

Energy Metabolism and Protein Utilization in Chicken- A Review

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ABSTRACT Evaluation of energy in the diet is very important in animal nutrition because food intake is strongly influenced by the energy content of the diet. This means that the intake of other nutrients, such as amino acids, is affected by their ratio to energy content. Poultry can control their energy intake over a range of energy: protein ratios. Energy: protein ratio also affects the growth and body composition. Therefore we need to know what extent the relationship between energy and dietary protein influences the bird's performance. To predict the energy value of the diet or its chemical constituents, researchers have been working on modelling using the equations of the major biochemical pathways in terms of ATP generation and utilization. The activity of feeding and the metabolism caused by digestion and assimilation of food increase the animal's heat production and it can be measured by calorimetry technique. Theoretically, surplus amino acids which are not needed for protein synthesis stimulate an additional increase in metabolic rate and lead to increased energetic costs of catabolism and excretion. However, it has sometimes been shown that there was no measurable diet-induced thermoregulatory effect when an imbalanced amino acid mixture was fed. All these aspects are discussed in this review.

(Key words : energy metabolism, heat production, amino acid, modelling, poultry)

INTRODUCTION

Energy, along with protein, is one of major cost factors of the poultry diet and as a consequence has been the subject of considerable research. Energy content of the diet should be seriously considered and is used as a basis to determine most nutrient concentrations because most animals tend to eat to satisfy their energy requirements assuming that the diet is adequate in essential nutrients. Poultry can control their energy intake over a range of energy: protein ratios. Energy: protein ratio also affects the growth and body composition. It is, therefore, very important to know to what extent the relationship between energy and dietary protein influences the bird's performance.

To study the utilization of metabolizable energy (ME), it is necessary to measure either the heat production of the animal or energy retained in the tissues, that used for productive work, or in a product. In cases where we know one of these quantities, then the other can be determined by subtracting the known one from ME. Net energy (NE) is equal to ME minus the heat increment and heat of fermentation. Heat increment can be defined as the heat production associated with nutrient digestion and metabolism over and above that produced prior to food ingestion. There has been a debate on

the choice of ME or NE for energy evaluation of poultry feedstuffs. Some scientists compared these two energy system (Halnan, 1951; Hill and Anderson, 1958; De Groote, 1974) and this subject was reviewed more recently by Pirgozliov and Rose (1999). Since NE accounts for more of the losses in metabolism of food or by the animal than other measures described, it should be the method of choice for food evaluation or standard of animal requirements. In poultry nutrition, however, the ME system is still more widely used because NE varies with environmental temperatures outside the comfort zone and because of the limited amount of data on feedstuffs and birds.

Dietary protein quality influences growth but also affects the environment because of different rates of nitrogen excretion. A reduction in nitrogen excretion and increased efficiency of nitrogen deposition can be achieved by matching the amino acid composition of the diet with amino acid requirements. This would also be expected to have implications for energy metabolism. The conventional expectation has been that a balanced blend of amino acids must lead to decreased energetic costs of catabolism and excretion (Baldini, 1961; Guillaume and Summers, 1970). However, MacLeod (1997) reported that heat production on an imbalanced, lysine-limited, amino acid mixture was no higher than on a balanced amino acid source

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with the same lysine concentration and there was no indication of stimulation of heat production by excess amino acids. Boorman and Ellis (1996) found no adverse effect of protein quality on lysine utilization and detected some indication of increasing net utilization with decreased protein quality. Although there have been many hypotheses, no complete explanation has been provided so far. In this article, background knowledge and studies on energy metabolism and the methods for its measurement and prediction are briefly presented. This review also discussed the relationship between energy utilization and protein quality in chicken, especially the effects of amino acid balance on thermogenesis.

UNDERSTANDING ENERGY METABOLISM

1. Measurement of Heat Production

Heat production can be measured in various ways. There have been many reviews about the techniques used for measurement of energy metabolism in farm animals and humans (e.g. McLean and Tobin, 1987; Blaxter 1989; McDonald et al., 1995). The principles are relatively simple and have changed little. However, there has been much progress in terms of technology for more precise and less labor intensive measurements.

The heat may be measured directly by physical methods or it may be inferred from quantitative measurement of some of the chemical by-products of metabolism. Direct calorimeters measure heat produced by the animal within them directly, using thermocouples or changes in the amount of heat produced in cooling the chamber. These types of calorimeters are quite expensive to build and to operate due to their complexity and are seldom used, especially for large animals.

Indirect calorimetry estimates heat production from quantitative measurements of oxygen consumption and carbon dioxide production during metabolism. Brouwer (1957, 1965) published an equation for calculating heat production from respiratory exchange.

$$\text{HP (MJ)} = 16.18 \text{ O}_2 \text{ (l)} + 5.16 \text{ CO}_2 \text{ (l)} - 5.93 \text{ UN (g)} - 2.42 \text{ CH}_4 \text{ (l)}$$

UN : urinary nitrogen

The open-circuit chamber method was one of the earliest types of calorimeters, having been devised by Pettenkoffer and Voit in 1875 (cited by McLean and Tobin, 1987), although at that time only the volume of air and its carbon dioxide content could be measured. There have been a large number of reports in the literature of open-circuit chambers. Jequier and Schutz (1983) have described an open-circuit chamber for human studies; open-circuit chambers have been combined with direct calorimetry for studies on man (Dauncey et al., 1978) and primates (Dale et al., 1967). Open-circuit chambers have also been widely used with poultry (Petersen, 1967; Misson, 1974), pigs, sheep and cattle (Verstegen et al., 1971; Vermorel et al., 1973; Young et al., 1975). A multi-chamber system for poultry has been built at the Roslin Institute, Scotland. This system has been described in detail by Lundy et al. (1978) and MacLeod et al. (1985).

An open-circuit calorimeter is an air-ventilated box containing the bird under investigation. The oxygen and carbon dioxide concentrations of fresh air entering and sample gas leaving the calorimeter and the flow-rate at which sample gas is withdrawn are measured at frequent, regular time intervals. Oxygen consumption is calculated from the difference between oxygen flow-rate into and out of the calorimeter. A continuous correction is made for changes in oxygen concentration in the calorimeter during the period of observation. Carbon dioxide production over the same period is calculated by analogous methods to those used for calculating oxygen consumption. Urinary nitrogen excretion can be determined by chemical analysis of cloacal excreta. Thus in calorimetric experiment under laboratory conditions the retention of energy in the body can be estimated, not directly, but as a difference between measurements of the intake of energy as food, and the sum of energy excretions and the heat produced (Blaxter, 1989).

2. Heat Production and Body Size

In the nutritional physiology of animals, it is important to compare the information obtained from calorimetric studies with more normal environmental conditions. Calorimetric data are obtained under very specific conditions, and it is not feasible to attempt to duplicate all of the situations which are encountered by animals in their normal environment or to

account for differences in age, size and species. In order to compare heat production between individual animals within or between species, the conditions under which the measurement are made must be standardized.

Early nutritional research showed that heat production was not directly correlated to body weight of animals and much effort was expended to develop means of predicting heat production and establish some overall law that applies to animals in general. In 1883, Rubner showed that the fasting metabolism of seven dogs, varying in body weight from 3.2 to 31.2 kg, was approximately constant when expressed per unit area of body surface (m^2). Voit (1901) published a table which showed that the fasting metabolisms of a number of different species were also proportional to their surface areas (cited by Blaxter, 1989). It has since been shown that the rate of cooling is proportional to surface area, which varies with the square of linear size or to the $2/3$ power of weight if specific gravity is constant. Surface area, therefore, varies with the square of linear size or the $2/3$ power of volume, so heat production can be related to body surface or volume. Despite the fact that surface area of a living animal is not constant due to various factors, it can be related reasonably well to surface area estimated by multiplying body weight by a fractional power. This is referred to as metabolic weight or metabolic size. There has been extensive controversy on this subject in the past. Kleiber (1932) and Brody and Proctor (1932) showed that when metabolism was related directly to body weight metabolism was proportional to a power of weight higher than $2/3$ (cited by Blaxter, 1989). Brody and Proctor found the power to be 0.734 and Kleiber estimated it to be 0.75. Kleiber (1961) stated that the slope as estimated from his original set of data was 0.739. In both sets of data errors were such that proportionality to the power 0.75 can be accepted as a valid estimate (Blaxter, 1989).

3. Basal and Fasting Metabolism

The minimal energy expended to maintain respiration, protein turnover and other vital metabolic process of a resting, thermally neutral and post-absorptive state is known as the basal metabolic rate (BMR). The post-absorptive state is used so that the heat increment or heat of fermentation do not add to the body heat production. Animals cannot be controlled to

keep their body at complete rest in post-absorptive state at a certain period of day. Therefore, the fasting metabolic rate is measured in domestic animals. Generally, smaller omnivorous animals reach the post-absorptive state earlier than ruminants. Mitchell (1962) stated that chickens reach this state in about 48 h and ruminants in 3~5 d.

The bird's calculated or measured BMR does not equal its daily basal requirement for dietary ME because BMR measurements are determined in fasted birds. Conversion of BMR into a basal ME requirement requires the addition of the amount of energy needed for the heat increment related to food consumption.

ENERGY UTILIZATION OF NUTRIENTS

1. Energy Source and Its Prediction

The dietary requirement for carbohydrates and fats is less exacting than those for proteins. Fats and carbohydrates are the main energy sources in the diet (Fig. 1). Protein, or rather the amino acids that constitute protein, can also be used as an energy source, but this only occurs in situations in which it is present in excess or imbalance, or where there is a shortage of fat and/or carbohydrates. The typical energy yields of these major nutrients, as determined by bomb calorimetry, are 4.49 kcal/g for carbohydrates, 5.61 kcal/g for protein and 9.17 kcal/g for fat (Blaxter, 1989). The actual amount of energy obtainable from these nutrients by birds is somewhat less, as this would require each of the nutrients to be absorbed completely by the gut. Both fat and carbohydrates can be fully oxidised in the body to CO_2 and water. But the nitrogen of protein is not released in its fully oxidised state since most is excreted as uric acid. This also reduces the energy available from protein to 4.3 kcal/g.

There are no specific storage protein molecules except skeletal muscle protein which is the largest potential reservoir of amino acids for egg protein during the laying period. When dietary protein is either scarce or absent, endogenous protein, particularly from skeletal muscle, is degraded to generate a source of amino acids. When the protein is provided in excess, it cannot be stored and becomes degraded and deaminated, providing carbon skeletons for biosynthesis of fats and carbo-

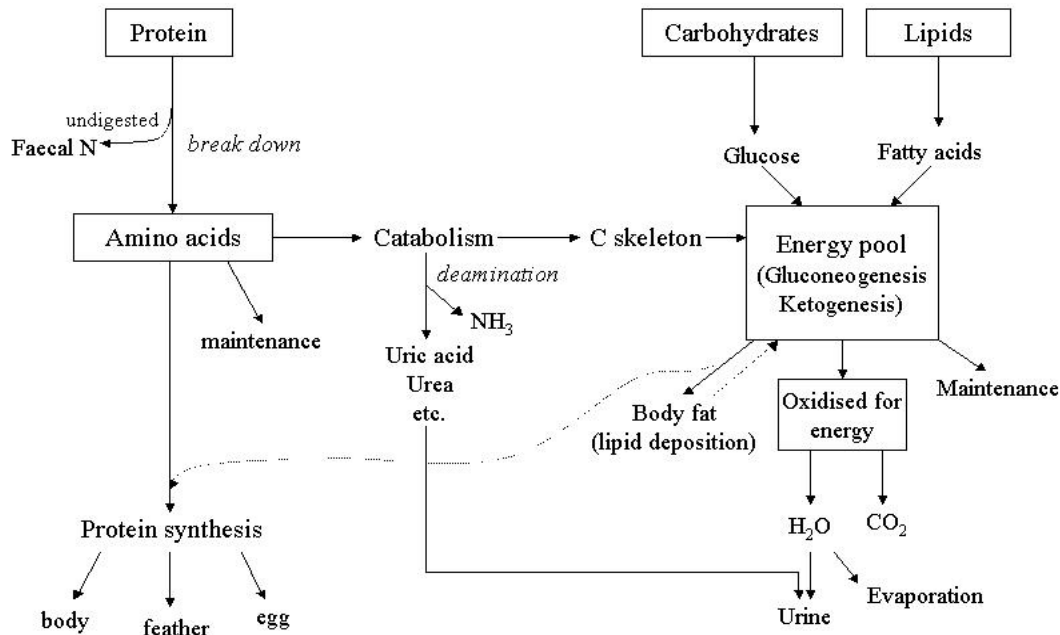


Fig. 1. Diagram illustrating the metabolism of energy-yielding nutrients in the body.

hydrates. In birds, the surplus nitrogen is excreted mainly as uric acid rather than urea or ammonia. The reason is considered to be an adaptation to the incubation requirements of the egg. During embryonic development, waste uric acid precipitates out of solution, preventing the osmotic imbalance that would occur if urea or ammonia were excreted. This osmotic advantage may also aid in water conservation in adult birds (Klasing, 1998).

Amino acids are absorbed by active transport processes involved with carrier proteins. Four carrier mechanisms were identified catering for the neutral amino acids, the basic amino acids, for dicarboxylic acid and for proline, hydroxyproline and glycine (Blaxter, 1989). These transport mechanisms, called symports, need energy. Similar active transport and diffusion process coupled to sodium ion movement apply to carbohydrate absorption. Glucose and galactose are absorbed by active transport and diffusion process while fructose absorption is passive. The heat production which accompanies active absorption arises from the ATP-dependent sodium transport component; it is the enthalpy change associated with oxidations which leads to ATP formation - the ultimate source of heat.

To predict the energy value of the diet or its chemical constituents, researchers (e.g. Schulz, 1975, 1978; Livesey, 1984,

1985; MacLeod, 1994, 2000) have been working on modeling using the equations of the major biochemical pathways in terms of ATP generation and utilization. Livesey (1984) calculated energy yield as ATP from carbohydrates, fats and proteins which have been absorbed and are available for cellular catabolism. His model treats all substances purely as energy sources and therefore corresponds with an ME form of evaluation.

In MacLeod's model (1994, see Fig. 2), the stoichiometric foundation for biochemically-based simulation of energy metabolism was derived largely from Schulz (1978). But different stoichiometric coefficients were used for amino acid breakdown due to the differences between mammalian and avian amino acid metabolism (MacLeod, 2000). Amino acid compositions of proteins in body, feather and egg were compiled from various sources.

Emmans (1984, 1994) reported a method for estimating the "effective energy" of diets or ingredients, in which ME is adjusted for the heat increment of feeding by applying linear coefficients to five measurable components of the interaction between the animal and its diet.

2. Energy Requirement and Its Response in Body Composition

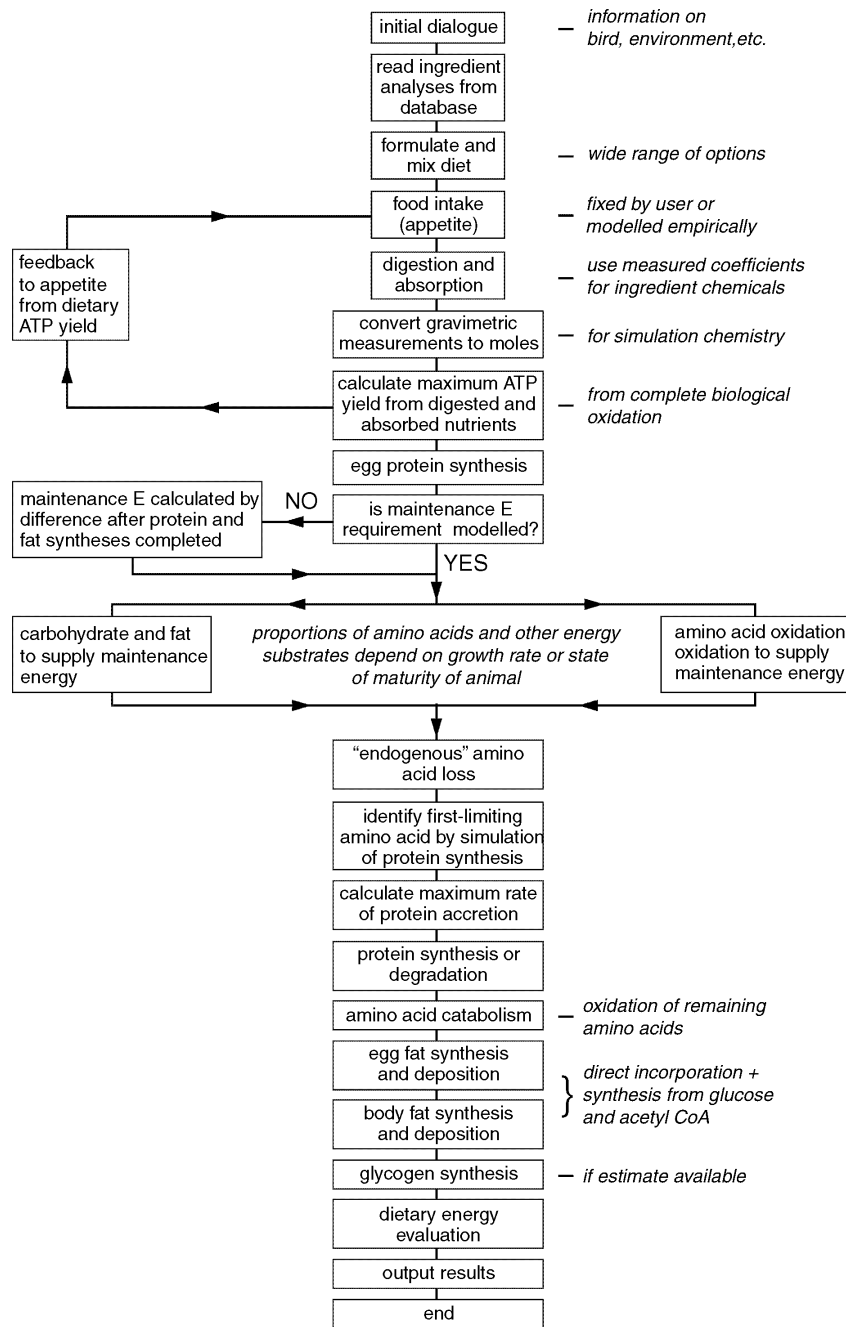


Fig. 2. Flow diagram of the energy metabolism simulation model of MacLeod (1994).

Energy content is widely acknowledged to exert a dominant role in the regulation of feed intake in growing poultry. Boomgaardt and Baker (1973) examined the effects of dietary ME concentration on the response of chicks to graded doses of methionine + cystine. Their results showed three distinct growth response curves for the three dietary ME concentrations; 2,600, 3,000 and 3,400 kcal/kg. However, the efficiency

of utilization of these amino acids is unaffected by energy content of the diet since a single response curve is obtained on plotting weight gain against methionine + cystine intake. D'Mello (1979) stated that dietary ME, within the range tested, exerts its effect principally through variations in feed intake and without affecting amino acid utilization.

In chicks, which are usually fed *ad libitum*, the energy:

protein ratio has been seen as important because the ME content of the diet determines feed intake (if other nutrients are non-limiting) and thus influences protein intake (Morris et al., 1999). D'Mello (1993) referred to reduced energy yield and amino acid utilization, but was not entirely convinced by the hypothesis. It should also be noted that MacLeod and Boyd (1994) reported that heat production was no greater from birds receiving lysine from a poor-quality protein source than from birds receiving the same dietary lysine concentration from a balanced protein mixture (cited by Boorman and Ellis, 1996).

Traditionally, broilers have been fed relatively high energy diets for better feed utilization and maximum growth (Leeson and Summers, 1991). Later, lower-energy diets have been tried in an attempt to resolve problems such as ascites, and it is now realized that overall growth rate is little affected (Leeson et al., 1995). Therefore, the broilers may adapt to low-energy feeds and simply eat more feed to maintain energy intake, much the same as does the Leghorn (Payne, 1967). Leeson et al. (1996) proved that the broiler has a good ability to control its feed intake based on desire to normalize energy intake and as energy intake is decreased, or there is increased protein intake, the bird deposits less carcass fat. Dozier et al. (2006) reported that increasing ME decreased feed intake and improved FCR in broiler chickens. In their later report (Dozier et al., 2007), these authors also stated that increasing dietary ME did not increase breast meat yield in broilers from 42 to 56 d of age.

It is known that many variables are affecting the energetic efficiency of ME use for tissue gain. The efficiency has been shown to vary with substrate source for lipogenesis at approximately 75, 84 and 61% for carbohydrates, fat and protein respectively (De Groote, 1969; Chudy and Schiemann, 1969; Hoffmann and Schiemann, 1971). However, high availability of fat ME for tissue gain depends on the fat being used for lipogenesis (Bossard and Combs, 1961). Protein utilization for tissue energy gain would be expected to be depending on the biological value of the protein source and should not be constant (De Groote, 1974). Wiernusz (2001) stated that, in order to achieve optimum carcass composition with maximum energetic efficiency in broilers, an energy requirement scheme must account for the variation in substrate-mediated heat pro-

duction.

3. Heat Increment and Protein

Ingestion of food increases both heat production and the energy retention in the body. A fed animal produces more heat than a fasted one. There have been a number of research studies that try to explain the increased HP after food intake. Several general theories explaining the heat increment have been produced. One of these older theories which is still valid is that of Rubner (1902, cited by Blaxter, 1989). He ascribed the specific dynamic action (SDA) to the waste heat produced by reactions necessary to support the physiological process of the body. All energy sources fed to an animal will increase heat production. But the increase caused by protein or amino acids has stimulated most research interest. The study of Rubner demonstrated that protein caused a larger increase in heat production than either carbohydrates or fat.

When fed as a high proportion of the diet, protein is a less efficient source of energy than carbohydrates or fat (Blaxter, 1989). In cases when protein is used as an energy source for maintenance or production, nitrogen must be excreted. Dietary protein also increases HP resulting from nitrogen excretion and HP associated with net synthesis of product. Additional effects of dietary amino acids on HP beyond this level and HP for the production would also be increased by protein because dietary protein stimulates protein turnover (Reeds et al., 1982; Reeds and Fuller, 1983). The energy cost of protein accretion has been estimated as 10.5 kcal ME/g (ARC, 1981). Of this amount, 5.65 kcal can be recovered by combustion of the protein. The cost of synthesis is, therefore, 4.85 kcal ME/g. A stoichiometric estimate of the cost of protein synthesis is 0.8 kcal ME/g (Millward et al., 1976). The difference of approximately 4.06 kcal ME/g protein is probably a consequence of protein-stimulated catabolism and turnover (Musharaf and Latshaw, 1999).

The results from many studies suggest that higher dietary protein will reduce energetic efficiency. The study of Rubner showed that the SDA of protein was expressed more markedly at high temperatures than low temperatures. The use of more synthetic amino acids and less intact protein permits essential amino acid needs to be met at lower concentration of dietary protein (Keshavarz and Jackson, 1992).

4. Effect of Amino Acid Balance on Thermogenesis

In the series of experiment by MacLeod (1990, 1991, 1992) using calorimetry system and comparative-slaughter techniques with high energy and low protein feeds, it was found that large differences in energy: protein ratio were accommodated mainly by changes in body composition, with no indication of regulatory changes in heat production or diet-induced thermogenesis. The conventional expectation has been that surplus amino acids which are not needed for protein synthesis must stimulate an additional increase in metabolic rate and lead to increased energetic costs of catabolism and excretion. The hypothesis from several studies (e.g. Guillaume and Summers, 1970; Okumura and Mori, 1979; Tasaki et al., 1970, 1976) has been that, when protein synthesis becomes limited by the first limiting amino acid, amino acids present in excess of the resulting requirement enter the pool of substrates available as energy sources. It suggests that this would lead to greater heat increment than would occur with a balanced amino acid mixture. Baldini (1961) found that heat production was increased in methionine deficiency diet. Guillaume and Summers (1970) also reported the increased heat production in diet containing methionine-cystine adequacy with other amino acids in relative excess. However, it can also be argued that the catabolism of surplus amino acids would, to some degree, spare the utilization of other substrates for heat production, without necessarily having a large effect on total metabolic rate.

MacLeod's experiment (1997) examined three dietary factors which have been implicated in elevation of metabolic rate: high energy concentration, low protein concentration and imbalanced amino acid mixture. He stated that heat production was closely correlated with rate of protein accretion, which in turn was more strongly associated with intake of lysine, the first-limiting amino acid than with total protein intake. Heat production on an imbalanced, lysine-limited, amino acid mixture was no greater than on a balanced amino acid source with the same lysine concentration.

Boorman and Ellis (1996) reported that there was no adverse effect of protein quality on lysine utilization and detected some indication of increasing net utilization with decreased protein quality. About this conflicting result, MacLeod (1997) suggested a possible explanation as follows; "At the extreme

protein imbalances of the present study, the amino acid pool was catabolized according to molar abundance. The smaller the proportion of lysine in the dietary amino acid pool the smaller may have been the proportion lost to catabolism; the excess non-limiting amino acids may thus have had a sparing effect."

In recent report by Kim (2014), the experiment was performed to test the assumption that imbalanced dietary amino acid mixtures must lead to increased heat production. The diets were formulated to have a wide range of crude protein concentrations but a fixed concentration of lysine, to be the first-limiting amino acid. With constant lysine at 11 g/kg and varying CP ranging from 180 g/kg to 300 g/kg, there was a 75% increase in N intake as CP concentration increased. This led to a 150% increase in N excretion, with no significant change in HP. Simulated HP agreed with the empirically determined results in not showing a trend with dietary CP rather correlated with the first limiting amino acid intake. These results suggest that HP was correlated with the first limiting amino acid intake rather than total CP intake. This agrees with previous study of MacLeod (1997) that there was little indication of regulatory diet-induced thermogenesis when imbalanced amino acid mixtures or excess amino acids were fed. The results imply the over-riding quantitative importance of the cost of protein accretion relative to that of nitrogen excretion. The additional energy cost of nitrogen excretion may be counter-balanced by the reduced costs of protein accretion.

CONCLUSION

There have always been needs to improve metabolic efficiency and growth rate and to optimize body composition of animal in nutritional research. Energy and protein contributing ingredients represent most of the feed cost for poultry. Therefore, providing feed formulated optimum energy and amino acids are critical to reduce the costs of production.

Protein deposition in the bird is an energy-demanding process and may only proceed if adequate dietary energy is provided assuming other nutrients are fulfilled. This fundamental relationship can be incorporated into the dietary association of energy and lysine, where the latter is used as the reference amino acid, as in the concept of ideal protein.

Future progress might be served by models based on this knowledge and descriptions of what the bird uses amino acids for. This modelling approach could enable prediction of the requirements of the birds which is difficult to detect in experiments. New techniques are now available to understand the mechanisms that were impossible to adequately address in the past. Development of molecular technique has enabled an almost exhaustive analysis of gene expression in various nutritional and physiological conditions. They allow a better understanding of the basic molecular mechanisms which regulate energy metabolism at the tissue or the whole body levels.

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