OPTIMISATION OF THE PROTEIN AND AMINO ACID SUPPLIES TO LAYING HENS

J.V. NOLAN and G.N. HINCH

Summary

This review examines the ability of poultry to self-select diets that meet their nutritional requirements. The issue of whether energy is the dominant factor determining choice is raised and an alternative possibility presented.

The role of learning or training in determining the accuracy of selection to meet nutrient requirements is examined, highlighting the sensitivity of the young chick to "food events" in the first days of life. The potential impact of learning is then reinforced in the mature bird and it is suggested that lack of training about foods may be an explanation for the variability in the success of choice systems to optimise nutrient intakes.

The ability of hens to select appropriately for amino acid and protein from a combination of feeds is examined, highlighting recent studies which show the ability of poultry to rapidly differentiate between feeds differing only in the level of methionine. The potential physiological mechanisms that may allow this to occur are discussed.

Finally the implications of these findings are discussed in the context of optimisation of amino acid intake.

I. MODERN FEEDING SYSTEMS

Birds require fairly precise ratios of energy and all essential nutrients in their diet (i.e. a ‘balanced diet’) to enable them to express their genetic potential for production. However, these requirements vary with genotype and are altered by factors such as ambient temperature, age of bird, stage of production and presence of disease, and are therefore difficult to determine precisely.

Currently, diets are usually made by mixing a number of feeds together to meet the putative requirements of birds for maintenance and production expressed in terms of daily requirements for metabolisable energy (ME) and individual amino acids (AA), minerals and vitamins. In this context, provision of protein or individual amino acids is probably best considered relative to ME intake or as absolute daily requirements for individual ingredients. Specification of dietary concentrations as percentages of the diet, though common, is more a matter of convenience for personnel involved in mixing the dietary ingredients. Values need to be adjusted in relation to the digestibility or metabolisability of the components and throughout the productive life of the bird.

Expression of the requirements for an amino acid (such as methionine) relative to the requirements for ME is based on a presumption that birds with free access to feed will adjust their intake primarily to meet their energy needs. Thus, nutrients should be provided in ‘matching’ amounts to meet the animals’ current needs as closely as possible while preventing deficiencies or excesses. The view that animals have an over-riding tendency to ‘eat for energy’ has, however, been challenged. Webster (1993), for example, has pointed out that an obese strain of rats offered diets with widely different ratios of protein:energy chose to adjust their intake in order to maintain a nearly constant pattern of protein deposition during growth while their patterns of fat deposition were more variable. It could be argued that the rats’ primary objective was to meet their protein requirement while tolerating over-supplies of energy. Indeed, there are reasonable teleological grounds for this suggestion. Animals undoubtedly have a fundamental requirement for energy to meet their needs for cell
survival. However, a ‘chicken and egg’ situation exists when we try to determine the importance of energy relative to other essential dietary ingredients. None of the necessary biochemical reactions by which energy is processed can proceed without enzymes to catalyze them – and enzymes are proteins that require amino acids for their synthesis and will only function if vitamins and minerals are present as co-factors. From this standpoint, it is not easy to see why birds should give priority to gaining just energy.

On the basis of earlier studies, Emmans (1991) has suggested that the adage ‘animals eat for energy’ should be re-cast to imply that animals eat for the most limiting dietary component to which could be added ‘provided this does not involve the simultaneous ingestion of toxic amounts of another dietary component’. Diets formulated against the above background can be presented to birds as a mash or as a pellet or crumble – the latter two having as one of their perceived advantages that each bite is a balanced diet containing all nutrients. Such a perception could be taken to imply that all birds in a flock have identical requirements, that the nutritionist knows best what the birds’ current requirements are, and that it is appropriate for all birds to be constrained to ingest exactly the same mixture of ingredients.

II. SELF-SELECTION FEEDING SYSTEMS

Diets for poultry have not always been formulated by nutritionists! To survive in its natural environment any animal must either possess innately, or acquire, the ability to select a nutritionally adequate diet from all of the nutritional and non-nutritional or toxic materials present in their environment. Red Jungle fowl in their natural environment were clearly able to do this by selecting feeds that fell essentially into one of two categories, viz. high-energy, low-protein feeds such as grass seeds, and low-energy, high protein ingredients such as snails, worms and vegetable materials (Cumming 1994). Until the 1960s, before cages were in common use, egg producers often kept their layers on the floor and offered them whole wheat, meat meal and shell grit in separate feeders. They were taking advantage of the often-demonstrated ability of modern birds to be able to select an appropriate diet from a range of suitable ingredients. This type of feeding system has been referred to more recently as ‘free-choice’ or ‘self-selection’ feeding and interest in this type of feeding system may increase with the current concerns for the welfare of caged layers and the increasing use of barn or ‘free range’ production systems.

Chah (1972) showed that birds offered calcium, protein and energy sources separately ingested calcium almost exclusively in the afternoon and evening and ingested less calcium than hens fed complete pellets (conventional diet). Energy and protein intakes by the choice-fed birds varied more during the day than for the conventionally fed hens, peaking in the middle of the day and showing a smaller peak in the evening before ‘lights-out’. They ingested 8% less ME, 9% less protein and 26% less calcium than their conventionally fed counterparts. Birds given complete diets may, therefore, be in the situation of having to eat more during certain times of the day to meet their changing diurnal needs for calcium or protein and, in doing so, having to ingest an excess of energy or a nutrient such as calcium or methionine at these times. Arguments such as this have led to suggestions that birds might produce better or be more efficient if allowed to self-select from an appropriate array of feeds.

Theoretical advantages of free-choice feeding were outlined by Emmans (1975). He argued that birds have different requirements for maintenance and production. The requirements of individuals will differ from the average for the flock so that no single diet can exactly supply the needs of each individual. He proposed a system of feeding in which each bird would be offered free access to two diets, one intended to meet its maintenance
requirements, and the other to meet its needs for production. The bird would then be able to choose from both diets to produce a mix that would more closely meet its individual needs (Emmans, 1975). This proposal effectively assumed that each bird would be able to choose proportions appropriate to its metabolic requirements.

III. THE MECHANISMS ENABLING SELF-SELECTION

Hogan (1973) showed that newly hatched chicks initially peck equally at food particles or sand. Ingestion of food leads, within about an hour, to increased pecking behaviour whereas ingestion of sand results in decreased pecking. Hogan concluded that ingestion of food, but not sand, produced positive post-ingestive effects that reinforced feeding behaviour. These findings were also found by Hale and Green (1988) with chicks at either 0.5 or 2.5 days of age. If, however, chicks were given some additional feeding experience of foods or sand they learnt to discriminate between the materials and came to prefer the foods.

It is now generally accepted that birds, like other animals, learn to recognise foods by their sensory characteristics and develop conditioned associations between the foods and their post-ingestive nutritional and metabolic effects. They will later exhibit stronger preferences for those foods that lead to more positive effects whereas those producing detrimental effects will subsequently be avoided (Rozin, 1968). Studies in which birds have been given dietary choice leave little doubt that they have the capacity to adjust their intakes of protein, minerals and vitamins as well as energy in order to achieve acceptable levels of production (see, for example, Graham, 1932; Li and Anderson, 1982). Moreover, domestic birds given diets deficient in a particular nutrient, for example calcium (Wood-Gush and Kare, 1966) or sodium (Hughes and Whitehead, 1979) or thiamine (Hughes and Wood-Gush, 1971), exhibit an increase in their searching and pecking behaviour which increases the likelihood that they will increase their knowledge of possible sources of nutrients.

The ability of young chicks to balance their diet from a smorgasbord of food ingredients was demonstrated by Funk (1932) and Dove (1935), but learning and recognition of different foods appears critical to their ability to select an appropriate diet. Newly hatched domestic chicks are very sensitive to particular shapes and colours (e.g. Dawkins, 1968). They peck preferentially at particles with round and regular shapes and brown-red colour. Natural feedstuffs, such as grains, vary in their shape, size and colour and when Adret-hausberger and Cumming (1985) exposed day-old commercial layer and broiler chickens to different seeds they found that both breeds exhibited an initial preference for sorghum. In contrast feral chickens selected wheat and maize; grey sunflower, rye, oat, rape, lucerne and barley seeds seemed to be less preferred by all breeds. When the seeds were stuck down and it was impossible to swallow them, the chickens were unable to establish an association between shape/colour and ingestive consequence and they then tended to peck seeds almost at random when tested 24 hours later. This suggests that the very first experience of pecking should be at food that is of a form, size and colour that may relate to later food exposures.

Karunajeewa (1978) evaluated the self-selection approach to feeding birds by giving them either conventional balanced mash diets based on barley or wheat, or a choice between the same ingredients given as a whole grains and a concentrate mixture. The choice-fed birds produced as well as those given the complete diets but they ingested 11% less food. Similarly, Leesoon and Summers (1978) found that free choice feeding decreased feed intake and increased production efficiency. They concluded that when birds were provided with a free-choice diet, each bird selected a diet closer to its own dietary needs.
IV. SELF-SELECTION (APPROPRIATE OR INAPPROPRIATE?)

There has been controversy about the ability of ‘choice-fed’ birds to ‘fine tune’ their dietary choices and demonstrations that birds may choose ingredients inappropriately are one reason why self-selection systems have not been adopted by commercial producers. Dove (1935) found a wide range of individual differences in the selection abilities of chickens. He attributed this variation to possible genotypic differences. Some chicks which selected a ‘balanced’ diet and grew at a rapid rate chose a ‘formulation’ that was remarkably similar to that of conventional starter diets. Other chicks were apparently unable to select a diet that would optimise their growth. These chicks apparently either did not possess innate knowledge about feeds or were unable to learn about the characteristics of the feeds available to them.

The ability of birds to differentiate between feeds depends on a learning process which involves the development of conditioned associations between the stimuli occurring in response to eating certain ingredients (post-ingestive consequences which may be positive or negative) and the stimuli invoked by their position or sensory properties. The latter are the means by which feeds that the animal has experienced are subsequently recognised. It can be argued that birds learn about feeds and exhibit feeding behaviour that will enable them to optimise their genetic potential for growth and production. This idea provides a general theoretical framework for considering feed intake regulation and nutrient selection in the manner just described, although Emmans and Kyriazakis (1995) have recommended caution in the overuse of the idea of optimisation, especially in the absence of evidence for it.

The relevant variables to be considered in the theory of diet selection are the animal (its genotype and current physiological state), the animal’s environment and the characteristics of the feeds available to it (Emmans 1991). The feed characteristics can include aspects such as composition, palatability and variety, the last two being more applicable to choice-fed birds. A number of studies have examined the contrast between a situation where one or a variety of foods are offered; in general these were foods that are apparently avoided in a two-choice situation and could be considered ‘unpalatable’, apparently they become ‘palatable’ when there is no choice given. Moreover, palatability may not be simply an attribute of a feed – it may reflect a bird’s experience/training/learning and its current physiological state and the palatability index of any feed may, therefore, change over time.

There are many other possible complications associated with choice feeding. In a comprehensive study, Farrell et al. (1989) compared the hen-day production of two strains of layers when fed a commercial layer crumble or given a choice of low (13%-16%) or high-protein wheat or sorghum (11%) with one of three protein concentrates based on either full-fat soybeans, sweet lupin meal or field peas. The protein concentrates were offered as mash or pellets in troughs that were separate from the grains and there were 6 birds per cage. Intake of the mash concentrate was consistently higher than of the pelleted concentrate and the choice-fed birds generally ingested excessive amounts of protein. Some individual treatments resulted in poor egg production and low gross economic margins relative to the commercial diet treatment. These workers concluded that self-selection programs required considerable ‘fine tuning’ to allow them to be useful in practical feeding systems. They identified trough design and birds per cage as issues requiring further attention. A further issue may have been the age and experience of birds when allocated to their experimental treatments as this was done in this experiment when the birds were 18 weeks of age after a conventional rearing on pullet starter and pullet grower mash. They had apparently not previously experienced the feed ingredients that were to be offered in the laying period.
In their review Cumming and Mastika (1987) concluded: "If choice feeding does not work efficiently the reason almost certainly lies in the method in which the choice feeding has been applied" and it would seem that training is an issue of practical significance if self-selected feeding is to be successful. A complete discussion of factors that may determine the success or otherwise of a self-selection feeding system is beyond the scope of this review but a number of factors are relevant.

1. A bird must first overcome neophobia associated with the presence of a novel feed at its feeding site.
2. It must then identify the material offered as potential food rather than non-food and peck at the material. Social mimicry plays a role at this stage if other birds are present.
3. The bird may need to practise pecking at the food in order to learn how to successfully prehend and ingest it, especially if the particle size and shape are new to the bird. Picard et al. (1999) have reported that there may be a burst of pecking activity when a bird is offered a novel food but in spite of the pecking activity, feed intake is low because the pecking does not result in successful prehension of feed particles.
4. After successful ingestion of a small portion of the food, the bird must form a conditioned association between the sensory properties (colour, beak feel) or position of this food and its post-ingestive consequences. Such associations may take time to develop, and reinforcement results in the formations of stronger conditioned associations.

Only by proceeding through steps 2, 3 and 4 (training) will the bird be able to recognise the food in the future and predict the potential consequences of ingesting it again.

V. PROTEIN AND AMINO ACID INTAKE

Rozin (1969) undertook a series of studies to determine whether there were separate processes for regulating the intake of energy and protein. Karunajeewa (1978) offered crossbred hens on litter a choice of protein concentrate (31% crude protein) and particulate calcium with either whole wheat or barley. He found their food intake was lower by 7 and 15%, respectively, than that of hens offered complete mash diets consisting of the same ingredients. Rate of lay did not differ between choice and mash diet feeding but choice-fed birds produced heavier eggs during the latter half of the laying cycle. He concluded that there were major benefits for choice-feeding from reductions in feed intake and the reduced energy costs associated with the use of whole grain. He also concluded that poor responses to choice feeding can often be attributed to inadequate intake of ME during the adjustment or learning period and non-separation of the calcium supplement.

In a study reported by Fuller (1962), White Leghorn pullets were allowed to self-select from a 33% protein concentrate, whole maize, whole oats and a mineral mixture from 8 to 21 weeks of age. These birds ate 13% less feed and performed more efficiently during the laying phase than those given a choice of a conventional mash (20.8% protein) and whole maize and whole oats. The energy intake was similar over a wide range of protein intakes which suggested that these growing pullets were eating to satisfy their energy needs with little regard for the protein level achieved. However, the range in protein options was such that it could be argued that there was no need for the birds to differentiate between protein sources.

Hughes (1979) suggested three ways that birds might achieve specific intake of individual dietary components: genetically programmed innate behaviour; learnt behaviour
based on an innate learning protocol; learnt behaviour based on socially acquired or personal experience; unable to learn. The current consensus is that birds can make appropriate choices where such choice will avoid deficiency or toxicity by a process of conditioned association between foods and their post-ingestive consequences (Rozin, 1991).

In recent studies we have confirmed that both broiler and layer cockerels are able to distinguish feeds identical in all but methionine concentrations and a colour (food dye) cue. The feeds offered consisted of mash feed formulated to meet bird requirements in all but methionine, one choice containing added methionine to provide an estimated marginal level of 0.29% and the other having no added methionine and with an estimated level of 0.19%. In one experiment four-week old broiler cockerels, not previously exposed to the foods, consistently selected the higher methionine food after an average 40 hours of choice feeding (Figure 1). In a second experiment 6-week old layer cockerels, exposed to the feeds independently for two days prior to choice feeding, choose within hours the feed containing the higher level of methionine.

![Graph showing intake of medium over low met diet](image)

**Figure 1** The percentage of the marginal methionine feed chosen by broiler cockerels offered a choice of marginal and deficient methionine feeds (Channon, 1999).

Such findings suggest that training has a major role to play in facilitating the ability to distinguish between feeds and possibly that the learning process is more rapid if the feeds are initially offered separately. However this requires confirmation.

These findings do raise questions about how the post-ingestive consequences of feeds differing in such small amounts of an amino acid are detected and collated? Diets that are amino acid imbalanced are known to induce hypophagic responses in most animals but the physiological mechanisms that enable them to recognise an under- or over-supply of individual amino acids are poorly understood (Leung and Rogers, 1986). Recent studies undertaken in rats by Gietzen et al. (1998) have attempted to elucidate the neurochemical
systems that may be involved in the initial recognition of a post-ingestive amino acid imbalance and in the development of conditioned responses to the diet producing the imbalance. They have demonstrated that, before intake of an imbalanced diet falls, there are changes in the activity of neurotransmitter substances (monoamines) in parts of the brain known to have monosynaptic connections to the anterior piriform cortex (APC) which is a chemically sensitive area of the brain. Gietzen et al. (1998) believe the APC becomes hyperexcitable in rats fed imbalanced diets when there is a lowering of the concentration of the limiting amino acid in this area. This may allow linkages to the hypothalamus (the traditional feeding behaviour centre) via alteration in noradrenalin or tyrosine concentrations in areas of the hind brain which in turn reduce feeding activity.

After intake had declined significantly, indicators of serotonin (associated with learning) were changed in the limbic system and in areas associated with the taste pathways. They believe that these latter changes which involve increases in serotonin concentration in the parabrachial nucleus and then in threonine concentration in the central nucleus of the amygdala are associated with the development of a conditioned aversion to imbalanced diets. They proposed: 'a circuit for the neural responses in the initial recognition of acute amino acid deprivation that begins with the activation of the APC and includes areas in the hind brain and hypothalamus. After a significant hypophagic response, serotonergic indicators were altered in areas of the taste pathway and the limbic system, suggesting that different circuits mediate the initial recognition and secondary responses to amino acid-imbalanced diets.' Such observations suggest that monogastric animals may be relatively more sensitive to deficiencies than to excesses of amino acids; however, the reality of this needs to be confirmed for poultry before such knowledge can be used to advantage.

IV. PRACTICAL LIMITS TO SUCCESSFUL SELF-SELECTION

Having established that birds can identify differences between feeds differing only in amino acid concentrations, consideration needs to be given to determining whether this ability to distinguish between feeds can be used to optimise intakes of protein or amino acids for individual birds. It appears that there are mechanisms whereby birds can identify differing amino acid levels and establish associations between the physiological outcomes and particular feed cues. If the associations are largely with deficiencies and imbalances then it could be argued that self-selection will only be effective where diets are marginal in an amino acid or protein.

The integration of a series of different physiological responses and cue combinations that would normally be associated with choice feeding is difficult to envisage as we still have no clear picture of the priority established if more than one imbalance occurs. It is possible that the feeding behavioural response to an imbalance is a generalised seeking behaviour, in which case optimisation for any one nutrient is unlikely. However, if training has previously allowed birds to learn about the physiological consequences of eating a particular feed then the accuracy and rapidity of correct/optimal choice may be improved.

Further studies are required to determine the relative importance of training on the ability of birds to make appropriate or optimal selections from a combination of feeds. If it can be shown that training increases the reliability of correct choice then the practical problems of offering choice feed delivery systems (Tauson and Elwinger, 1986) can be reduced.
REFERENCES


