Factors affecting energy metabolism and evaluating net energy of poultry feed

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ABSTRACT Different energy evaluating systems have been used to formulate poultry diets including digestible energy, total digestible nutrients, true metabolizable energy, apparent metabolizable energy (**AME**), and effective energy. The AME values of raw materials are most commonly used to formulate poultry diets. The net energy (**NE**) system is currently used for pig and cattle diet formulation and there is interest for its application in poultry formulation. Each energy evaluating system has some limitations. The AME system, for example, is dependent on age, species, and feed intake level. The NE system takes AME a step further and incorporates the energy lost as heat when calculating the available energy for the production of meat and eggs. The NE system is, therefore, the most accurate representation of energy available for productive purposes. The NE prediction requires the accurate measurement of the AME value of feed and also an accurate measurement of total and fasting heat production using nutritionally balanced diets. At present, there is limited information on NE values of various ingredients for poultry feed formulation. The aim of this review is to examine poultry feed energy systems with the focus on the NE system and its development for chickens.

Key words: energy metabolism, net energy, evaluating system, chickens

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INTRODUCTION

Nutrients such as proteins, carbohydrates, and fats, when assimilated, yield energy that is vital for body functions. The most commonly used system of ingredient energy evaluation is apparent metabolizable energy (**AME**) corrected to zero nitrogen retention (**AMEn**). This has been successfully used for decades, where available energy is calculated as gross energy ingested minus energy excreted in the feces and urine. The true metabolizable energy system was proposed by researchers to include endogenous energy losses in the calculation (McNab and Fisher, 1981). This was a rapid test taking around 24 h with small amounts of feed or single ingredients given to fasted adult birds. In most areas, the AMEn system is deemed as the most practical energy evaluation system in poultry. Large amounts of AMEn data are available for various feedstuffs as well as predicted energy values based on simple chemical components. The AMEn values of feeds have been measured using growing and adult birds.

It has been well-documented that adult birds utilize the energy of feedstuffs to a greater degree with less variation than growing broilers (Garnsworthy et al., 2000; Svihus and Gullord, 2002; Cozannet et al., 2010a). As different bird breeds (meat or egg producers) and ages differ physiologically in their digestion and absorption of nutrients, different energy values may be obtained from ingredients (Begin, 1967; Pym and Farrell, 1977; Lopez and Leeson, 2005; Cozannet et al., 2010b). In addition, AME values depend on the composition and form of the test diet (Nitsan et al., 1997; Noblet et al., 2010). For instance, AME values obtained for high-fat ingredients are often underestimated and those for high-protein ingredients are typically overestimated in the AME system compared to carbohydrates (De Groote, 1974; Carré et al., 2014).

The AME values reported are most often corrected to zero nitrogen retention in body tissues or AMEn. They may also be standardized to 50% nitrogen retention (AMEs) as suggested by Cozannet et al. (2010a). The correction for nitrogen retention is somewhat controversial. Sibbald and Slinger (1963) had doubt about the soundness of correction to zero nitrogen retention and stated that since the amount of tissue protein which is catabolized is small relative to the amount stored by growing birds, or deposited in eggs by laying birds, the imposition of a penalty is a questionable procedure. Lopez and Leeson (2007) demonstrated that correction to zero nitrogen retention imposes about 4 to 5% penalty on the AME values of high protein ingredients. However, little or no difference in overall performance was demonstrated as long as diets were formulated with either all AME or all AMEn values. Dale and Fuller (1984) also confirmed that correction for N retention underestimates the AME of high protein ingredients

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such as soybean meal as compared to cereal grains. Correction of AME values to zero nitrogen retention makes the values for individual ingredients more consistent across various bird types such as adult roosters and growing broilers (Mollah et al., 1983; Hätel, 1986; Bourdillon et al., 1990b; Farrell et al., 1997). Although the AME system is simple to use and is the current default system it does not consider energy partitioned for maintenance, production (meat, egg), and heat increment (**HI**). The net energy **(NE)** system is more comprehensive with respect to energy partitioning and is currently used in cattle and pig diet formulation (Ferrell and Oltjen, 2008; Noblet et al., 2010). This NE system considers energy for maintenance, as well as HI, being the energy wasted as heat. De Groote (1974) compared NE and AME systems for feedstuff energy evaluation in broilers and reported better feed efficiency when using the NE system. This suggests that there may be an economic advantage in taking HI into account during feed energy evaluation. Pirgozliev and Rose (1999) evaluated 40 different feedstuffs with a wide range of AME and NE contents using NE values predicted by Fraps (1946). They reported that NE values gave an improved evaluation of utilizable energy for feedstuffs compared to the AME system, as the latter overestimated the energy values used for production (**NEp**) in high protein feedstuffs of animal origin compared to cereals, cereal by-products, and high-protein vegetable ingredients. Therefore, they proposed the NE system would be more predictable from chemical analysis of feed, provided that digestibility coefficients for protein, fat, and carbohydrate were known for the feedstuff. The major criticism against the NE system is the tedious nature determining HI of ingredients as it required comparative slaughter or live animal indirect calorimetry (**IC**). Calorimetry accuracy depends on highly experienced operators and flawless equipment. De Lange and Birkett (2005) lamented that the NE system was unable to estimate the energy requirements for maintenance (**NEm**) and production (NEp) because of inaccuracy in methodology for heat production (**HP**) calculations using IC. Further, the NEp of different body tissue stores cannot be precisely explained by the NE system. Emmans (1994) proposed an alternative evaluation system called the effective energy model. In this system, the effective energy of a feed or feedstuff is estimated from AME, digestible crude protein, digestible fat, and fecal organic matter. This system is similar to NE, with HP calculated as the difference between effective energy intake and AME. However, the application of effective energy values is debatable. The Emmans Model assumes that higher fecal organic matter (undigested organic matter) increases HI resulting in decreased NE of diets. According to the effective energy model, a diet with increased fiber has decreased NE as dietary fiber is not well digested in poultry. However, later research indicated no effect of dietary fiber on HP, HI, and NE: metabolizable energy (**ME**) in broilers (Noblet et al., 2010; Carré et al., 2014). Moreover, both the effective energy and AME systems involve corrections that may underestimate useable energy values of feedstuffs.

ENERGY PARTITIONING IN THE BODY

The AME value is obtained by subtracting urinary and fecal energy (determined as excreta energy as poultry species void their urine and feces together) from the total gross energy consumed as shown in Figure 1. The NE value is then calculated by deducting heat loss or HI from the AME value. The NE value represents the energy available for maintenance, growth, and production. Further removal of maintenance energy results in NEp. Total heat production (**THP**) is made up of heat produced for maintenance or fasting heat production (**FHP**) and HI. The latter includes the thermic effect of diet and heat production associated with the activity (**AHP**) as a normal level of animal physical activity (van Milgen et al., 1997; Noblet et al., 2010).

TOTAL HEAT PRODUCTION

The THP accounts for approximately 50% of ME intake in broilers (van Milgen et al., 2001) with reported values of 54% for layers (Luiting, 1990). The THP can be measured by calorimetry or comparative slaughter. Both direct calorimetry (**DC**) and IC methods are used to assess energy expenditure. The DC measures actual THP from an enclosed chamber of animals whereas IC estimates the energy expenditure from gaseous exchange (O_2 consumption and CO_2 production) as a result of substrate oxidation (Chepete et al., 2004). During gas exchange measurements, the respiratory quotient (**RQ**) can be calculated by dividing the volume of CO_2 produced by the volume of O_2 consumed. Oxidation of various substrates (fat, protein, and carbohydrate) produce varying RQ values and the total amount of O_2 consumed over a given period depends on the rate of nutrient oxidation (Blaxter, 1967).

Oxidation of carbohydrates, fats, and proteins during metabolism leads to the production of metabolites and heat energy. The average heat of combustion of protein when completely oxidized is 22.2 kJ/g. Oxidization of glucose and tripalmitin (as typical carbohydrate and fat sources) produces the following amounts of energy, respectively (McDonald et al., 2011):

$$C_6H_{12}O_6 + 6O_2 \Rrightarrow 6CO_2 + 6H_2O + 2820\,\text{kJ}$$

$$C_3H_5(COO - C_{15}H_{31})_3 + 72.5O_2 \Rrightarrow 51CO_2 + 49H_2O + 3202\,\text{kJ}.$$

The Brouwer equation (Brouwer, 1965; McLean, 1972; Czerkawski, 1980) was developed to calculate THP in ruminants. The equation, THP (kcal = 3.866 O_2 (volume consumed) +1.200 CO_2 (volume produced) −1.431 g N excreted in urine −0.518 CH_4 (volume

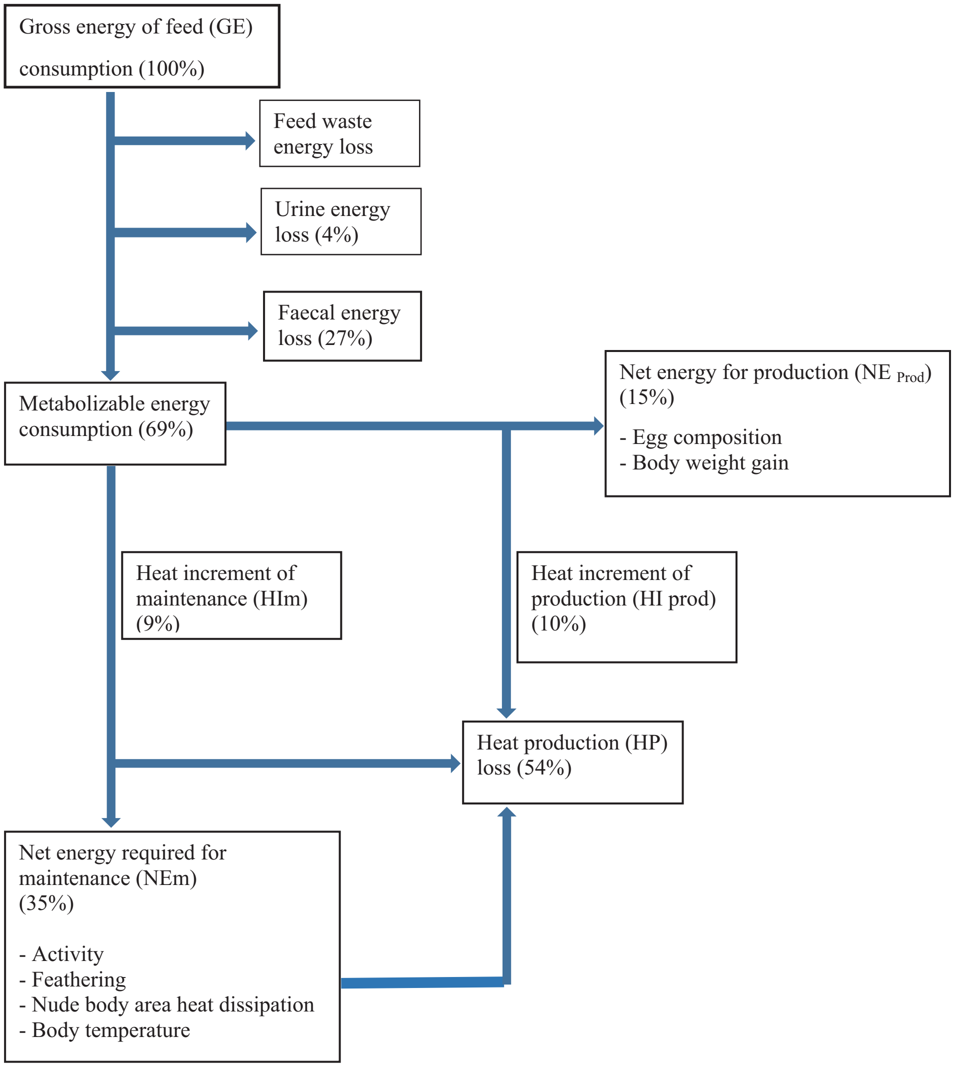

Figure 1. Gross energy partitions in laying hens (Luiting, 1990).

produced). In IC, the O_2 and CO_2 contribute approximately 75 and 25% respectively to THP, while the CH_4 and N contribute about 1% (McLean, 1972). Romijn and Lokhorst (1961) reported THP for cockerels and hens and various strains of ducks using IC during feeding and fasting and used a variation of the Brouwer equation, THP kcal = 3.871 O_2 (litres) +1.194 CO_2 (litres) −0.048 (N in urine (g) × 6.25). The separation of N from feces and urine was not reported. Measurements of THP using IC in poultry usually ignore the minor contributions of CH_4 and N (Farrell, 1972; Zubair and Leeson, 1994) because the error in not including these two terms in the calculation of THP in birds is less than 0.2% (Romijn and Lokhorst, 1961).

Both IC and DC methods have limitations. Both need accurate measurements and appropriate methodology. In DC the THP measured may not be the same as emitted by the animal if the time period is too short and some heat may be absorbed by surrounding materials (Blaxter, 1967). The DC is not able to accurately measure rapid changes in metabolism that occur for example during exercise (Kenny et al., 2008; Kenny et al., 2017)

Other techniques, such as the comparative slaughter technique, calculate THP from measured retained energy (RE) in body tissues. The comparative slaughter method was introduced by Fraps (1946). In this approach, the birds are divided into 2 groups, and the first group is slaughtered at the beginning of the experiment and their body energy content is measured by bomb calorimetry. The second group is slaughtered at the end and their body energy content is measured. The difference between the initial and final body energy content is used to calculate the RE (McDonald et al., 2011). This method is time-consuming as it involves serial slaughter and measurement of birds. In addition, the sampled birds at the beginning of the measurement must be representative of the birds used for the final measurement.

Body tissue stores of fat and muscle can be measured with non-invasive indirect techniques including computed tomography scan (Bentsen and Sehested, 1989; Remignon et al., 1997; Glasbey and Robinson, 2002), magnetic resonance imaging, and echography (Grashorn, 1996). The dual-energy X-ray absorptiometry (**DEXA**) technique has been used with IC to provide a better understanding about dynamics of energy utilization, its partitioning and deposit in different parts of the body as different tissues (Swennen et al., 2004a; Caldas et al., 2018). While body composition data for poultry is traditionally determined by whole carcass grinding (comparative slaughter technique) through wet chemistry analysis, the DEXA method is recommended as a reliable and non-invasive alternative for in vivo measurements of the body composition of broilers (Mitchell et al., 1997; Swennen et al., 2004a; Salas et al., 2012), laying hens (Schreiweis et al., 2005), and broiler breeders (Salas et al., 2012; Caldas et al., 2018). These non-invasive techniques are useful for gross muscle mass and depot fat measurements. However, care must be taken in interpretation of whole body results as intramuscular fat and protein associated with connective tissue are less easy to discern than with whole carcass grinding.

RESPIRATORY QUOTIENT

The RQ is the ratio between the volume of carbon dioxide produced by an animal and the volume of oxygen used. The RQ changes with diet composition, metabolic rate, physiological status, and feed intake (van Ouverkerk and Pedersen, 1994). The RQ for oxidization of carbohydrates, protein, and fat is 1.0, 0.74, and 0.70, respectively, in uricotelic species (McLean et al., 1987; Walsberg and Wolf, 1995). Utilization of protein as a source of energy involves more complex metabolic pathways and a higher metabolic rate. Dietary composition in terms of carbohydrates, protein, and fat affects the RQ of growing broilers with a tendency for lower values with diets both higher in fat and protein but higher values when carbohydrates are supplied as the main ingredients of the diets (MacLeod, 1990). The RQ is higher in broilers fed low-protein diets, as broilers mostly retain energy as fat with more efficient fatty acids synthesis (lipogenesis) compared to low-fat counterparts fed isocaloric diets (Swennen et al., 2004b). Furthermore, the use of body resources to provide energy affects RQ such as in the state of limited feeding or fasting. In such cases, fat reserves are oxidized resulting in lower RQ values. On the other hand, during lipogenesis, or the conversion of carbohydrates to fats results in increased RQ as is the case in growing birds. When fasting, RQ values can be as low as 0.70 (Blaxter, 1989), while during growth with excess dietary energy, RQ values become higher than 1 (King, 1957; Blaxter, 1989). Due to de novo lipogenesis, RQ values can be much higher than 1 as, in this pathway, no O_2 is consumed and only CO_2 released (Rivera-Torres et al., 2010). Researchers showed that de novo lipogenesis accounted for 60% of total lipid retention and increased as birds grew older (Rivera-Torres et al., 2010). During periods of starvation, body oxidation patterns change such that more fat than protein is catabolized (Chwalibog et al., 2004). Fasted laying hens showed lower RQ in the last day of a 3-D calorimetry measurement, implying that the birds were oxidising more body fat reserves to meet energy requirements as starvation continued (Ning et al., 2014).

The RQ can also be influenced by the level of feed intake as an increased level of feed intake resulted in higher THP and RQ as shown in pigs (Noblet et al., 1994).

Since the body changes its metabolic patterns for energy utilization at maturity, RQ values can be affected by bird age. Choct (2004) showed RQ values greater than 1 with less variability in growing broilers compared to 56-wk-old layers fed the same ingredients. Chepete et al. (2004) found an average RQ of 0.94 and 0.91 for Hy-Line W-36 pullets and layers, respectively. Broiler breeder hens showed the lowest RQ values at 43 wk of age compared to the beginning of egg production (Caldas et al., 2018). Those researchers assumed that at 43 wks of age, birds oxidize fat or protein to meet the requirement for energy compared to the beginning of production where energy is provided mostly by carbohydrates. Broiler breeders use glucose for egg lipogenesis at the beginning of production but mostly use dietary fat for egg lipid synthesis at the end of production (Salas et al., 2017).

The mode of CO_2 excretion from the body affects the level of CO_2 measured in calorimetry chambers and thus RQ values in laying hens. Walsberg and Wolf (1995) reported RQ values of less than 0.71 during fasting possibly due to incomplete oxidation of fat and non-pulmonary loss of CO_2 through non-respiratory sinks for CO_2 or excretion as bicarbonate ions. Therefore, CO_2 production varies in layers at different levels of egg production.

FACTORS AFFECTING HEAT PRODUCTION

It has been well-documented that animal THP varies owing to different factors. Energy intake is positively correlated to HP (Chudy et al., 2003; Ning et al., 2013; Ning et al., 2014) as greater feed intake increases metabolic rate and thus releases more heat. Feeding diets with different nutrient composition changes THP; dietary protein and amino acids contents are more important contributors to THP than other dietary nutrients. MacLeod (1997) found that protein retention in the body increased following higher intake of lysine (first-limiting amino acid) and this resulted in greater THP in broilers. However, supplementing diets with extra amounts of other essential amino acids did not affect THP.

Utilization of AME in different body tissues alters HP with different anabolic pathways. Protein synthesis and the excretion of nitrogenous compounds from body during protein turnover, require more energy compared to anabolism of other tissue components (Latshaw and Moritz, 2009). Synthesis of each gram protein requires

380% more oxygen compared to the synthesis of each gram fat (Teeter et al., 1996). In the same way, broiler breeder hens generate more heat at the end of the production period as they retain dietary energy in muscles and catabolize fat to meet energy requirements (Caldas et al., 2018).

Photoperiod affects metabolic rate, and accordingly, THP will change based on the diurnal patterns and physical activity. Physical activity accounts for 20 to 25% of THP in laying hens (MacLeod et al., 1982; Boshouwers and Nicaise, 1985). Physical activity costs about 10% of ME intake in different species such as growing broilers, pigs, and calves (Noblet et al., 2010). The THP is significantly decreased in the dark period compared to the light period as physical activity is less during darkness (Chepete et al., 2004). This is also the case for modern pullets and layers. Lighting period and intensity change THP and physical activity in laying hens (Li et al., 1992; Ning et al., 2014). This is an important point for poultry production, as different lighting schedules might affect THP and NE of layers fed the same diets. The THP decreases after oviposition, as the hen loses weight with less energy required for keeping the egg warm within the same temperature range of the body tissues (Pesti et al., 1990).

The disease affects metabolism, energy balance, and nutrient digestion. Broilers challenged with necrotic enteritis showed lowered feed intake and lower energy intake, RQ, and NE. Infected birds had decreased body temperature and THP probably as a consequence of hypothyroidism (M'Sadeq et al., 2016).

FASTING HEAT PRODUCTION

The basal metabolic rate is FHP adjusted to zero activity (Noblet et al., 2015). Also, FHP and metabolizable energy for maintenance (**MEm**) can be calculated by extrapolating to zero ME intake from regression estimation of different ME intakes on different THP produced (Birkett and de Lange, 2001; Noblet et al., 2010; Ning et al., 2013). The FHP should be measured at the thermoneutral zone or the environmental temperature where the animal produces a constant minimal level of heat loss to maintain body temperature in homoeothermic status (Arieli et al., 1980). Increased levels of ambient temperature from the thermoneutral zone decrease THP and MEm (Vohra et al., 1975; Chudy et al., 2003). The FHP accounts for 80% of MEm variation; therefore, the factors affecting FHP might affect MEm as well (Vohra et al., 1975). Likewise, the main source of variation in THP is due to variation in MEm and is affected by physical activity, feathering, FHP, body composition, and temperature (Luiting, 1990).

The FHP is assumed to be an allometric function of body weight. The fasting metabolic rate was defined as FHP $= a \times \mathrm{BW}^b$, where a is a constant coefficient as kcal, BW is body weight (kg), and BW^b is metabolic BW (kg) which correlates bodyweight to surface area (Vohra et al., 1975). Researchers applied regression estimations to find the correct power to express metabolic BW (Close et al., 1973; Bikker, 1994; Noblet et al., 1994). The power of 0.75 for metabolic BW was originally stated by Kleiber (1947) for a wide range of animals, although Noblet et al. (2015) recommended 0.70 for growing broilers. Lopez and Leeson (2005) reported that applying the power of 0.75 underestimated MEm estimations of smaller and younger broilers, and 0.60 is more accurate for these birds. Since MEm accounts for 42 to 44% (large portion) of ME intake (Lopez and Leeson, 2005), accurate estimation of MEm is necessary for correct calculations for production requirements.

The ME intake alters FHP and thus the efficiency of ME intake for MEm. Higher ME intake showed higher FHP compared to lower ME intake; in addition, starvation decreased THP and FHP during a 3-D calorimetry measurement, and the more elongated the starvation the less the contribution of feed to HP (Ning et al., 2013). The efficiency of ME intake for MEm was higher (0.67 to 0.80%) when feed intake met maintenance requirements compared to lower values (0.57 to 0.69) when consumption was higher than maintenance requirements (Sakomura, 2004). MacLeod (1990) reported that dietary composition had no effect on MEm and FHP in growing broilers.

As birds grow their maintenance requirement changes (Sakomura, 2004). The composition of BW gain at different stages of growth affects MEm (Sakomura et al., 2005). Growing birds require higher MEm than adult birds. Mature birds tend to deposit energy mostly as fat resulting in lower MEm. However, growing birds use dietary energy for protein synthesis that requires complicated metabolic pathways and thus embraces higher energy cost for the body (Blaxter, 1989).

Different bird types vary in FHP and MEm requirements. The MEm of broilers was reported to be 594 to 618 kJ/BW $^{0.75}$ per day (Liu et al., 2017); however, values for laying hen strains were 469 to 502 kJ/BW $^{0.75}$ per day (Jadhao et al., 1999; Sakomura, 2004). FHP values obtained in broilers were 410 to 460 kJ/BW $^{0.70}$ per day (Noblet et al., 2015) and 386 to 404 kJ/BW $^{0.75}$ per day (Liu et al., 2017) which were higher than values for layers at 370 to 395 kJ/BW $^{0.75}$ per day (Farrell, 1975; Wu et al., 2016).

The MEm is not a constant value and varies with ambient temperature. The MEm of different bird strains increased with decreasing environmental temperature (Sakomura, 2004). The MEm of broilers was negatively correlated by the quadratic effect of ambient temperature (Sakomura et al., 2005). Birds must produce heat when they are housed below the thermoneutral zone and when temperatures exceed thermoneutral zone, birds must expend energy to dissipate heat in order to maintain body temperature (Leeson and Summers, 1997). The environmental effect of energy requirements can be discussed from an endocrine point of view. Thyroid hormones play a pivotal role in body temperature homeostasis. Both ambient temperature and feed intake affect thyroid hormone production. For example, hens fasted for more than 4.5 h had lower triiodothyronine (**T_3**) as reported by May (1978) and produced less THP as described by Klandorf et al. (1981). Increased ambient temperatures beyond thermoneutral decreased T_3 level in plasma and HP as the latter is predominantly controlled by T_3 hormone and not by thyroxine in laying hens (Klandorf et al., 1981).

The MEm requirements vary with body feather coverage, for similar reasons. Layers housed at the thermoneutral zone with 0% feather coverage required 38% more MEm than their peers housed at the thermoneutral zone with 100% feather coverage (Peguri and Coon, 1993). Accordingly, birds with poor plumage were found to be more resistant to heat stress than birds with normal feather coverage as the former is able to dissipate heat more easily (Balnave, 2004).

The AHP and MEm requirements change according to housing conditions. The AHP accounts for 20 to 25% of THP variations or 8 to 10% of MEm requirements (van Milgen et al., 2001). Broiler breeder hens reared on the ground produced more THP, lost more energy as AHP and required 20% higher MEm compared to those kept in the cages (Sakomura, 2004).

Lighting program changes AHP and THP of birds as activity level and THP decrease during the dark period (Ning et al., 2014). Birds are also more active under a continuous lighting program than in lighting programs that allow a daily dark rest period. However, Ohtani and Leeson (2000) observed that THP of broilers reared under an intermittent lighting program (multiple light and dark in a day) was higher than of those under continuous lighting presumably due to higher activity under intermittent lighting.

The diurnal pattern of FHP and THP will change according to metabolic status during the day. Damme et al. (1987) found an increased metabolic rate in hens just before oviposition, which resulted in the increased level of FHP and THP followed by a sharp fall to the resting level after oviposition.

HEAT INCREMENT AND NET ENERGY

The proportion of gross energy lost via excreta is approximately 30%, that is to say, about 70% of the gross energy of a common diet fed to poultry is metabolized. From AME to NE, the amount of energy lost as heat is approximately 75% for most common ingredients fed to poultry. This means that 25% of ME is lost as heat during the digestive and metabolic utilization of energy. Indeed, a recent study reported a thermic effect of balanced feed accounting on average for 26% of ME intake in broilers (Wu et al., 2019), while it can be lower (20 to 23%) with low protein or low fat diets (Swennen et al., 2004b).

The NE:AME of nutrients are different as the highest values are reported for fats and lowest one for protein (Pirgozliev and Rose, 1999; Carré et al., 2002, 2014; Wu et al., 2019). An increase in HI with elevated protein levels might be due to two factors: catabolism of protein leads to nitrogenous wastes that require energy to be excreted; protein accretion and turnover requires energy to fuel metabolic pathways (Musharaf and Latshaw, 1999). The level of dietary fat and protein was found to affect measured HI and NE:AME in broilers (Wu et al., 2019) and also layers (Barzegar et al., 2019). Earlier studies, however, did not show level of dietary protein, fat or fiber to effect NE:AME or HI, (Noblet et al., 2003; Noblet et al., 2010; Carré and Juin, 2015). With different levels of fiber, it was suggested by Carré et al. (2014) that the low variation in NE:AME may be due to its low digestibility in broilers as opposed to pigs (Noblet et al., 1994). However, a recent study in broilers indicated that digestible neutral detergent fiber had a negative effect on NE:AME (Cerrate et al., 2019).

Feed and ME intakes also alter NE:AME efficiency and HI. Liu et al. (2017) reported higher levels of feed intake in broilers lowered NE:AME. They stated that when feed intake increased, the proportion of ME used for HI increased and resulted in less NE and a lower NE:AME ratio. In addition, laying hens with access to ad libitum feed showed higher HI and lower NE:AME than the feed-restricted hens (MacLeod et al., 1979),

The utilization of AME for NE depends on the form of energy that is retained. Utilization of AME for fat retention is more efficient compared to that for protein retention (Farrell, 1975; Noblet et al., 1999). Utilization of AME for NEp produces more heat than that for NEm. Blaxter (1989) showed that different energy sources as protein, carbohydrates or fat used for maintenance showed 20% higher efficiency than for production, which means that HI was less when the nutrients were used for maintenance than for growth and production. Feeding animals to the level of maintenance produces heat that is used for basal heat requirements of body (thermostasis) and spares dietary energy to be used for FHP; however, feeding above maintenance requirements, produces heat that is surplus to basal requirements and hence it is wasted, leading to decreased energy efficiency (Musharaf and Latshaw, 1999).

ENERGY PARTITIONING FOR GROWTH AND PRODUCTION

Partitioning of ME as MEm and RE in body fat (**RE_f**) or body protein (**RE_p**) is based on metabolizable energy intake (**MEI**). Where MEI = MEm + $(1/K_f \times RE_f) + (1/K_p \times RE_p)$ (Boekholt et al., 1994), MEm is ME for maintenance as a function of BW, K_f and K_p are the efficiencies of utilization of ME for fat and protein retention respectively. The values for K_f (86%) and K_p (66%) have been estimated using statistical models with different feed restriction levels applied in broilers (Boekholt et al., 1994).

As stated earlier, the utilization of energy for protein deposition (NEp:ME) is lower than for fat deposition. The original reported efficiency values of 66% for protein accretion and 86% for fat accretion in broilers (Boekholt et al., 1994) and applied later by Lopez and Leeson (2005) indicate that the energy required for protein deposition in the body is less than that for fat (8.6 *vs* 11.1 Kcal/g ME). Applying the energetic efficiencies of 60% for protein and 80% for fat in growing pigs, the deposition of protein (9.6 kcal/g) requires less energy than the deposition of fat (12.0 kcal/g) (van Milgen and Noblet, 2003).

Genetic selection is a progressive process which affects the pattern of RE over time for different chicken strains. Lopez and Leeson (2008a) calculated RE_p:RE and RE_f:RE as 51 and 49% (in broilers) and 62 and 38% (in layers). More recent values of RE_p:RE and RE_f:RE were 55 and 45% in broilers (Wu et al., 2019) and 96 and 4% in laying hens (Barzegar et al., 2019). It can be concluded that poultry geneticists' criteria are focused on improving the efficiency of RE_p and decreasing the RE_f both in broilers and laying hens.

Examining RE as a balance of MEI and THP in the body, the amount retained as NE per unit of product (egg) and BW gain in layers can be ascertained. The efficiency of ME for deposition in the egg was lower than for growth (62 vs. 65%) in layer hens, whilst those correspondent values were 64 and 47% in broiler breeder hens (Rabello, 2001; Sakomura, 2004). The egg energy content remained constant while MEI increased in hens (Chudy et al., 2003). Retention of energy in the body depends on bird energy balance. Layers do not retain energy as fat unless they are in positive energy balance; nonetheless, they can retain energy in protein, eggs or body tissues regardless of body energy balance status (Farrell, 1975). When energy is provided only to meet MEm requirements, energy is totally retained as protein without any fat deposits in broilers (Boekholt et al., 1994). Also in layers, the efficiency of ME for egg production is higher when body tissues are used for egg production compared to utilizing a dietary energy source for egg production (Blaxter, 1989).

Given that the energy storage in body tissues is a balance of energy intake and energy loss, this balance can be changed in different environmental situations. For instance, in hot environmental situations, both high temperature of the environment plus the HI of diet represent the main sources of energy inputs. This extra flow of energy, which is beyond the thermoneutral zone, must be dissipated from the body to maintain body temperature homeostasis (Daghir, 2008). Minimizing excess protein and replacement of carbohydrates with fat as an energy source reduce the HI of the diet, increase the NE:AME, enhance feed intake and maintain performance (Dale and Fuller, 1979; Gous and Morris, 2005).

The stage of growth affects body composition and energy retention. Broilers are leaner at a young age and thus the proportion of energy intake deposited as protein is more efficient than fat deposition. Protein retention accounted for 23 to 30% of BW gain during first few weeks of age in turkeys, although fat was deposited to a greater extent than protein in older turkeys (Rivera-Torres et al., 2010). The same pattern of energy retention on age was observed during the laying period of hens. Caldas et al. (2018) observed a negative correlation between protein and energy retention in broiler breeder hens. Lean body mass decreased from peak production until 50 wk of age with the opposite trend for fat mass in the same period, which soared after 50 wk of age. In other words, at the beginning of the production period, birds sacrificed muscle protein to maintain egg production. After 50 wk of age, when egg production is reduced they catabolize more energy from fat resources.

Diet composition can change energy and protein metabolism in birds. Broilers fed low-protein diets consumed more energy from isocaloric diets with an increased level of THP and more RE as fat compared to their counterparts fed low-fat diets (Swennen et al., 2004b). Low-protein diets are formulated with a high level of fat and the extra caloric effect of fat might be a reason for higher RE as fat. The extra caloric effect of fat may be due to enhanced of digestibility and energy utilization of non-lipid nutrients in the diet. It is perhaps also true that utilization of fat produces less heat and hence more NE, accentuating the amount of energy available for production. Furthermore, low-protein fed broilers showed higher protein retention compared to high protein fed broilers (Swennen et al., 2004b).

Different strains of chickens have a different body composition that may affect growth and energy utilization. During the first 6 wk of life, layer chickens showed a sharp increase in RE as protein compared to broilers. Broilers undergo physiological changes including feather growth, which requires protein and influences body protein retention during the first weeks of their life (Lopez and Leeson, 2005). Different broiler lines show different responses to energy retention. Lean broiler lines have higher protein retention compared to fat retention and high fat lines degrade dietary amino acids resulting in higher uric acid excretion and lower potential for protein retention. However, no difference in ME intake, THP, HI, and MEm were observed (Geraert et al., 1988; Geraert et al., 1990).

COMPARISON OF ENERGY EVALUATION SYSTEMS

Different feed energy systems can be compared if the measurements performed are under standardized conditions, i.e., with the same genotype, sex, age, housing, and controlled temperatures. Furthermore, energy partitioning should be expressed as per metabolic BW as opposed to BW. The exponent used to convert BW to metabolic BW should be constant for the MEm and energy partition calculations. Estimation of MEm when BW rose to the exponent 0.60 is more accurate (in particular for younger and smaller birds) with less residual variance compared to the estimations using 0.75 (Lopez and Leeson, 2008a).

Initially, Fraps (1946) evaluated 62 individual feedstuffs to determine productive energy using a comparative slaughter technique in growing chickens. Results showed that NEp from high protein feedstuffs (animal sources) were lower than those originating from high starch ingredients (cereal sources). Furthermore, the NEp took into account the total amount of fat and protein retention without any differentiation. This method is arduous and time-consuming and the outcomes may change depending on error sources. The advantages of utilizing IC methods to determine NEp include rapid estimation of HP and shorter restricted feeding times with basal metabolism being less affected. The IC method reduces the errors associated with carcass analysis and shortens the total experimental period (Farrell, 1974). Comparing different methods of NE measurement under the same situation, the reported values of energy partitions were different. The THP variation (based on metabolic BW) was 1% when measured by either IC or by the comparative slaughter method (Farrell, 1972). The THP measured by IC was 3% higher (kcal/bird per day) than that measured by the comparative slaughter method with 10-wk old cockerels (Fuller et al., 1983). The ME intake, THP, RE, NE and NE:ME measured by comparative slaughter were the same as measured by IC in broilers (Liu et al., 2017). However, Barekatain et al. (2014) reported that applying the comparative slaughter method resulted in less THP and higher NE, NE:ME, and RE compared to IC method.

Dietary AME or NE can be predicted from the chemical composition of poultry feedstuffs (Janssen, 1989; Pirgozliev and Rose, 1999; Cozannet et al., 2010a; Carré et al., 2014; Barzegar et al., 2019; Wu et al., 2019). A recent study with broilers used digestible nutrients to predict AME or AMEn and then predicted NE from AME and total nutrient levels (Cerrate et al., 2019).

GUT MICROBIAL COMMUNITY AND NUTRIENT UTILIZATION

The gastrointestinal tract (**GIT**) includes microbial communities having substantial metabolic functions that improve the nutritional performance and health status of the host. The establishment of chicken microbiota increases rapidly after hatch (Apajalahti et al., 2004) and starts when the hatchling contacts bacterial colonies residing the eggshell surface. Because of a commensal microbe-host interaction, there is evidence confirming the beneficial effect of intestinal bacteria in feed digestion, GIT development, vitamin synthesis, boosting the immune system and host energy metabolism (Rakoff-Nahoum et al., 2004; Forder et al., 2007; Klasing, 2007). Diet-based complex carbohydrates such as non-starch polysaccharides and resistant starch are not degraded in the small intestine but enter the large intestine and ceca where they undergo bacterial fermentation. The end product of this degradation is short-chain fatty acids that may be absorbed and used as an energy source (Rinttilä and Apajalahti, 2013). Researchers found a significant correlation between the cecal microbial profile and efficiency to convert GE to ME (ME:GE) with enhanced FCR (Rinttilä and Apajalahti, 2013). Antibiotic growth promoters (**AGP**) have been used to alter GIT micrflobiota and thereby increasing energy value of the feed. In some world areas AGP have been banned due to concern over potential development of antibiotic resistance of pathogens and accumulation of antibiotic residues in the environment (Barton, 2000; van den Bogaard and Stobberingh, 2000).

Other feed additives such as enzymes increase energy availability due to their effect on digestion. Olukosi et al. (2008) observed a significant improvement in BW, NEp, RE as fat, and RE as protein following supplementation with phytase. Broiler feed supplemented with phytase was found to have higher NEp compared to ME and was more responsive to BW than ME. Cowieson et al. (2018) also reported a higher BW gain, improved RE, NE, and NE:AME in broilers diets with supplemental exogenous protease. In that study, protease addition increased NE more than AME (+107 vs. +73 kcal/kg). Enzyme application, particularly carbohydrases, improves nutrient digestibility and energy metabolism due to hydrolysis of polysaccharides resulting in release of encapsulated starch and protein thus reducing THP and increasing NE of diets (Choct et al., 2010; Nian et al., 2011). Barekatain et al. (2014) reported enzyme supplementation (xylanase, protease, amylase, and glucanase) increased NE, NE intake, and RE, but did not change THP in broilers. Enzymes also reduced the weight of the GIT which accounts for more than 50% of HI and MEm (Nian et al., 2011).

Probiotics are defined as live microbial feed additives with beneficial effects on the host by improving its intestinal microbial balance (Fuller, 1989). The mode of action of probiotics is to uphold a beneficial microbial population which includes competitive exclusion and immune system modulation (Yang et al., 2009). The competitive exclusion effect of probiotics in lowering microbial load, maintaining the overall health of gut microbiota, and preventing a number of potential food-borne pathogens has been confirmed in broilers (Pascual et al., 1999; Higgins et al., 2007; Mountzouris et al., 2019). As probiotics have been shown to increase nutrient digestibility, ME (Mountzouris et al., 2010; Reis et al., 2017), and broiler performance (Bai et al., 2013; Harrington et al., 2015) they may also enhance NEp.

CONCLUSION

The implementation of an NE system instead of the AME system for poultry feedstuff energy evaluation is in its early stages of development and not without debate (De Lange and Birkett, 2005; Noblet et al., 2010; van der Klis et al., 2010; van der Klis and Jansman, 2019; Zuidhof, 2019). Currently, the AME system is considered as the default method but lacks the ability to distinguish energy use for different body functions. While the NE system gives more accurate energy values compared to AME, its application is complicated in practice. The main component to calculate NE is THP that can be measured using serial slaughter or with IC. Such measurements depend on dietary nutrient levels, age, and category of birds, body composition, physiological status, and environmental conditions. The energy partitioning for different metabolic purposes as growth and production in different body tissues can be defined by the NE system. It is anticipated that using the NE system will result in a more accurate estimation of energy value of ingredients for productive use. Determining the NE value of ingredients must be conducted using balanced diets with defined environmental conditions and will require accurate measurements of AME. Further research is required to confirm whether an NE system will offer advantages in terms of economic performance.

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