Simulation modelling for predicting responses in broiler breeder and laying hens

R.M. Gous
University of KwaZulu-Natal, Pietermaritzburg, South Africa

Summary

Simulation modelling offers a greater understanding of the underlying principles of nutrition and production in an animal system, and such models may then be used for many different purposes. The emphasis in this paper is on predicting the food intake of a flock of commercial laying hens, and the response of broiler breeders to nutrient intake, for which an understanding of systems such as the attainment of sexual maturity in a flock of pullets and the physiological control of egg production in hens is essential. The potential performance of a laying hen is dependent on the age at which it becomes sexually mature, on its genetically-determined internal ovulatory cycle length and egg weight, and the rates at which these change over time, all of which may be satisfactorily modelled. Using stochasticity, the potential laying performance of a flock may be simulated from these individual responses. Whereas laying hens are usually given ad libitum access to feed, the daily food intake of broiler breeders is restricted. But in both cases it is useful to be able to predict the amount of energy and of each nutrient that is required for maintenance and egg production. In order to achieve these goals, a comprehensive understanding is required of the factors influencing the attainment of sexual maturity in these birds, of the ovulatory cycle and how this changes during the laying cycle, of the changes that occur in egg and body component weights over time, and of the physiological, environmental and social factors that may prevent each bird from consuming sufficient of a given feed to meet its potential performance each day. Without a comprehensive simulation model that incorporates all these concepts it is unlikely that the consequences of offering feeds of different quality to flocks of laying hens or broiler breeders on the rate of egg production and the weight and composition of the eggs produced could be accurately predicted. Nor is there a better way of optimizing the feeding of these birds than of being able to predict these consequences before the feed is offered to the flock.

Much of the information required to develop such a model has been published, not necessarily with a...
view to its use in a simulation model, but there are still some concepts that have not been researched, where further information would be valuable. Thus, by developing a simulation model for predicting responses in laying hens and broiler breeders, the relevant information from the literature has been synthesized into a workable theory for each system, the various systems have been integrated, and gaps in our knowledge of these systems have been identified. Such models are never complete or perfect, but by describing them comprehensively further development and refinement is more likely to be achieved.

**Predicting the age at sexual maturity**

The age and body weight of a bird on the day it lays its first egg has a very strong influence on future egg weight and the number of eggs laid, which are important considerations for both the layer and broiler breeding industries. These characteristics can be modified by lighting and/or the nutritional control of growth: in full-fed, egg-type hens, a 10-d delay in sexual maturity that has been achieved through a lighting programme results in an increase of 1.3 g in mean egg weight and a reduction of 7 eggs over 52 weeks lay, but the total egg output will be similar (Lewis and Morris, 2006). Clearly, to predict the laying performance of a hen, her age at sexual maturity must first be defined, and this can be predicted.

Important considerations in predicting sexual maturity in hens are that gonadal development proceeds whatever lighting programme is used, that lighting modifies the age at sexual maturity, that changing photoperiods have a greater influence than do constant photoperiods (Lewis and Morris, 2006), and that the response of a broiler breeder to light differs from that of a commercial laying hen because broiler breeders, unlike commercial laying hens, exhibit photorefractoriness (Lewis et al., 2003).

In full-fed commercial pullets lighting is the most important environmental factor influencing age at first egg (AFE) (Lewis et al., 2002). When pullets are reared under constant day lengths the length of the photoperiod used can influence AFE (Lewis et al., 1998), and when one or two changes are made to the daylength during rearing, the length of each photoperiod also has an influence (Lewis and Perry, 1994; Lewis et al., 1996). Whilst the initial and final photoperiods are the principal components of a lighting programme influencing AFE in full-fed pullets, the effects of a given change in photoperiod are not the same at all ages. Lewis et al. (2002) proposed a model to predict AFE of full-fed pullets when changes were made to the photoperiod during rearing. The four components of the model, each of which is calculated separately, deal with the genetic differences in AFE in birds maintained on constant photoperiods from hatching, the change in AFE as a function of age at transfer to the final photoperiod, the acquisition of sensitivity to increases in photoperiod in the young pullet, and the onset of spontaneous rapid gonadal development, i.e. the proportion of birds maturing under the influence of the initial photoperiod, without responding to a late change in photoperiod. It is assumed that a pullet will lay its first egg at the age expected for a long-day rearing treatment even if the photoperiod is reduced during the final 13 days before that egg is due, this being the length of time taken for final rapid development of the largest ovarian follicle (Etches 1996). Lewis and Morris (2008) modified their original model to accommodate subsequent evidence related to the effect of FSH on the process of sexual maturity.

Following a series of trials with broiler breeders, a similar empirical model was developed by Lewis et al. (2007) to predict the age at sexual maturity of these birds, taking into account their body weight at 20 weeks and the fact that they are photorefractory, which means that they do not respond to light in the same way that commercial layers do. Only one change in photoperiod is accommodated in this model. The photosexual response in broiler breeders is strongly influenced by the feed allowance and hence the rate of prepubertal growth. Regressions for birds given either a constant photoperiod or a single increase indicated that mean age at 50% lay advances by 2 d for every 100-g increase in body weight at 20 weeks. Because broiler breeders exhibit juvenile photorefractoriness they require up to 20 weeks to dissipate this, although faster growth allows quicker dissipation. As a consequence, a group of birds grown to a typical weight of 2.1 kg at 20 weeks do not start to be photoresponsive until about 10 weeks and are not uniformly responsive until 19 or 20 weeks. A transfer to a stimulatory photoperiod before a bird has dissipated photorefractoriness causes a delay of about 3 weeks in its sexual development, and these results in a bimodal distribution of ages at maturity when a flock is photostimulated between 10 and 20 weeks. A flock of broiler breeders with typical feed restriction starts to mature spontaneously under the
influence of the initial photoperiod from about 25 weeks.

These empirical models for commercial laying pullets and for broiler breeders enable the prediction of AFE for individuals making up a laying flock. Using means and standard errors for each of the parameters in the models it is possible to allocate randomly an ASM to each bird in the simulated flock, which contributes to its potential rate of laying, as will be described in the next section.

**Modelling potential egg output**

Describing the potential rate of lay of a laying hen is complex because of the number of interacting factors and the fact that the potential varies over time within each individual. 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. Johnston and Gous (2003) extended this model by defining 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.

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. 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 using mean values and standard errors for each of the parameters in the model (Johnston and Gous, 2003). Such a population of birds would generate a range of ovulation times, the distribution of which is unimodal and positively skewed 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.

Different approaches have been used to model the decline in rate of lay over time. Most of these have been empirical in nature (Gavora et al., 1971; McNally, 1971; McMillan et al., 1986; Foster et al., 1987; Yang et al., 1989; Koops and Grossman, 1992 and Fialho and Ledur, 1997), all of which are severely limiting when making use of a mechanistic approach for describing the decay in the rate of laying of an individual hen over time. Emmans and Fisher (1986) suggested that the hen’s internal cycle length increased with time from first egg, resulting in a linear decline in the rates of ovulation and oviposition with age. They suggested that, at the start of the laying period, some hens had the capacity to lay at a rate greater than one egg in 24 h, but that laying performance of these birds was constrained by the external cycle length. Eventually, the internal cycle length would become longer than the external cycle length, when ovulation rate would begin to decline. However, there is evidence to show that sequence length tends to rise initially (Lewis and Perry, 1991; Johnston, 2004), with most hens exhibiting a single characteristically long (prime) sequence about the time of peak egg production, which then declines at different rates between individuals (Robinson et al., 1990), so the model of Emmans and Fisher (1986) is unsatisfactory in describing the change in ovulation rate over time.

In order to reproduce these changes in sequence length over time, the internal cycle length initially needs to be longer than 24 hours, before decreasing with advancing time from first egg to close to, or below, the daylength, and subsequently increasing. External cycle lengths longer or shorter than 24 h can be accommodated when such an approach is used. When the ovulation curves of individuals in the flock are integrated, the characteristic laying curve is faithfully reproduced. 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.

Although it is not of interest commercially, a simulation model should be able to predict the consequences of feeding very low concentrations of a limiting nutrient. In two response trials conducted by Bowmaker and Gous (1991), broiler breeders continued to lay at a rate of an egg every 7 to 10 d when given a fixed amount of feed severely deficient in either lysine or methionine. At some point, as the nutrient supply is reduced, ovulation will cease and
the bird will go out of lay, but questions remain about the ability of hens to sustain production, albeit very low, when nutrient supply is more than marginally limiting.

The reproductive rates of flocks of commercial laying hens and broiler breeders may be simulated by making use of the Monte Carlo method which requires the choice of appropriate values for the means and standard errors of the parameters in the various equations used to simulate ovulation rate, the rate of decay in internal cycle length and the incidence of pause days, internal layings and soft-shelled eggs (Johnston and Gous, 2006; 2007a). The potential performance of each hen in the population is simulated in this way, thereby producing information necessary for predicting the nutrients required by each hen on each day of lay. For more precision in determining these nutrient requirements, the weight of the egg and the proportions of yolk and albumen in the egg need to be known.

Modelling egg weight and composition

When modelling the nutrient requirements of a hen over a production cycle, based on the daily outputs of each nutrient, egg weight needs to be predicted as the sum of the three components, since each has a unique chemical composition, and these proportional changes will therefore influence the nutrient requirements of the hen. Egg weight increases as hens age, but the eggs contain proportionally more yolk and less albumen and shell. However, at a given age, larger eggs contain proportionally more albumen (Johnston and Gous, 2007b). Yolk weight is dependent mainly on the genotype, but within a strain because it is related to hen age it may be calculated using an appropriate (logistic) function. Allometric functions may then be used to predict albumen weight from yolk weight and shell weight from the weight of the egg contents. The methods described by Johnston and Gous (2007b) for this purpose appear also to work satisfactorily for broiler breeders (Gous and Nonis, 2010) 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. These relationships differ not only between laying hens and broiler breeders, but also between strains.

The position of an egg in the sequence also influences the proportions of the weight of the egg and its components. The weight of consecutive eggs within a sequence gradually decreases (Belyavinet et al., 1987, Miyoshi et al., 1997) and similar patterns have been observed with yolk weights (Bastian and Zarrow, 1955; Zakaria et al., 1984; Zakaria, 1999) with the heaviest yolks occurring more frequently in the first two places of a sequence (Gilbert, 1972). Egg shell weight tends to be heaviest in the terminal egg of the clutch (Miyoshi et al., 1997), presumably because the lag in oviposition time is longest for this last egg, which means a longer period of time is devoted to shell deposition.

When essential nutrient intake is constrained this will have consequences on both rate of lay and egg weight: Morris and Gous (1988) showed that these are equally reduced when the feed is marginally deficient in an amino acid, but that the deficiency becomes more severe, rate of lay is reduced to a far greater extent than is egg weight. So there is very little scope for the laying hen nutritionist to manipulate egg size without also affecting rate of lay. Why this appears attractive is that the coefficient of variation for rate of lay is very high (around 25 %) whereas that for egg weight is only between 6 and 8 %. So it is far more difficult to show statistically significant differences in rate of lay between treatments than in egg weight, and consequently the wrong message has been broadcast, that rate of lay is not affected by a decrease in amino acid supply, but that egg weight is. It is very important to realise that egg weight cannot be adjusted nutritionally without also adjusting rate of lay.

The revenue derived from the sale of commercial eggs is a function of the size of the egg, given that in most markets eggs are graded according to weight, and that the price for each grade is usually different. The weights of eggs produced on any one day by a flock of hens will be normally distributed around the mean, so the proportion of the total that fall into each grading category can be determined mathematically, and the revenue derived from the sale of a given number of those eggs may be calculated accordingly. As egg output increases, as a result of an increase in the supply of a limiting nutrient, both the number of eggs produced and the mean egg weight will be equally affected if egg output is close to the potential of each hen, and the additional revenue derived as a result of the higher nutrient supply can be calculated. But because the effect of a more severe deficiency influences rate of lay more than egg weight, this relative change in the outputs needs to be accounted for when determining the revenue derived from the sale of eggs.
Predicting body weight and composition

A large proportion of the daily intake of energy and amino acids by a laying hen or a broiler breeder hen is used for maintenance, so the prediction of the bird’s maintenance requirement, when determining its optimum daily intake of energy and amino acids, is of considerable importance. In most factorial models these maintenance requirements are based on body weight, but because body lipid does not need to be maintained, a more accurate basis for calculating these requirements would be the body protein content of the bird. Emmans and Fisher (1986) and Fisher (1998) have raised this issue in the past, and the concept has been successfully incorporated into some broiler (EFG Software, 1995) and pig (Ferguson et al., 1997) growth models. But little useful information is available on the carcass protein content of layers or broiler breeders during lay or the extent to which this varies over time, to enable such calculations to be made of the maintenance requirements of these birds.

Changes in body composition of the broiler breeder hen have been measured during the rearing period (Bennett and Leeson, 1990), at the end of the rearing period (Blair et al., 1976; Pearson and Herron, 1980, 1981, 1982; Spratt and Leeson, 1987; Renema et al., 1999), during the period when the ovary and oviduct are developing (Bowmaker and Gous, 1989), and at the end of the laying period (Blair et al., 1976; Pearson and Herron, 1980, 1981, 1982; Spratt and Leeson, 1987; Attia et al., 1995; Wilson et al., 1995). However, the pattern of changes in body composition over time in the mature hen has not been rigorously investigated.

Pearson and Herron (1980) found that feather-free body protein content of a broiler breeder hen continued to increase between 22 and 34 weeks of age. However, a large part of this increase will be in the growth of the ovary and oviduct (Bowmaker and Gous, 1989). Differences in age at sexual maturity between birds in the flock will also contribute to the variation in the apparent increase in body weight during this period, with early maturing birds no longer growing, and perhaps even losing weight, whilst those not yet sexually mature would continue to grow until they have laid their first egg.

In laying hens it is well established that body protein content is maximal at sexual maturity and that little further protein growth occurs during lay (Fisher and Gous, 2008). It could be argued that broiler breeder hens are further from their somatically mature protein weight at sexual maturity than are laying hens, and hence that body protein growth may still be a priority when the opportunity arises. Such might be the case in poor egg producers, where body protein may be deposited if the number of pause days becomes excessive, but there is no evidence to substantiate this. Provision for slow body weight gain in broiler breeder hens is often recommended, assuming a mean gain of about 650 g from 50% egg production to the end of lay. However, it has been demonstrated in mammals that protein growth does not occur when the animal is in a lactating state, equivalent to the egg production state in hens. Sows, for example, show very little protein growth, if any, during gestation (Shields and Mahan, 1983; King, 1987), whilst losing considerable amounts of body protein during lactation (Whittemore and Yang, 1989).

As the weight of body protein remains relatively stable throughout the laying period, and as any growth in body protein may be regarded as taking place among non-laying hens only, it should not be necessary to assume that protein growth is obligatory when determining nutrient requirements of laying hens or broiler breeder hens. Also, because changes in body lipid content are the consequence of the way in which the hen has been fed, it is unnecessary to make provision for any obligatory gain in body protein or lipid during lay. Maintenance requirements may thus be considered to be constant over the laying period for those birds that continue to lay in closed cycles, and these should be based on the body protein content at the age of first egg.

Predicting food intake

To be of any real value, models that attempt to optimise the feeding of laying hens and broiler breeders must be capable of predicting voluntary food intake. Where this variable is an input to the 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, and not an input to, a model. A reproducing animal needs to be supplied with nutrients in order to meet the requirements for maintenance of the body and for reproduction. The theory of food intake and growth proposed by Emmans (1981, 1989) is based on the premise that birds attempt to grow at their genetic potential, which implies that they attempt to eat as much of a given feed as would be...
necessary to grow at that rate. The same principle can be applied to laying hens (Emmans and Fisher, 1986). To calculate the daily energy and nutrient requirements of a laying hen, her protein weight (for maintenance) and potential protein and lipid output (in eggs) needs to be known. By comparing these requirements with the content of nutrients in the feed, the ‘desired’ feed intake can be determined: this is the amount of feed that would be needed to meet the requirement for the first limiting nutrient in the feed (Emmans, 1981). The bird may not be capable of consuming this amount of feed, its intake possibly being constrained by either the bulkiness of the feed or the inability to lose sufficient of the heat generated to the environment. In this case feed intake will be less than desired and performance would be compromised.

This theory has been shown to predict food intake and hence growth and carcass composition with considerable accuracy (Ferguson and Gous, 1997, 2002; Ferguson et al., 1997). Burnham et al. (1992) and Gous et al. (1987), among many others, have shown that broilers and laying hens 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.

The critical features of a model to predict food intake in hens would be predictions of the body protein weight of the bird and its potential egg output on each day, from which nutrient requirements for maintenance and output may be calculated; a description of the nutrient content of the feed on offer; and a description of the effective temperature of the environment in which the bird is housed. Although the principle of predicting food intake is the same for growing and reproducing birds, the description of potential growth and of egg output differs markedly between the two.

The situation with broiler breeder hens differs from that of 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 may not always be achieved, thus the actual food intake would be 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. Whether the consequences of underfeeding are more likely to be evident with broiler breeders than with commercial laying hens, given that laying hens are fed ad libitum, would depend on the daily amount of food allocated to the breeders in relation to their potential egg output, and on the density of the feed allocated to the laying hens and the environmental temperature to which they are subjected.

Not all hens in a broiler breeder flock will consume exactly the same amount of feed, some birds being more aggressive than others. These differences in intake may be accommodated in a simulation model by allocating an aggressiveness factor to each hen based on a range of deviations from a mean of zero. The correlation between aggressiveness and potential egg output is not known, but could be varied in the model to determine the consequence of differences in this relationship.

In determining nutrient requirements, rules must be applied to account, for example, for the size of amino acid pools for potential albumen formation (which must be filled before ovulation can proceed), and for the rates at which lipid can be deposited in, or withdrawn from, body reserves as a means of accounting for differences in energy balance. If it is assumed that birds and animals have an inherent ratio between body lipid and protein, which they attempt to maintain at all times (Emmans, 1981, 1989), where possible, the bird will make use of excess lipid reserves as an energy source. This has an impact on the voluntary food intake of hens, with energy being stored on non-laying days, and being utilised on laying days, which would tend to buffer the changes in food intake required on these days. Presumably there is a minimum amount of body lipid that needs to be maintained, that will be unavailable as an energy source, although even this may be utilised when food supply is severely limiting.

**Optimisation**

Until recently, mechanistic models developed for poultry have dealt with the simulation of responses in a single bird. Such responses are usually linear to the point where the genetic potential is reached. Poultry nutritionists are interested in responses to nutrients in economically important outputs such as body weight (or protein) gain, breast meat yield, egg output, 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 (Fisher et al., 1973). 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. In the models of commercial laying hens and broiler breeders described here, the theory is applied to an individual and then a population is simulated using appropriate means and standard errors for the variables concerned. The responses thus obtained are acceptable representations of reality, and are thus ideal for determining the optimum method of feeding these simulated flocks.

Optimising the feed and feeding programme for a flock of laying hens can be achieved with three components, namely, a feed formulation program, an egg production model and an optimisation routine. The flow of information for such a procedure bears similarities to the continuous quality improvement model of Deming (1986), which consists of four repetitive steps (Plan, Do, Check, Act), this continuous feedback loop being designed to assist managers to identify and then reduce or eliminate sources of variation. In the case of the nutritionist, the optimiser defines nutritional constraints for practical layer or breeder feeds, which are passed to the feed formulation program where the least-cost feed that meets these constraints is determined. The characteristics of this formulated feed are then passed, as input, to the laying hen model. The performance expected from this feed when given to a defined flock of hens in a given environment is predicted by the model, and this predicted performance is then passed to the optimiser to complete the cycle. The next cycle starts with the optimiser modifying the feed specifications, moving, according to some in-built rules, to an optimum point. A single feed could be fed throughout the laying period, or different feeds might be more beneficial as the flock ages. In the case of broiler breeders, both the composition of the food and the amount to be supplied may be altered during the laying period. The objective function to be maximised or minimised can be defined in terms of any output from the simulation model, but realistically would be an economic index of some sort. Examples are maximising the margin, based on the value of egg output and the cost of feeding; or, in the case of broiler breeders, because of the high value of the hatched chick, maximising the number of eggs per hen.

Conclusions

The major limitation in determining the optimum economic amino acid and energy supply for a flock of laying hens and broiler breeders has been the inability to predict how much of a given food the flock would consume. Thus, even though it is possible to determine the optimum intakes of these nutrients as their marginal costs and the marginal revenue for eggs change, it is not possible to convert these into concentrations in the feed. The models described here now offer the possibility of being able to predict food intake, and as a result the optimisation of feeds for laying hens and broiler breeders is now possible. Predicting food intake is only possible once the potential laying performance of each hen can be predicted, which is in itself dependent on a large number of interacting systems, all of which can now be simulated, although not perfectly.

References
