

The role of mathematical modelling in optimising animal production

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Introduction

The economic crisis that has dominated the headlines recently has brought into focus the problem that animal nutritionists face when formulating feeds for poultry and pigs. Huge increases in input costs, problems in acquiring raw materials and a reduction in demand for product lead to technical challenges that need immediate response. This situation is very different from that where the producer controls the market, and demands a closer look at all aspects of the production process. The nutritionist, mill manager, farm manager and marketing department need to work together to maximise profitability in the entire enterprise rather than regarding each department as an independent cost centre. Feed formulation, the topic of this paper, is only a small part of the total process but, whereas in the past it was not possible to take account of all aspects of production when formulating feeds for animals, advances in simulation modelling now improve the prospects for achieving this goal.

Poultry nutritionists base their nutritional strategies on the concept of a 'nutrient requirement'. This is seen as a characteristic of the bird and is the nutrient content required to support 'maximum' or 'optimum' production. Such requirements are published as tables by learned committees (e.g. NRC, 1994), by national extension services in many European countries, by breeding companies and by some universities and research institutes. Within a company the nutritionist will attempt to adapt these requirements to local circumstances taking some account of the business's objectives and also of economic circumstances. The basis on which such adaptations are made are often tenuous and lacking in critical scientific rigour.

The application of systems thinking and modelling to the problem of feed formulation leads to the replacement of the above approach with one in which nutritional decisions are made entirely in terms of the objectives of the business. Nutrient specifications are chosen that will maximise a desired objective function such as margin/m² per annum. Feeding animals to achieve some company objective is not the same as feeding them to meet a 'requirement'. Economic circumstances will change from time to time, and different nutritional strategies will be needed to maximise margins. Also, nutritional decisions will depend on the stage in the production process at which margin is to be assessed. For example if nutrition is optimised for margin at the farm gate, with live bird weight (and perhaps downgrading) affecting revenue then nutritional responses in growth, feed conversion ratio and mortality will need to be considered. If, however, margin is measured based on the production of processed portions or meat then nutritional responses in these characteristics, as well as those operating at the farm gate, will affect the outcome. These are real differences, each requiring specific nutritional decisions. Modelling enables these differences to be accommodated.

The process followed is not dissimilar to that proposed by Deming (1986) to improve product quality, except that in this discussion it is profitability and not quality that is being targeted, which is not to say that quality should not also be considered. The nutritionist's role at present is to complete the Plan/Do/Study/Act (PDSA) cycle by changing the formulation specifications and measuring the resultant response that is obtained in the field over a number of cycles. Decisions about which nutrients to manipulate, and by how much, are generally made with reference to the shadow price of

each limiting nutrient without regard to the value of the end product. Progress, if at all, is at best slow, but may be elusive. Opportunities arising from changes in input costs or product value need to be grasped immediately if maximum benefit is to be gained, and this is only possible if performance can be predicted rather than measured in the field. The PDSA cycle could then be completed in seconds rather than months and the company would benefit in good and in bad times. The role of nutritional modelling in this process is thus to predict nutritional responses so that the PDSA cycle can be automated through the process of optimisation. It should be made clear that the 'optimum' feeding strategy referred to throughout this discussion is that which will maximise or minimise the objective function defined by management.

Predicting performance

Predicting responses of poultry to nutrients has been the goal of nutritionists and modellers for a long time. The controlled feeding model of a growing pig (The Edinburgh Model Pig) was the first serious and successful attempt to integrate information about an animal, its feed and the environment in which it was kept, with a view to simulating its performance (Whittemore, 1976; Whittemore and Fawcett, 1976). This provided the impetus for the development of further models, of modifications to existing models and of research targeted at filling the gaps in our knowledge of critical aspects of the theory incorporated into these models. The most important subsequent contribution to response modelling was the theory proposed by Emmans (1981) to predict voluntary food intake in poultry and pigs, which raised the value of prediction models inestimably by making food intake an output from, as opposed to an input to, the growth model. Models incorporating this theory are thus more realistic and useful, providing the nutritionist with a tool for making decisions about the most appropriate course of action to take under different circumstances. Advances continue to be made, and it is now possible to optimise the feeds and feeding programmes of broilers and pigs, through the integration of a feed formulation program, a simulation model and an optimisation routine (Gous and Berhe, 2006). However, because models require a complete statement about each step in the chain of events, some interpolation must of necessity be used where appropriate data are missing (Whittemore, 1981). All models contain some such conjectures, so none can claim to be absolutely accurate. Also, as models become more sophisticated, the list of variables that may be predicted increases.

Until recently, mechanistic models developed for pigs and poultry have dealt with the simulation of responses in a single animal or bird. Such responses are usually linear to the point where the genetic potential is reached (Fisher *et al.*, 1973). Poultry nutritionists are interested in responses to nutrients in economically important outputs such as body weight (or protein) gain, breast meat yield, egg output, food intake and conversion efficiency, numbers of chicks produced per hen, etc. Because such responses are usually measured using groups of birds, they are invariably curvilinear, being the result of integrating the responses of individuals making up that population. Populations of birds therefore cannot have 'requirements' for nutrients: what nutritionists seek are the optimum economic dietary contents of each nutrient, and for this they need to know how populations respond to increasing dietary contents of the essential nutrients. Descriptions of such responses, whilst taking account of marginal costs and revenues, are therefore invaluable in determining how to maximise or minimise the objective function chosen for any given commercial operation. Clearly, being able to predict these nutrient responses may be seen as the foundation of a successful nutritionist.

Many empirical models have been developed that attempt to optimise performance (Kenny *et al.*, 2004; Eits *et al.*, 2005 a and b; and for a summary of others, see France and Kebreab, 2008), but these are not discussed further in this paper as they are not designed to predict performance but simply to predict the composition of the feed that will maximise performance or profitability. Being empirical in nature they are limited in their ability to respond to changes in the important variables

such as genotype and environment. Their greatest limitation is that none of these empirical models can predict food intake, which is the basis for being able to predict performance.

Predicting food intake

To be of any real value, models that attempt to optimise the feeding of animals must be capable of predicting voluntary food intake. Where this variable is an input to a model, as is most often the case, it is naïve to believe that feeding programmes can be successfully optimised, when the composition of the food offered has such important effects on voluntary food intake. Food intake must therefore be an output from a model, and not an input. The theory of food intake and growth proposed by Emmans (1981, 1989) is based on the premise that birds attempt to grow or reproduce at their genetic potential, which implies that they attempt to eat as much of a given feed as would be necessary to achieve these goals. This 'desired' food intake (DFI) is defined as the amount of the nutrient required divided by the content of that nutrient in the feed, and can thus be determined for each of the essential nutrients, and energy, required by the bird or animal. That nutrient resulting in the highest DFI is by definition the first limiting nutrient in the feed on offer. The process of calculating the DFI for each nutrient is relatively straightforward. Where this DFI cannot be achieved through constraints of gut capacity or environmental heat demand, the food intake is said to be constrained (CFI) and the actual food intake, being the lower of DFI and CFI, would in this case equal the constrained intake.

This theory has been shown to predict food intake and hence growth and carcass composition with considerable accuracy (Ferguson and Gous, 1997, Ferguson *et al.*, 1997). Broilers (Burnham *et al.*, 1992) and laying hens (Gous *et al.*, 1987) have been shown to increase food intake as the limiting nutrient in the feed is reduced, attempting thereby to obtain more of the limiting nutrient, until a dietary concentration is reached where performance is so constrained that food intake falls. The common misconception that 'birds eat to satisfy their energy requirements' is clearly naïve and of no value in predicting voluntary food intake.

A growing or reproducing animal needs to be supplied with nutrients in order to meet its requirements for maintenance of the body and feathers (in the case of poultry), for the growth of all other components of the body, including feathers, and for reproduction. In order to predict voluntary food intake it is necessary to predict the amount of each of these essential nutrients required by the bird or animal each day. This requires a description of the genotype (its body protein weight and potential growth rate or egg output on that day), the food being offered, and the environment to which the animal is being subjected. Each of these provides challenges for the modeller, many of which have been described previously (Emmans and Fisher, 1986). The approach suggested by Emmans (1989) to describe and evaluate broiler genotypes, for example, begins with a definition of potential protein growth, and the live weight of the animal is built up from this, using the allometric relationships that exist between protein, water, ash and lipid, i.e. a bottom-up approach. He has shown that a few, simple, assumptions can lead to a description of a growing animal that is sufficient for predicting its performance in non-limiting conditions and for calculating what these conditions are. It seems sensible to be able to predict performance in non-limiting conditions before the more difficult question is tackled, namely, that of defining growth in limiting conditions. Values for the genetic parameters that define a growing animal can be measured by rearing animals in environmental conditions that are as near to ideal as possible. Under these conditions, growth curves are obtained that represent the genetic potential for a particular genotype. The growth curves obtained in this way allow comparisons to be made between breeds and strains. Examples of such investigations are in Hancock *et al.* (1995), and Gous *et al.* (1999).

The resources needed to meet these requirements can be determined from knowledge of the growth rate and composition of the various components of the body and/or eggs being produced. The

resources available for supplying these requirements, which are present in various feedstuffs, need to be described in the same terms as are used to describe the nutrient requirements. The requirement for protein depends on the amino acid composition of that protein and the rate at which it is being produced. The sum of each amino acid required for the maintenance and the growth of feather and of body and egg protein constitutes the daily requirement for each of the amino acids. The retention of lipid, water and ash has no protein requirement. The scale on which the amino acids required by the animal are measured, and on which the amino acids in the feed are described must be the same. The conventional wisdom is to express this in terms of digestibility. The marginal efficiency with which the first limiting amino acid is used for protein retention above maintenance is not necessarily constant, but can be modified by the supply of other amino acids and by the supply of energy (Kyriazakis and Emmans, 1992). Values for these marginal efficiencies need to be measured using response experiments, but the methodologies used for measuring and interpreting such responses have not been resolved. A discussion on this topic is not appropriate here, but is important when interpreting results of published trials and when designing future response experiments.

Describing the potential rate of lay

Describing the potential rate of lay of a laying hen is complex as this differs between individuals and over time within individuals. The mathematical model of Etches and Schoch (1984) demonstrated that two functions, representing two independent but interacting systems of the hen's asynchronous ovulatory cycle, were able to predict realistic ovulation times and intra-sequence ovulation intervals. However, a major disadvantage of their model is that predictions are restricted to sequences of between 2 and 9 ovulations only. For each ovulation sequence, a different set of discrete values for the parameters is required, these values apparently having been somewhat arbitrarily chosen by the authors. Of greater value for modeling purposes is a set of continuous functions, representing the changes required to the values of the different parameters, such that the prediction of any sequence length is possible. This approach (Johnston and Gous, 2003) has considerably enhanced the value of the model described originally by Etches and Schoch (1984). Mean rate of lay in a flock of hens at a particular age is determined by the individual patterns of sequential laying at that time. The slope of the initial rise in flock egg production to peak rate of lay is influenced by the distribution of ages at sexual maturity and by the lengths of the individual prime sequences. The incidence of internal laying at onset of maturity plays a role in modifying rate of lay but not ovulation rate. The persistency of lay after peak will be determined by the rate at which sequence lengths of individual hens shorten over time, as well as by the number of pause days. Hence the prediction of sequence length is a logical step in predicting the performance of a flock of laying hens over an entire laying cycle.

One of the advantages of the method used by Johnston and Gous (2003) to model egg production is that it lends itself to stochasticity. Within a population of birds, individuals of the same age show considerable variation about a mean sequence length, which may be due to variation in the length of the open period for LH release, or variation in follicular dynamics. This variance may be accounted for by using mean values and standard errors for each of the parameters in the model. Such a population of birds would generate a range of ovulation times, the distribution of which would be unimodal and positively skew in young hens, becoming bimodal with age. Reproductive senescence in hens manifests as an increase in the intra-sequence ovulation and oviposition intervals with time, as well as an increase in the number of pause days. With this information it is possible to determine the nutrients required daily by laying hens for reproductive purposes.

The environment as a constraint to achieving the desired feed intake

High temperatures are the most common reason for birds and animals not achieving their desired feed intake. It has been demonstrated (Ferguson and Gous, 1997 and 2002, Ferguson *et al.*, 2000a and b) that as the protein or amino acid content of a feed is reduced, pigs will increase intake in an attempt to meet their requirements for potential growth, the extent to which they are able to compensate for the deficiency being dependent on the amount of heat the pig can lose to the environment, which in turn is dependent on the environmental temperature. The results of these experiments are all accurately simulated using the pig growth model (EFG Software, 2006) developed using the theory of growth of Emmans (1981, 1987 and 1989).

Whereas birds benefit in cold weather from the insulative properties of their feather cover, this thermal barrier constrains the amount of heat that may be lost to the environment in hot weather. As the potential growth rate of broilers is increased by genetic selection, their inability to lose sufficient heat to the environment is becoming a major constraint in commercial broiler operations worldwide. Accounting for all the factors that contribute to the environmental heat demand placed on the birds, such as temperature, humidity, wind speed and thermal radiation, and then accounting for the response of the bird to this 'effective' temperature, is a major challenge when modelling the response of broilers to nutrient supply.

In very few models is food intake an output to the model, the majority needing this variable to be input in some way or other. In such cases it is difficult to imagine that the effects of the environment on food intake can be successfully modelled. But even where food intake is an output, such models presently take a relatively naïve approach when describing the environment, usually describing only the environmental temperature and the relative humidity. Yet wind speed and radiation are important elements in determining the environmental heat demand on the animal, as is the fact that birds are capable of differential blood flow redistribution (McArthur, 1981) to the bare appendages of the body (wattles, comb and legs). By managing the vasoconstriction/vasodilation of the arterio-venous shunts of the skin in those anatomical regions, the bird is able to control sensible heat dissipation (Hillman *et al.*, 1982, Hillman and Scott, 1989, Willmer *et al.*, 2000). Accounting for these additional factors impacting on the response of the bird to its environment implies that a dynamic approach is necessary.

It is still not clear from the literature what the micro-environmental conditions are at which the bird is at least thermoregulatory effort, which would seem to be a prerequisite for predicting the environmental effects on birds when they are not in this state. Many of the experiments involving the effect of thermal stress on birds have been conducted using constant temperatures applied over long periods of time, which implies that the physiological and productive responses of the bird are in a steady-state (such as the model suggested by Mount (1979) for a homoeothermic animal), thus ignoring the important point that the environment has a dynamic, cumulative effect on chickens (Blanco and Gous, 2006). We have argued that responses of chickens to environmental conditions are dynamic, and depend not only on the thermoregulatory abilities of the birds and the conditions of the environmental variables to which they are exposed, but also on the time of exposure to such conditions. Birds varying in body weight will achieve thermal equilibrium with the environment following different lengths of exposure, depending on the environmental conditions as well as on their thermal properties (feather cover, comb and wattle size, acclimatisation, etc). Blanco *et al.* (2004) have modelled these thermal responses, considering the animal characteristics as well as the environmental conditions.

It appears that there is much still to be done in explaining these thermal responses in a dynamic, time-dependent manner before being able to take accurate account of environmental heat demand when predicting voluntary food intake.

Optimisation

Once food intake has been predicted the performance of the growing or reproducing bird or animal can also be predicted leading to the possibility of determining the feeds and feeding programme that will maximise or minimise the objective function defined by management. The process involves a feed formulation program, a model that simulates performance, and an optimisation algorithm, which is a numerical method for finding a value x such that $f(x)$ is as small (or as large) as possible, for a given function f , possibly with some constraints on x (Wikipedia, 2009). Many such algorithms are available.

In this case the optimiser works from a given starting point and then varies the diet composition or feeding programme until the combination of circumstances which maximises (or minimises) the objective function is reached. The feeds being formulated, invariably at least cost, at this stage are optimised for the conditions used. Normally the objective function will be some measure of productivity such as margin/m² per annum, or breast meat yield at a given body weight, but any output parameter from the growth model may be used for this purpose.

The optimiser works by iteration and the time taken to reach a solution can be an issue in some circumstances. Various ways of working around this problem are available and indeed it progressively becomes less severe as computer power increases.

A practical approach to optimisation

The optimum feeding programme for broilers and pigs is that which results in the highest profit for the enterprise. To be of economic relevance, objective functions should include revenue, space and time, the most obvious example being margin/m² per annum. This takes account of the both the fixed and variable costs of production and the income derived from the sale of product. In broiler production, fixed costs are invariably high, so throughput is particularly important. Reducing the age at slaughter by one or two days results in considerable savings in fixed costs. Such objective functions are more sensible than attempting to minimise feed conversion ratio, for example.

Determining the optimum concentrations of amino acids relative to energy in each feed, the optimum nutrient density, and the optimum length of time (or amount) that each feed should be fed, is therefore both a nutritional and an economic decision. At present the EFG programs optimise each of these three aspects of commercial broiler and pig feeding programmes. These options are described more fully below. The information required for optimisation consists of feed costs at different levels of amino acid provision, a description of all the relevant animal responses, both fixed and variable costs affecting the production system, and details of revenue. The complexity of the information required would depend on the level of organisation at which the optimisation is to be made. If profit of the broiler grower is to be maximised at the farm gate, then responses in liveability, growth and feed conversion ratio will probably suffice. However, and more realistically, a wider view will be required, and the effect of broiler nutrition on slaughterhouse variables (eviscerated yield, rejects etc.) and further processing (carcass composition) will need to be defined. Mack *et al.* (2000) emphasised the importance of broiler companies considering all aspects of the production cycle when making nutritional decisions.

Optimising amino acid contents in each feed

The optimum relationships between the essential amino acids and energy change during the growing period, and the optimiser determines the relationship within each specified feeding period that maximises (usually) or minimises the objective function. The objective is to determine the optimum amino acid to energy ratio in each of the feeds in the feeding programme such that the overall performance is maximised. The objective is not to determine independently the optimum ratio in

each of the feeds on offer. Because the performance on one feed impacts on the performance on subsequent feeds, this is an essential prerequisite in optimising the feeding of broilers.

To optimise dietary amino acid contents the process works only with lysine. The contents of the other essential amino acids are controlled by reference to an (user-controlled) 'ideal' protein ratio. In the present versions of the program both amino acid and energy contents are optimised simultaneously, although the user may fix either of these, thereby increasing flexibility.

Optimising nutrient density

Where a given ratio between the essential amino acids and energy in each feed is to be maintained, the program will optimise the nutrient density in each of the feeds in the feeding programme, by maximising the objective function over the entire growth period. As Fisher and Wilson (1974) have shown, the optimum nutrient density depends on such factors as sex, the ratio between input and output costs, and mixing and transport costs. These factors, and others, may be considered by the user in determining the optimum nutrient density of each of the feeds in the programme.

Optimising the feeding schedule

Many broiler or pig producers do not have the opportunity of having feeds mixed according to their specifications, but are constrained to make use of proprietary feeds. An almost infinite variety of options is open to such producers in designing their feeding schedule, which can be based on amounts fed in each period or on fixed feeding periods for each feed. The optimum feeding schedule is dependent on the composition of the feeds, their respective prices, the revenue to be derived from the sale of the product, and many other biological and economic considerations.

The system is extremely versatile, allowing for a wide range of management practices to be considered. The broiler growth model, for example, allows for multiple harvesting (cropping) from single- or mixed sex flocks, and calculates revenues from any mixture of whole-bird sales and processing. Typical economic variables are included although these are readily customised to fit with individual enterprises.

In the pig model, account is taken of the effect of genotype, feed and environment on all the usual production parameters, but in addition, the carcass grade. Any grading system can be defined in the model, and prices are allocated to each grade, these being considered when optimising the feed and feeding programme for these animals.

The situation with broiler breeder hens differs from that of broilers and full-fed laying hens in that a daily allowance of feed is allocated, this being less than would normally be consumed if the birds were given *ad libitum* access to feed. Yet the principles applied to voluntary intake prediction, described above, remain: the difference is that the desired food intake of the birds is hardly ever achieved, thus the actual food intake is that constrained by the farm manager. Consequently, egg output will be a function of the amount of limiting nutrient remaining after the maintenance requirement of the hen has been met. It is doubtful that broiler breeders have a requirement for growth, once sexual maturity has been achieved, thus it could be argued that body protein and lipid deposition, or utilisation, leading to a change in body weight, should be regarded as being a consequence of the nutrients consumed and not as an obligatory daily process. This being the case, the balance of ME intake remaining after accounting for maintenance and egg production would be converted into body lipid with varying efficiencies depending on whether the dietary lipid was deposited directly as body lipid or first converted to CO₂ and H₂O (Emmans, 1994). Similarly, any excess protein would be deaminated and converted into body lipid. This is a more sensible approach than assuming that a broiler breeder hen has a need to grow body protein or lipid during the reproductive phase.

All that remains then is to predict potential rate of laying as well as the weights of albumen and yolk that would make up the contents of each egg produced. The methods described by Johnston and Gous (2006) for this purpose appear to work satisfactorily for broiler breeders (Gous and Nonis, 2009) as long as appropriate functions are used to describe the relationships between age and yolk weight, albumen and yolk weight, and shell and egg content weight, which differ between strains. Account can be taken of differences in age at sexual maturity, maximum rates of lay, rates of decay in ovulation rate over time, and the variation that exists between individuals in all these respects. Rules must be applied to account, for example, for minimum egg weights when essential nutrient intake is severely constrained, for the size of amino acid pools for potential albumen formation, and for the rates at which lipid can be either deposited in, or withdrawn from, body reserves as a means of accounting for differences in energy balance.

Because the egg production period of broiler breeders is so long (about 35 weeks), experiments designed to determine the optimum feeds and feeding programmes fail because of the almost infinite combination of variables that could be applied during this period. Furthermore, it has been demonstrated that the response of a bird or animal to a feed depends on what was being fed previously (Kyriazakis et al., 1991; Gous and Nonis, 2009) which adds a further dimension to the possible feed treatments that could be explored over the laying period, and points to the futility of attempting to determine the optimum feeds and feeding programmes by experimentation. Short term trials are certainly not the answer. The approach described above, of accurately predicting the effects of daily allocations of a given feed on performance, is far more likely to result in optimum solutions under the varying circumstances likely to be encountered in practice.

Discussion

For practical reasons only energy and amino acid levels need to be considered in the optimisation process, thereby reducing the size of the problem. The range of responses that need to be predicted is not fixed although it will have to be quite extensive if the models are to be useful: the actual range will of course depend on the particular markets involved. As with all optimisation routines it is possible to find a 'local' minimum or maximum that is not the best option available in the nutrient space being investigated. To overcome this problem different starting points are often used, which increases the time taken to reach the optimal solution. Other methods are available that explore the entire space and then produce three dimensional plots of the response surface, which assist in sensitivity analysis; determining which factors are of importance, and under which circumstances.

It has been 30 years since the Edinburgh Model Pig entered the scientific arena and since then the progress that has been made in predicting performance of broilers and pigs has been enormous. The Edinburgh Broiler Model (Emmans, 1987) was an improvement on the Pig Model, mainly because it predicted voluntary food intake as opposed to using a controlled feeding approach. The theory used to predict food intake (Emmans, 1981) has had major advantages for modellers, as it has been successfully applied in simulating the effect of, among others, changes in dietary amino acid and protein content, environmental temperature, infection and social stress. It has led to food intake being an output from models instead of being an input, which has enabled models to be used to optimise feeds and feeding programmes, a process not possible unless food intake is accurately predicted. It has spawned many useful scientific studies that have corroborated the theory, and it has led to a simplified method of accounting for the heat produced by an animal when consuming a given feed, known as the effective energy system (Emmans, 1994). And because the effective (or net) energy value of a feed is a function of both the feed and the animal being fed, what would be the advantage of describing feeds in these terms if a model were not available to determine the value of this feed to the animal itself? Those early models stimulated useful and purposeful research targeted at filling the gaps in our knowledge of critical aspects of the theory incorporated into these models, this being useful in itself in improving the scientific value of research.

In spite of the progress made in the past decades, there are still challenges that lie ahead for those wishing to predict responses to nutrients in poultry. Many of these have been raised through the development of existing models. For example, the need to understand how to describe the environment and the way it impacts on broiler performance has greater meaning when this information can be linked to a prediction of the constraining effect of high temperatures on voluntary food intake. It has been demonstrated that significant changes have taken place in broiler genotypes over time, and that the genotypes available today differ substantially in their composition and in the way they deal with marginally deficient feeds, yet updating the description of these genotypes would be of little value if this information could not in some way be used to simulate the performance of these birds under varied feeding and environmental conditions, from which optimum feeds and feeding programmes could be predicted. Also, it only really matters whether the efficiency of utilisation of an amino acid by a broiler for growth is 0.75 or 0.80 if this is to be used to predict the requirement by the broiler for that amino acid: this information is of no value if the requirement for the amino acid is being derived purely from the results of a growth trial.

Apart from the problems described above, there are others that still need to be resolved to provide nutritionists with the tools to make informed decisions about poultry feeding. The voluntary food intake of laying hens, for example, has not yet been modelled mechanistically, with nutritionists still relying on empirical equations based on energy requirements such as those of Emmans (1974) as the basis for such prediction. Yet the principles are the same as those for predicting food intake in broilers, the main difference being in the definition of potential performance. But a model has now been developed that adequately describes the ovulatory cycle of a laying hen, from which laying performance and egg composition throughout the laying cycle may be modelled (Johnston and Gous, 2006). What remains is to model the effect of inadequate nutrient intake on egg production. Similarly, the performance of broiler breeder hens, in response to daily nutrient allocations, needs to be adequately modelled. There remain opportunities for simulation modellers to address these and other challenges in the future.

Sadly, the world does not seem to be as enthusiastic about models as are the modellers themselves. This is partially the result of scepticism brought about through bad experiences with (bad) models. Many sets of empirical equations have been termed 'models', some of which are robust and useful, such as the model to predict age at first egg of laying pullets for any specified pattern of photoperiod used during the rearing period (Lewis *et al.*, 2003), whilst many others are simply equations representing the result of a single experiment, with little or no predictive value outside of the experiment itself. It is the latter that have justifiably caused this scepticism. One of the challenges faced by those predicting responses to nutrients is to convince the poultry Industry that good models have the potential to be of immense benefit to nutritionists, geneticists and other decision makers in the Industry. The important principle is that models should be 'open' –the user must know on what ideas and assumptions the model is based. Models which are 'black boxes' and closed to the user are not likely to contribute much to the improved management of nutrition. It is imperative also that the methods used by scientists to measure the numbers that make theories work are robust and unambiguous such that the resultant models can be used to assist the poultry Industry to become more efficient especially when designing their feeds and feeding programmes.

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