(\pm 55.63)$ for MEC and

4.94(\pm 2.60) for MEC², with P-values of 0.057 and 0.063 respectively. The R² value in these equations was only 11.1 and 10.5% respectively.

Table 4.4 *Mean responses of Hy-line Brown hens to dietary protein and energy content over the last four weeks of the trial*

Dietary Treatment	ME MJ/kg	CP g/kg	FI g/bird d	BDW g/bird d	EW g/bird d	ROL /100bird d	EO g/bird d
1	11.87	116.8	109.2	-0.9	44.6	71.0	31.8
2	11.84	134.2	112.7	1.5	54.9	86.2	47.4
3	11.80	151.7	103.6	1.2	54.1	84.0	45.5
4	11.77	169.1	110.2	2.3	57.3	87.6	50.2
5	11.73	186.6	102.5	2.3	56.2	85.9	48.3
6	11.70	204.0	112.8	2.1	57.1	83.9	48.0
7	10.69	117.1	108.7	0.4	51.3	80.9	41.5
8	10.70	134.1	112.5	0.8	53.7	86.1	46.4
9	10.71	151.2	104.0	1.0	51.8	81.2	42.1
10	10.72	168.3	96.0	1.8	54.3	84.3	46.0
11	10.74	185.4	103.5	2.3	54.7	84.7	46.5
12	10.75	202.5	108.2	1.4	54.8	82.4	45.2
13	9.50	117.3	110.8	-0.2	44.8	73.1	32.8
14	9.56	134.0	111.3	1.4	53.7	84.4	45.3
15	9.62	150.8	123.3	1.2	54.4	82.7	45.3
16	9.68	167.5	110.7	1.4	55.3	84.8	47.0
17	9.74	184.3	119.7	1.9	56.0	86.1	48.4
18	9.80	201.3	108.2	1.6	55.2	86.5	47.9

For full description of headings see acronyms on page viii

4.3.2 Bodyweight change

When all terms were fitted to the model, using protein and energy contents, only the CP² term was significant (P=0.005); the coefficient was -0.0494 (\pm 0.0167) with an R² value for the full model being 43.8%. Where all the non-significant terms were dropped from the model, both CP and CP² proved significant (P=0.002 and 0.007, respectively), the resultant regression coefficients being 1.72 (\pm 0.523) and -0.0469 (\pm 0.0166) respectively. The R² value for the restricted model was 40.7%.

When the full model of protein and energy intake on change in body weight were fitted only, CPI², MEI and CPI*MEI had significant effects. The relevant regression coefficients for CPI², MEI and CPI*MEI were -0.033 (\pm 0.011), -0.028 (\pm 0.012) and 0.000921

(± 0.00034) with P values of 0.004; 0.022 and 0.01, respectively. The R^2 value for the full model was 37.7%.

4.3.3 Rate of laying

Rate of laying was significantly affected by both the protein content of the feed and its squared term (CP^2), when all terms were included. The regression coefficient for both terms was 9.56 (± 4.139) and -0.285 (± 0.0968), with an R^2 of 30.1% and the P values being 0.025 and 0.005, respectively. Where only CP and CP^2 were included, with a constant term, the respective coefficients were 9.90 (± 3.016) and -0.284 (± 0.094), with an R^2 of 29.3% and $P=0.002$ and 0.004, respectively. There was no significant interaction between protein and energy content.

Where rate of laying was regressed against the intakes of both protein and energy, only CPI and CPI^2 proved significant ($P=0.012$ and 0.028, respectively), the coefficients being 5.06 (± 1.94) and -0.1210 (± 0.0534) respectively. The restricted model resulted in these coefficients changing to 4.938 (± 1.862) and -0.119 (± 0.0513) respectively, the R^2 value for the equation being reduced from 27 to 24.1% by dropping the non-significant terms. The P values for the restricted model were 0.011 and 0.025, respectively.

4.3.4 Egg weight

Egg weight increased at a rate of 5.764 (± 2.820) g for each 1% increase in dietary protein content, this and CP^2 being the only variables that proved to be significant ($P=0.046$; 0.005) when the full model was fitted. The R^2 value for the full model was 42.6%. Where CP and CP^2 were fitted alone, they proved to be highly significant ($P=0.001$ and 0.005, respectively). The coefficients were 6.942 (± 2.062) and -0.191 (± 0.064) respectively, and the R^2 value was reduced to 41.4%.

Where egg weight was fitted against the full model of intakes of protein and energy, only CPI and CPI^2 significantly influenced egg weight ($P=0.056$ and 0.004, respectively), the relevant coefficients being 2.993 (± 1.530) and -0.135 (± 0.045), with an R^2 value of 43.1%. These coefficients changed to 4.071 (± 1.266) and -0.0945 (± 0.035) respectively when the

non-significant terms were dropped from the model, the R^2 value being reduced, as a result, to 37.8%. The P values were 0.002 and 0.009, respectively.

4.3.5 Egg output

As with rate of laying and egg weight, only the protein content of the feed affected egg output when the full model was fitted, the significant regression coefficient being 9.64 (± 4.338) for CP and -0.2996 (± 0.1015) for CP^2 , with an R^2 value for the equation of 36.4%. When the non-significant terms were dropped from the model, the resultant coefficients for CP and CP^2 were 10.539 (± 3.156) and -0.295 (± 0.0984) respectively. The R^2 value of the restricted model was 35.9%.

Also, egg output was significantly ($P=0.012$ and 0.028 , respectively) influenced only by protein intake and CPI^2 when the full model of intakes was fitted. In this case the R^2 value was 35.5%, and this reduced to 31.7% when all the non-significant terms in the equation were dropped. In the latter case, the coefficients for CPI and CPI^2 were 5.654 (± 1.941) and -0.132 (± 0.0534), with P values of 0.005 and 0.017 respectively.

4.4 DISCUSSION

The objective behind this experiment was to determine the influence exerted by dietary energy and protein on feed intake and performance of laying hens, when varying amounts of these nutrients were offered to the birds. Because the basal feeds used did not conform to the formulation specifications, the trial could not be analysed as a factorial, but the effect of protein and energy content on the performance variables had to be assessed by means of regression, using the observed contents of protein and metabolisable energy in the feed, and in some cases, the intakes of protein and energy. Little loss of information occurred as a result of this change in method of analysis, but the main effects of protein and energy could not be displayed in the same way as is normally done with an analysis of variance.

It is apparent that food intake was influenced to a greater extent by the dietary energy content than by protein. This is generally the case in laying hens as long as adequate amounts of protein and other essential nutrients are included in the feed (Morris, 1968). By consuming more food as the ME content decreased, the protein intake on these low-energy feeds would have increased beyond that necessary for maximum production, resulting in a wastage of dietary protein, but the differences were not sufficient to cause a significant interaction to occur between protein and energy in this trial.

Energy intake increased linearly with dietary energy content, with birds eating 84.3 (± 18.1) kJ more energy for each MJ increase in ME content. These results agree with the theory of Morris (1968) that birds will over-consume energy as dietary energy levels are increased. Although the birds over-consumed energy on the highest ME feed, performance was unaffected by this over-consumption, being solely related to the protein content of the feed. Rate of laying, egg weight, and hence egg output were all influenced by the protein content of the feed, these three variables increasing at a decreasing rate as protein content was increased. Perhaps the ME contents were not sufficiently far apart for these to have influenced egg production; but in addition, the hens tended to overcome the differences in ME content by consuming different amounts of feed depending on the ME content.

The regression coefficients describing the response in body weight gain, rate of laying, egg weight and egg output give some indication of the effect of an increase in dietary protein

content on these variables. The statistical procedure used when fitting regressions results in changes in these coefficients depending on the other variables included in the regression, which makes the interpretation of these results problematic. For example, the regression coefficient for rate of laying was 9.56% for a 1% increase in protein content when all terms were included, and 9.90 when only CP and CP² were included. In each case the squared term was negative, suggesting that the response was not linear, but became less as the protein content was increased. The equivalent coefficients for egg weight were 5.76 and 6.94g / % CP, and for egg output, 9.64 and 10.54g / % CP. These values in each case do not change by a large margin, but the difference does suggest that more data are needed before the true effect of dietary crude protein on these variables can be accurately predicted. It is for this reason that researchers attempting to determine the true response of laying hens to dietary protein content should make use of the results of as many trials as possible when modelling such responses.

It is of interest to note that when the production variables rate of laying, egg weight and egg output were regressed against protein and energy intakes, instead of protein and energy content, only protein intake proved to be significant in describing these dependent variables. Because these intakes are confounded with food intake it is more useful to consider the response to dietary protein and energy contents than their intakes. Once again the regression coefficients varied marginally depending on whether the full or the restricted model was fitted, and in this case there was no significant effect of either protein or energy intake on the change in body weight over the experimental period.

The coefficients obtained in this trial will be of use when determining the overall response of laying hens to dietary protein and energy, which is the subject of the following chapter, in which the optimum combination of protein and energy is determined for laying hens under various economic circumstances.

CHAPTER 5

A MODEL TO PREDICT THE COMBINATION OF DIETARY ENERGY AND PROTEIN THAT WILL MAXIMISE PROFIT

5.1 INTRODUCTION

Protein and energy have the major influence on the voluntary food intake of the hen, together making up about 85% of the total feeding cost. Any alterations made to the dietary energy or protein content would influence the cost/ benefit ratio associated with the feeding of the diet, given that the cost and intake of the feed would change, as would the performance of the hens being offered the feed, and hence the income (revenue) generated. To achieve maximum profitability from the operation, it is necessary that the marginal cost of feeding be related to the value of eggs produced. Such that optimum nutrient intake can be estimated under changing economic conditions and allowing the formulation of a diet that will meet the hens' daily needs (Fisher and Morris, 1970; Morris and Blackburn, 1982).

A major problem with the Reading Model approach to determining the optimum economic intake of the essential amino acids (Fisher and Morris, 1970) is that these optimum intakes must be converted to concentrations before the feed can be formulated. This requires that the voluntary food intake by the hens is known, or can be predicted. No simulation models are available as yet that can predict food intake in laying hens of a given genotype kept in a given environment and provided with a given food. Until such models are available, other means must be found to determine the optimum combination of protein and energy in the feed.

The two trials reported in the previous chapters produced results that may be used for the purpose of finding an optimum economic combination of protein and energy that will maximize profit for the birds used in the trial, and perhaps for similar strains housed in similar conditions. By fitting regressions to the various outputs from the trials, profit contours could be produced, which would indicate the combinations of protein and energy that resulted in similar profits, as well as identifying the combination that results in

maximum profitability. Changes in the optimum combination brought about by changes in input costs or revenue could then be investigated.

5.2 MATERIALS AND METHODS

5.2.1 Prediction of feed intake with changes in dietary energy and protein content

Prediction of food intake is complex, because it must consider the ability of the bird to adjust its intake in relation to the nutrient concentrations in the diet, and to the prevailing environmental conditions. In an effort to test the accuracy of the results reported in the previous chapters, the equation of Morris (1968) was used to predict food and energy intakes. This equation however can only be used when the characteristic energy intake of a diet of a measured ME content is known; energy intakes on feeds with different dietary energy concentrations can then be calculated. As the ME contents of the feeds used in the two trials reported here were measured, the energy, and hence, food intakes by hens given access to feeds differing in ME content could be predicted using the equation of Morris (1968):

$$E = y + (0.1306y - 146.6)(x - 11.3)$$

where E = energy intake kJ ME/d

y = typical energy intake of strain when given a feed containing 11.3 kJ ME/g

x = energy content of feed in kJ ME/g

No such equation exists for predicting food intake when the protein content of a feed is altered. Using linear regression analysis performed on a range of relevant data obtained from previously published papers (Table 5.1) it was possible to estimate relative changes in food intake as the protein content of feeds was altered (Figure 5.1). From each data set the highest feed intake was given a value of 100 (F100), and intakes for levels that were below or above this value were calculated relative to the highest intake. This resulted in two groups of data sets, one being above and the other being below F100 respectively. Regression (meta) analyses was performed on these data and two regression equations (illustrated below in Figure 5.1) were obtained, one for protein contents below that which

gave maximum food intake and the other for those protein contents that were fed above that required to maximise food intake.

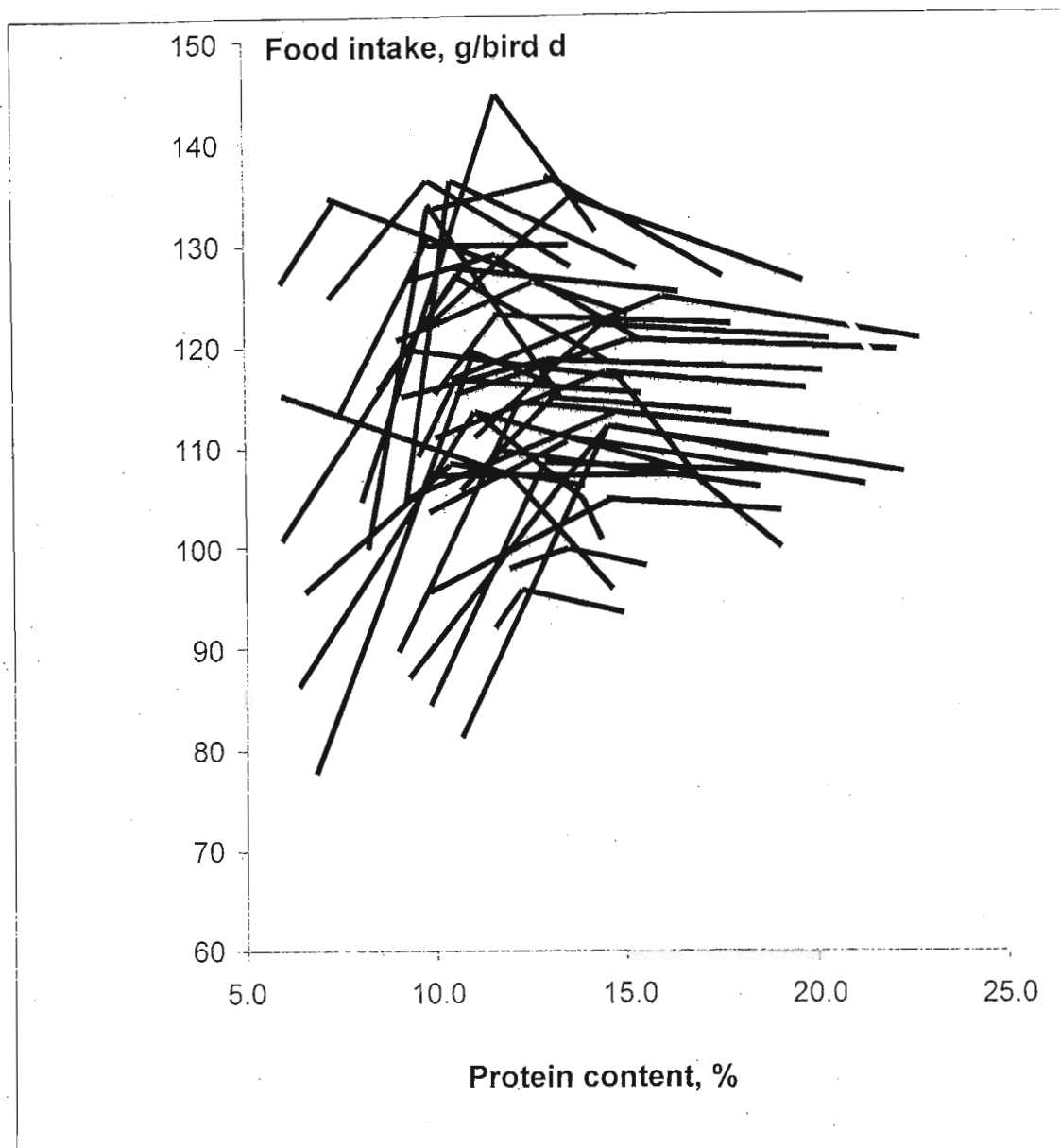


Figure 5.1 The relationship between dietary protein content and feed intake using 31 data sets in 9 published experiments (Table 5.1) with laying hens. The equations (derived from the data in Table 5.1) used were $Y = 67.723 + 1.841X$ ($R^2 = 31.8$) for protein contents below that giving maximum food intake, and $Y = 98.717 - 0.1980X$ ($R^2 = 14.4$) for protein contents above that giving maximum food intake)

Starting with a knowledge of the characteristic food intake of the birds on the trials conducted here, on a feed with a given ME content, these slopes could then be used to predict food intake with changes in dietary protein content.

The effect on food intake of changing the protein content of the feed was calculated by assuming that a feed containing 150g protein/kg would result in the highest food intake, this being the case in Chapter 4 of this study. Adjusting food intake for protein contents below and above 150g/kg using the regression coefficients derived above (illustrated in Figure 5.1), a two-dimensional matrix of dietary energy and protein contents was constructed, with predicted energy intakes for the range of protein and energy contents being shown in Table 5.2. Food and protein intakes predicted for the same range of protein and energy contents are in Tables 5.3 and 5.4, respectively.

Table 5.1 *Data sets used for the prediction of characteristic food intakes*

Authors	Number of data sets
De Groote (1972)	3 (<i>Nutrient density for battery-caged LH hens</i>)
Fisher and Morris (1970)	1 (<i>Methionine requirement</i>)
Gous <i>et al.</i> (1987)	9 (<i>Methionine, Isoleucine & Lysine experiments</i>)
Griessel (1980)	3 (<i>Isoleucine experiment</i>)
Huyghebaert and Butler (1991)	1 (<i>Threonine experiment</i>)
Jensen <i>et al.</i> (1990)	2 (<i>Experiment 3 and 4</i>)
Morris and Blackburn (1982)	2 (<i>Experiment 1 and 2</i>)
Pilbrow and Morris (1974)	8 (<i>Lysine requirements for 8 strains of laying hens</i>)
Sykes (1972)	1 (<i>Energy requirements</i>)

Table 5.2 *Predicted energy intakes (kJ/ bird d) by laying hens for a range of dietary protein and energy contents*

Dietary ME content		Dietary Protein content, g/kg					
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	1146	1186	1232	1285	1281	1276	1270
13.5	1145	1183	1227	1277	1273	1268	1263
13.0	1143	1180	1222	1269	1265	1261	1256
12.5	1142	1177	1216	1262	1258	1253	1249
12.0	1141	1174	1211	1254	1250	1246	1242
11.5	1140	1171	1206	1246	1242	1239	1234
11.0	1139	1168	1201	1238	1235	1231	1227
10.5	1138	1165	1195	1230	1227	1224	1220
10.0	1137	1162	1190	1222	1220	1216	1213

Table 5.3 *Predicted feed intakes (g/ bird d) by laying hens for a range of dietary protein and energy contents*

Dietary ME content		Dietary Protein content, g/kg					
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	81.8	84.7	88.0	91.8	91.5	91.1	90.7
13.5	84.8	87.6	90.9	94.6	94.3	93.9	93.5
13.0	88.0	90.8	94.0	97.6	97.3	97.0	96.6
12.5	91.4	94.2	97.3	100.9	100.6	100.3	99.9
12.0	95.1	97.8	100.9	104.5	104.2	103.8	103.5
11.5	99.1	101.8	104.9	108.3	108.0	107.7	107.3
11.0	103.5	106.2	109.1	112.5	112.3	111.9	111.6
10.5	108.4	110.9	113.8	117.2	116.9	116.6	116.2
10.0	113.7	116.2	119.0	122.2	122.0	121.6	121.3

Table 5.4 *Predicted protein intakes (g/ bird d) by laying hens for a range of dietary protein and energy contents*

Dietary ME content MJ/kg	Dietary Protein content, g/kg						
	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	8.2	9.7	11.6	13.8	15.1	16.5	18.1
13.5	8.5	10.1	11.9	14.2	15.6	17.0	18.7
13.0	8.8	10.4	12.3	14.6	16.1	17.6	19.3
12.5	9.2	10.8	12.8	15.1	16.6	18.2	19.9
12.0	9.6	11.2	13.2	15.7	17.2	18.8	20.7
11.5	10.0	11.7	13.8	16.3	17.8	19.5	21.4
11.0	10.4	12.2	14.3	16.9	18.5	20.3	22.3
10.5	10.9	12.7	14.9	17.6	19.3	21.2	23.2
10.0	11.4	13.3	15.6	18.3	20.1	22.1	24.2

5.2.2 Predicting the cost of feeding

In order to calculate the daily feeding costs for all 63 feeds in the matrix (seven protein contents ranging from 100 to 200 g/kg, and nine energy contents, from 10 to 14 MJ/kg) the cost of each of the feeds had first to be determined. Four 'corner' feeds (Table 5.6) were formulated using the WinFeed 1.1 (1996) formulation program to obtain the cost of each of these feeds, using current ingredient prices. The amino acid specifications used were for a 2.0 kg laying hen with a potential egg output of 58g/d, using the coefficients of response in Table 5.5, suggested by McDonald and Morris (1985). The resultant amino acid intakes were converted to dietary contents using the predicted food intakes given in Table 5.2. Using the costs of the four corner feeds, the cost of the remaining 59 feeds was calculated. These costs were multiplied by the predicted food intake to determine the cost of feeding the birds each day (Table 5.7).

Table 5.5 *Coefficients of response used in calculating the daily amino acid intakes, and the resultant intakes, required by a laying hen weighing 2.0kg and producing 57g egg output/d.*

Amino acid	¹ Coefficients of response		² Amino acid requirement mg/d
	Maintenance mg/kg body weight	Egg output mg/g egg output	
Lysine	9.99	73	716
Methionine	4.77	31	334
Tryptophan	2.62	11	171
Isoleucine	7.97	67	283
Leucine	12.50	32	776
Methionine + Cystine	8.30	80	465
Arginine	8.90	53	667
Threonine	6.90	32	457
Histidine	3.30	16	613
Valine	8.90	76	659
Phenyl. + Tyrosine	13.50	32	834

¹⁻² *From McDonald and Morris (1985)*

Table 5.6 *Ingredient and nutrient composition (g/kg) of the four basal feeds and prices of ingredients (R/ ton) used.*

Ingredients	HE/LP	HE/HP	LE/LP	LE/HP	Cost of ingredient
Maize	546.0	265.0	540.5	461.0	1400
Wheat Bran	143.9	53.6	339.1	90.1	1000
Soybean full fat	82.5	306.8	-	36.5	2700
Soybean 46	-	-	-	215.7	2200
Sunflower 37	-	150.0	-	92.0	1700
Sunflower oil	120.0	120.0	14.5	-	6600
Limestone	91.8	89.2	93.6	89.2	400
DL- Methionine	-	0.2	-	0.2	33760
L- Lysine HCl	1.0	-	1.9	-	22690
Vit-min premix	1.5	1.5	1.5	1.5	12980
Salt	2.7	2.9	2.3	2.9	550
Monocalcium phosphate	8.4	9.5	4.1	9.5	2780

Nutrient composition	HE/LP	HE/HP	LE/LP	LE/HP
CP	100.0	200.0	100.0	200.0
ME (MJ/ kg)	14.0	14.0	10.0	10.0
Lysine	7.5	9.0	3.8	8.8
Methionine	3.5	3.2	1.8	3.2
Tryptophan	1.7	5.8	0.8	6.1
Isoleucine	6.3	6.5	3.1	6.5
Methionine + Cystine	6.3	12.9	3.1	12.7
Calcium	3.5	3.5	3.5	3.5
Avail. Phosphorus	0.5	0.5	0.5	0.5

Table 5.7 *Calculated cost of feeding (c/bird d) for a range of dietary protein and energy contents, with a maize price of R1400/ton.*

Dietary ME content	Dietary Protein content, g/kg						
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	10.3	11.2	12.2	13.2	13.7	14.2	14.7
13.5	10.7	11.5	12.5	13.6	14.1	14.6	15.1
13.0	11.0	11.9	12.9	14.0	14.5	15.0	15.5
12.5	11.4	12.3	13.3	14.4	14.9	15.5	16.0
12.0	11.8	12.8	13.7	14.8	15.4	15.9	16.5
11.5	12.3	13.2	14.2	15.3	15.9	16.4	17.0
11.0	12.8	13.7	14.7	15.8	16.4	17.0	17.6
10.5	13.4	14.3	15.3	16.4	17.1	17.7	18.3
10.0	14.0	14.9	16.0	17.1	17.7	18.4	19.0

Table 5.8 *Calculated cost of feeding (c/bird d) for a range of dietary protein and energy contents, with a maize price of R700/ton.*

Dietary ME content	Dietary Protein content, g/kg						
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	7.1	8.2	9.3	10.5	11.4	12.2	13.0
13.5	7.3	8.4	9.5	10.7	11.5	12.3	13.1
13.0	7.6	8.6	9.7	10.9	11.8	12.5	13.3
12.5	7.9	8.9	10.0	11.2	12.0	12.8	13.6
12.0	8.1	9.1	10.2	11.4	12.2	13.0	13.8
11.5	8.4	9.4	10.5	11.6	12.4	13.2	13.9
11.0	8.8	9.8	10.8	12.0	12.8	13.5	14.3
10.5	9.1	10.1	11.2	12.4	13.2	13.9	14.7
10.0	9.5	10.5	11.5	12.7	13.4	14.2	15.0

5.2.3 Predicting egg weight and rate of lay

Estimates of the relative egg weights and rate of lay (Tables 5.9 and 5.10, respectively) were predicted from the equations of Morris and Gous (1988):

$$\text{Relative egg weight} = 1 - 0.07353x - 0.10424x^2 \quad (R^2 = 0.764)$$

$$\text{Relative rate of lay} = 1 - 0.03734x - 1.02927x^2 \quad (R^2 = 0.877)$$

Where x = amino acid intake for a particular diet/amino acid intake for the diet which supported maximum egg output

To calculate egg weight and rate of lay (Tables 5.9 and 5.10), estimates of relative egg weight and rate of lay were multiplied by the response in egg production of Hy-Line Brown laying hens reported in Chapter 4, with a maximum egg weight of 58g/bird d and a mean rate of lay of 88 eggs/100 bird d, respectively.

Table 5.9 *Predicted mean egg weights (g) by laying hens for a range of dietary protein and energy contents*

Dietary ME content	Dietary Protein content, g/kg						
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	52.8	53.7	54.6	55.5	56.0	56.5	56.9
13.5	53.0	53.8	54.7	55.7	56.2	56.6	57.0
13.0	53.2	54.0	54.9	55.8	56.3	56.8	57.1
12.5	53.4	54.2	55.1	56.0	56.5	56.9	57.3
12.0	53.6	54.4	55.3	56.2	56.6	57.1	57.4
11.5	53.8	54.6	55.5	56.4	56.8	57.2	57.5
11.0	54.0	54.9	55.7	56.6	57.0	57.3	57.6
10.5	54.2	55.1	55.9	56.8	57.1	57.5	57.7
10.0	54.5	55.3	56.2	56.9	57.3	57.6	58.0

Table 5.10 *Predicted mean rate of lay (%) by laying hens for a range of dietary protein and energy contents*

Dietary ME content MJ/kg	Dietary Protein content, g/kg						
	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	46.5	53.8	61.7	69.9	74.1	78.0	81.6
13.5	48.0	55.4	63.2	71.3	75.5	79.3	82.7
13.0	49.6	57.0	64.8	72.8	76.8	80.5	83.7
12.5	51.3	58.7	66.4	74.3	78.2	81.8	84.7
12.0	53.0	60.4	68.1	75.8	79.6	83.0	85.7
11.5	54.9	62.3	69.9	77.3	81.0	84.1	86.5
11.0	56.9	64.3	71.8	78.9	82.4	85.2	87.2
10.5	59.0	66.3	73.7	80.5	83.7	86.2	87.8
10.0	61.2	68.5	75.6	82.0	85.0	87.1	88.0

5.2.4 Predicting income and profit

The proportions of eggs falling into different egg weight categories, using the South African egg grading system, for mean egg weights ranging from 40 to 75g were calculated assuming a coefficient of variation of 0.08 in egg weight, and assuming that the distribution of egg weights is normal (Appendix). A description of the egg grades used in South Africa, as well as current local prices for the different grades is given in Table 5.11. Mean egg prices (VAT included) from local supermarkets were used as reference.

The mean revenue per dozen (Table 5.12), for each of the 63 combinations of dietary protein and energy, was calculated as the product of the proportion of egg weights falling into each grade (Appendix), and the number of eggs produced per day for each of the three egg price scenarios (current, +15% of current, and -15% of current). This was done using the VLOOKUP function in MS-Excel. Profits (revenue-minus-feeding costs) for the three egg price scenarios were calculated (Table 5.13 and 5.14).

Similar calculations for profitability were conducted for the three egg revenues when the maize price was halved. Multiple regression analyses were then performed on each of the

data sets, with profit (the dependent variable) being regressed against dietary protein and energy, as well as their squared terms and the covariance between these two dietary characteristics. These regression equations were used to produce profit contours, thereby obtaining a graphical illustration of the effect of dietary protein and energy on profitability under different pricing scenarios.

Table 5.11 *Current prices for different egg grades (standard), and when these are either increased or decreased by 0.15 (April 2003 prices)*

<i>Egg grade</i>	Weight Range (g)	Price (R/dozen)		
		Standard	+ 15%	- 15%
Small	< 45	7.98	9.18	6.78
Medium	46- 51	8.38	9.64	7.12
Large	52- 61	8.58	9.87	7.29
Extra-large	62- 66	9.58	11.02	8.14
Jumbo	> 66	9.98	11.48	8.48

5.3 RESULTS

The objective of this exercise was to predict what combination of protein and energy would yield the highest income over feeding cost, and to determine whether this optimum combination would change as the cost: benefit ratio changed. The revenue derived from the eggs produced for each of the 63 combinations of dietary protein and energy is given in Table 5.12. The highest revenue generated was at the highest concentrations of dietary protein at all levels of energy, and with the low energy feeds resulting in higher revenue than the high energy feeds.

Table 5.12 *Revenue (c/hen d) under current egg prices for laying hens fed a range of feeds varying in protein and energy.*

Dietary ME content MJ/kg	Dietary Protein content, g/kg						
	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	9.5	11.0	12.6	14.3	15.1	15.9	16.7
13.5	9.8	11.3	12.9	14.6	15.4	16.2	16.9
13.0	10.1	11.6	13.2	14.9	15.7	16.5	17.1
12.5	10.6	12.1	13.7	15.4	16.2	16.9	17.5
12.0	11.0	12.5	14.1	15.7	16.5	17.2	17.7
11.5	11.4	12.9	14.5	16.0	16.8	17.4	17.9
11.0	11.8	13.3	14.8	16.3	17.0	17.6	18.0
10.5	12.2	13.7	15.2	16.6	17.3	17.8	18.2
10.0	12.8	14.4	15.9	17.2	17.8	18.3	18.5

The profit (revenue minus feeding cost) generated by these combinations of dietary protein and energy were calculated for three egg price scenarios, and the results of these calculations using current egg prices is given in Table 5.13. Even though the revenue was highest on high protein, low energy combinations, because of the high cost of feeding, such feeds were not as profitable as the high protein high energy feeds, where the maximum profit was generated. To reduce space, only the profit at current egg prices is given; the consequence of changing the egg price on profit generated is illustrated in the contour plots presented later.

The consequence of lowering the cost of maize by 0.5 was then addressed, using the same three egg price scenarios, and the results of one of these (again using current egg prices) is given in Table 5.14. The consequence of reducing the maize price at current egg prices, apart from increasing the profit for all combinations of protein and energy, was to move the combination yielding the highest profit from high protein; high energy to low protein, low energy feeds. The results of these calculations were used to generate the profit contours presented below.

Table 5.13 *Revenue minus feeding cost (c/hen d) under current egg prices for laying hens fed a range of feeds varying in protein and energy.*

Dietary ME content	Dietary Protein content, g/kg						
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	1.5	2.2	2.9	3.3	3.5	3.5	3.3
13.5	1.5	2.2	2.9	3.2	3.3	3.2	2.9
13.0	1.7	2.4	3.0	3.2	3.3	3.1	2.7
12.5	1.6	2.3	2.8	3.1	3.0	2.7	2.2
12.0	1.6	2.2	2.7	2.8	2.7	2.3	1.6
11.5	1.6	2.2	2.6	2.5	2.3	1.7	0.9
11.0	1.7	2.2	2.5	2.4	2.0	1.3	0.2
10.5	1.5	2.0	2.2	1.9	1.4	0.5	-0.9
10.0	1.4	1.8	1.9	1.4	0.7	-0.5	-2.1

Table 5.14 *Revenue minus feeding cost (c/hen d) under current egg prices for laying hens fed a range of feeds varying in protein and energy, following a 0.5 reduction in maize price.*

Dietary ME content	Dietary Protein content, g/kg						
MJ/kg	100	115	131	150	165	182	200
Characteristic intake, g/d	101	104	107	110	110	109	109
14.0	4.7	5.3	5.8	6.0	5.8	5.5	5.0
13.5	4.8	5.4	5.9	6.1	5.9	5.5	4.9
13.0	5.1	5.7	6.1	6.3	6.0	5.6	4.9
12.5	5.2	5.8	6.2	6.2	5.9	5.3	4.5
12.0	5.3	5.9	6.2	6.2	5.8	5.2	4.3
11.5	5.4	6.0	6.3	6.2	5.7	5.0	3.9
11.0	5.7	6.2	6.5	6.2	5.7	4.8	3.5
10.5	5.8	6.2	6.4	6.0	5.3	4.2	2.7
10.0	5.8	6.2	6.3	5.8	4.9	3.7	1.9

Profit contours were produced as a means of illustrating the effect on profit (revenue minus feeding cost) of combinations of dietary protein and energy, using the data generated above. In performing multiple regression analyses on each of the data sets generated, with profit (the dependent variable) being regressed against dietary protein and energy, as well as their squared terms and the covariance between these two dietary characteristics, the squared terms were never found to be statistically significant and were therefore dropped from the analysis. The equations generated for each of the six datasets (three egg price scenarios at two maize prices) are given in Table 5.15. In all cases the dietary protein and energy contents, as well as the interaction between these, were highly significant, resulting in low residual mean squares. These regression equations were used to generate profit contours for each of the six scenarios, and these are given in Figures 1 to 6.

Table 5.15 *Regression coefficients for predicting revenue minus feeding costs for laying hens fed a range of energy and protein concentrations, using the data generated in Tables 5.13 and 5.14, when egg prices were normal (Scenario I), increased (Scenario II) or decreased (Scenario III) by 0.15, with and without a change of -0.5 in the cost of maize.*

	Constant	ME	CP	ME x CP	R.M.S.
Normal maize price					
I	19.410	-1.398***	-1.593***	0.130***	0.572
II	24.458	-1.690***	-1.712***	0.145***	0.675
III	14.089	-1.082***	-1.454***	0.113***	0.457
0.5 of the normal maize price					
IV	24.686	-1.433***	-1.378***	0.103***	0.616
V	29.750	-1.730***	-1.494***	0.119***	0.720
VI	18.963	-1.087***	-1.211***	0.084***	0.505

***P < 0.001

5.4 DISCUSSION

Under current or standard egg prices (Figure 5.1), the lowest profitabilities (0.7 to 1.4 c/bird d) were at ME contents below 11MJ/kg and CP contents between 125 and 150g/kg. Revenue in this region generated the highest revenue (18.5c/bird d), but because the cost of feeding is between 3 and 4c higher than at the higher ME contents (19 vs. 15.5), mainly because of the high food intake at this low ME content (121 vs. 97g/bird d), this becomes the least profitable combination.

Increasing egg prices by 15% resulted in increase in the revenue (± 2.0 c/bird d) and profits of twice those obtained under current egg prices at similar combinations of dietary CP and ME (Figure 5.2). However, the combination of protein and energy resulting in the highest profit remained the same. This was not the case when the revenue was decreased: in this case (Figure 5.3) profit was reduced, as expected, but the range of protein contents over which the maximum profit remained the same was extended, to encompass contents from as low as 110g/kg.

When profit was increased as a result of a decrease in maize price, the effect on the optimum combination of protein and energy in the feed was not the same as that resulting from an increase in egg price. In this case (Figure 5.4) the combination yielding the highest profit moved from high protein and high energy feeds to low protein and low energy feeds. Feeds high in energy and protein consist of high-energy-containing ingredients such as full-fat soya and sunflower oil, so a decrease in the cost of maize has little effect on the cost of such feeds relative to that of low energy feeds, especially when these contain low protein contents. The effect of a decrease in the cost of maize was greatest, therefore, on the low protein feeds, and especially the low protein and low energy feeds. Consequently, maximum profit shifted to the low protein low energy feeds, where egg production was lower and feed price was reduced considerably relative to the other combinations of protein and energy.

The effect on feed cost of a reduction in maize price was so dramatic that the optimum combination of dietary energy and protein did not change even when the egg price was changed considerably (Figures 5.4 to 5.6). Under such circumstances it would, therefore be unnecessary to alter the composition of the feed as the value of eggs produced was altered.

But, with a change in ingredient prices, the optimum combination of protein and energy would change depending on whether the ingredient supplied predominantly protein or energy. It would be necessary to conduct such an exercise in order to determine the optimum combination of protein and energy.

Until a suitable model for predicting the amount of a given food that a laying hen will consume each day when kept in a given environment is produced, the method outlined in this chapter could be used under all circumstances to ascertain the optimum feeding strategy for different breeds and strains, as long as the potential performance of the breed in use is known.

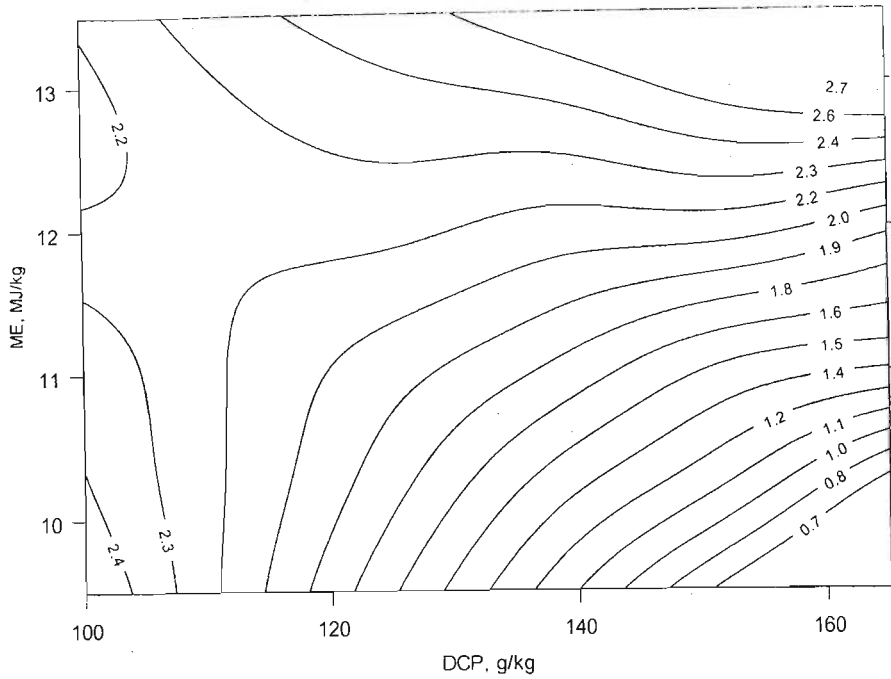


Figure 5.1 *Contour plot of the effect of combinations of dietary energy and protein on profit (c/bird d) under standard egg prices and high maize price.*

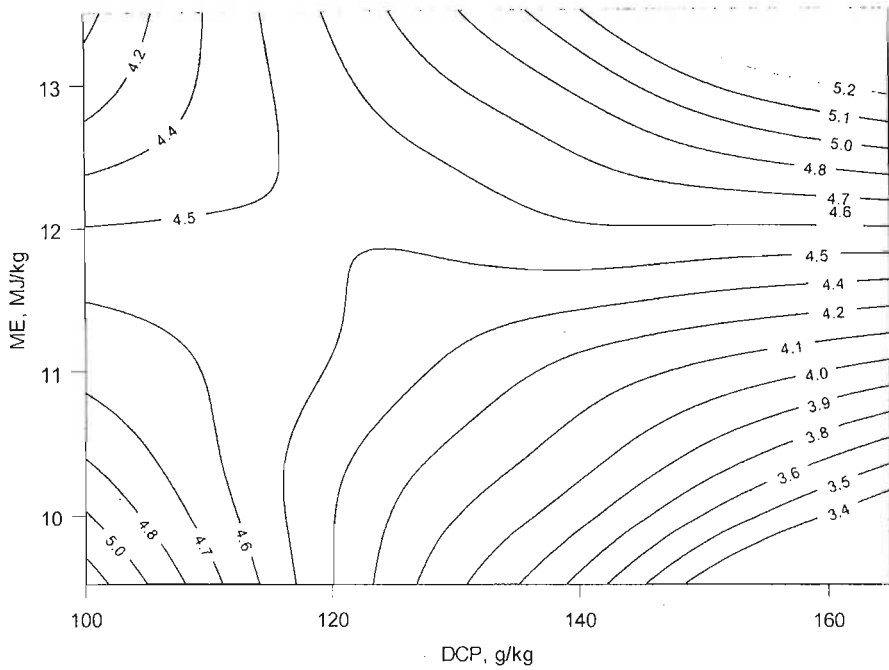


Figure 5.2 *Contour plot of the effect of combinations of dietary energy and protein on profit where maize price is high and egg prices were increased by 0.15.*

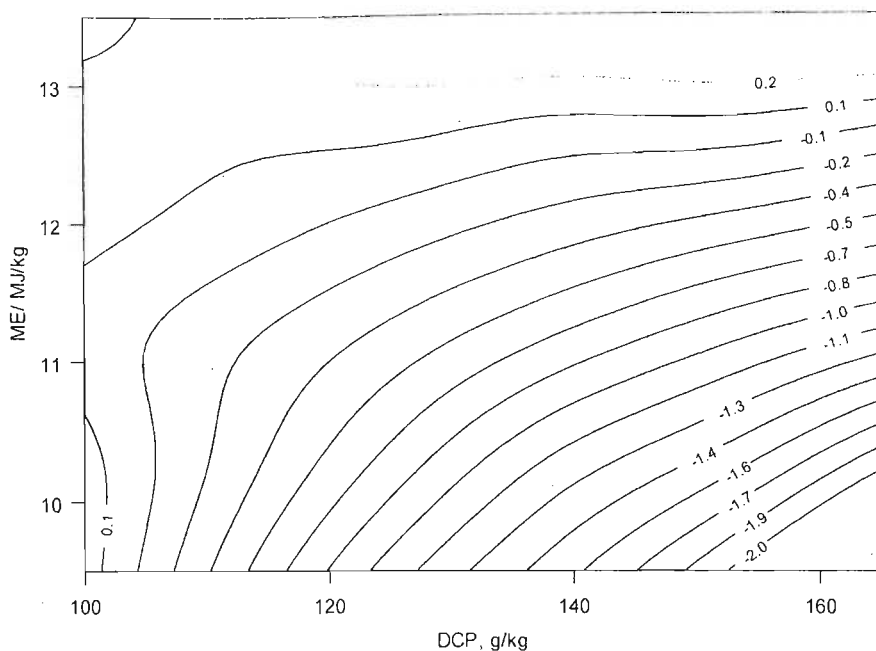


Figure 5.3 *Contour plot of the effect of combinations of dietary energy and protein on profit where maize price is high and egg prices were reduced by 0.15.*

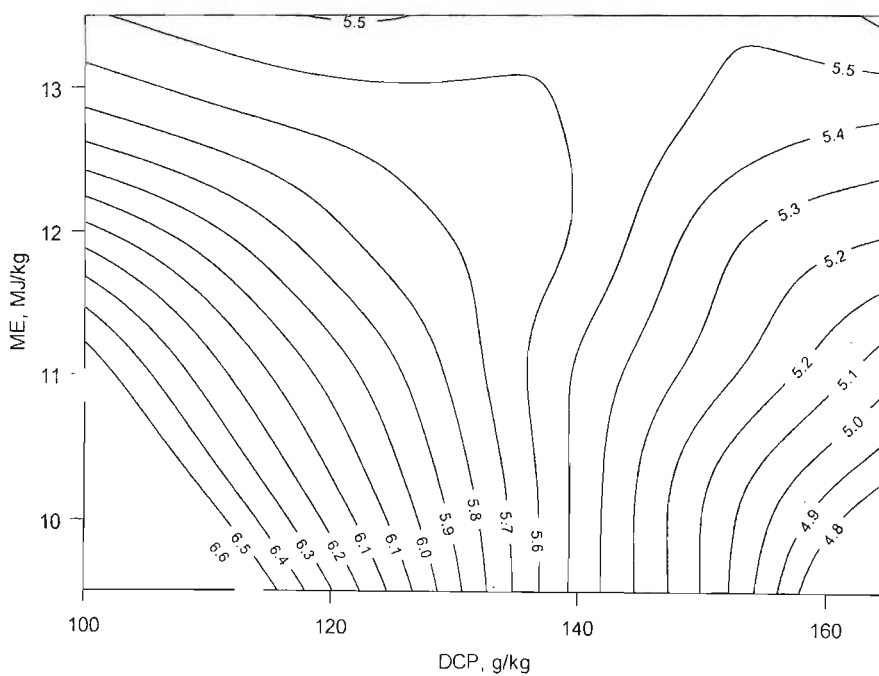


Figure 5.4 *Contour plot of the effect of combinations of dietary energy and protein on profit under normal egg prices and a low maize price.*

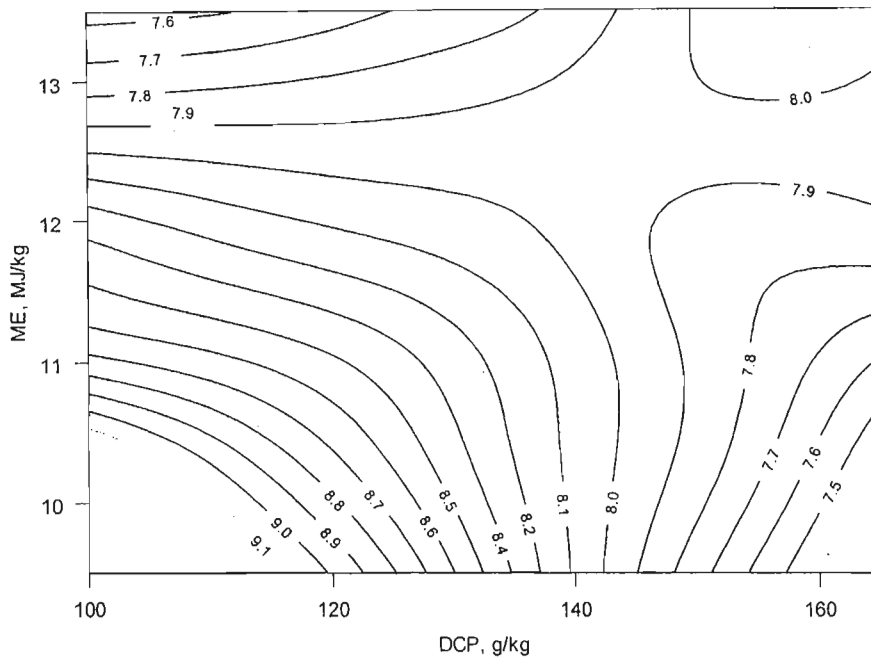


Figure 5.5 *Contour plot of the effect of combinations of dietary energy and protein on profit where egg revenue was increased by 0.15 at a low maize price.*

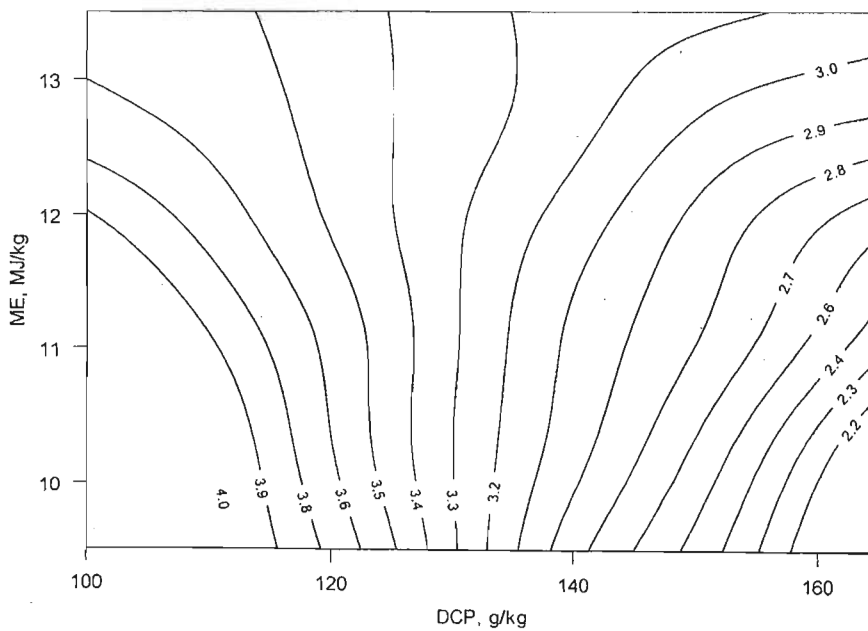


Figure 5.6 *Contour plot of the effect of combinations of dietary energy and protein on profit where egg revenue was decreased by 0.15 at a low maize price.*

GENERAL DISCUSSION

Providing the optimum daily nutrients for laying hens is both a biological and an economic problem, requiring detailed definitions of the nutrient requirements of the birds being fed, the nutritional value of ingredients being used to meet optimum dietary energy and protein needs of producing birds, and the relevant costs and returns. In the South African egg industry, feed constitutes 64 to 70% of total production costs, and the availability of good quality protein ingredients and grains, which constitute about 50% of total ingredients, fluctuates from season to season and from year to year, causing ingredient prices to change, sometimes dramatically. Ingredient prices also fluctuate depending on the strength of the local currency relative to others, often not recovering linearly to a strengthening Rand value, whilst producer prices normally increase far too slowly to recover production costs. Due to the financial implications that these fluctuations have on profitability it would be useful to have some means of determining how the composition of feeds for laying hens should be altered in order to maximise profitability under these changing circumstances.

The difficulty in optimizing the feeding of laying hens is that there is no accurate method of predicting food intake, but this is a prerequisite if the cost of feeding is to be predicted. Over the years, papers have been published on predicting food intake, based on the energy content of feed, but this is not the only feed attribute that influences food intake, so it is naïve to use only the energy content for this purpose. Whereas the Reading model has been used successfully to interpret responses of laying hens to amino acid intakes and to predict optimal economic estimates of amino acids that should be included in the feed, this also relies on being able to predict food intake. But until a satisfactory theory is developed to predict food intake, some other means of determining the optimum feed for laying hens needs to be found.

As a means of addressing the problem, two experiments were conducted, in which three strains of laying hens between 33 and 48 weeks of age were used, to produce data from which the optimum combination of dietary energy and protein for different strains of laying hens could be derived. The major objective of the study was therefore to determine the optimum feeding strategy by applying a cost: benefit analysis. This was done by predicting feed intake, and hence feeding costs, and egg output, and hence revenue, with

changes in dietary protein and energy, using estimates obtained from the present, and past, studies, of the changes that are likely to occur when these feed attributes are altered. The use of profit contours enabled evaluations to be made of the effect on profitability of changes in egg price and maize price. The changes in the optimum combination of dietary protein and energy that occurred when these prices were changed indicated that the theories used were sufficiently sound to justify the use of such a method in the decision-making process.

The results from this study showed that to maximise profit when egg revenue is high, a combination of high protein and high energy would be favoured, and that this combination would not change much when the egg revenue was reduced, given that almost the same change was applied over all combinations of protein and energy. The greatest change observed was where the ingredient price was altered: in the case of a substantial drop in the maize price, the optimum combination changed from high protein, high energy feeds to low protein, low energy feeds. This was because the cost of high energy, high protein feeds decreased only marginally, whereas the low energy, low protein feeds dropped substantially as a result of the decrease in the price of maize, resulting in a significant drop in the cost of feeding. A different result could be expected if the price of one of the other ingredients, such as a protein source, were altered.

In conclusion, the nutrition of the laying hen is not currently suffering from any shortage of information relating to nutrient requirements for both maintenance and egg production. Nevertheless, it is worth continuing to measure responses of laying hens to dietary energy and protein, as the data may assist modellers to produce sufficiently accurate models of food intake, thus making response assessment easier and less costly.

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APPENDIX

Table I. *Proportion of egg grades used to calculate the revenue in Chapter 5*

Egg weight	Small	Medium	Large	Extra Large	Jumbo
45	28.9	62.8	8	0.3	0.1
46	20.8	65.4	13.1	0.7	0.3
47	14.4	64.4	19.6	1.6	0.6
48	9.6	60.2	26.8	3.3	1.4
49	6.3	53.8	33.6	6.0	2.7
50	4.0	46.0	39.4	10.0	4.9
51	2.5	37.8	43.3	15.0	8.3
52	1.5	30.0	45.0	20.8	12.8
53	0.9	23.0	44.3	26.9	18.6
54	0.5	17.2	41.4	32.6	25.5
55	0.3	12.5	37.2	37.2	33.3
56	0.2	8.8	32.2	40.2	41.6
57	0.1	6.1	26.8	41.5	50.0
58	0.1	4.2	21.6	40.8	58.2
59	0.0	2.8	17.0	38.6	65.7
60		1.8	13.0	35.2	72.4
61		1.2	9.7	30.9	78.3
62		0.8	7.1	26.4	83.2
63		0.5	5.1	22.0	87.3
64		0.3	3.6	17.8	90.4
65		0.2	2.5	14.1	92.9
66		0.1	1.7	10.9	94.9
67		0.1	1.2	8.3	96.3
68			0.8	6.3	97.4
69			0.5	4.6	98.1
70			0.4	3.3	98.7
71			0.2	2.4	99.1
72			0.2	1.7	99.4
73			0.1	1.2	
74			0.1	0.8	
75				0.6	