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REVIEW

Optimisation of dietary energy utilisation for poultry – a literature review

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SUMMARY

Feed energy is an important production factor in poultry, representing 75% of the total cost of feed. Therefore, maximising energy digestion and utilisation is essential for cost-effectiveness and sustainability in poultry production. Consequently, accurate energy evaluation of raw material and animal requirements for energy is valuable for precision feeding and optimised benefits in growing chickens. Two key strategies to enhance the utilisation of energy from feed ingredients are the use of exogenous enzymes, such as carbohydrases, and accurate energy requirement prediction. Exogenous carbohydrases can enhance nutrient digestion and absorption, especially in diets with viscous ingredients, in which carbohydrases can enhance the digestibility of saturated fat and protein, by 33% and 3%, respectively, and about 4% energy utilisation. This can improve not only energy utilisation, but also gut health by reducing nutrient flow into the hindgut, as the presence of undigested nutrients fuels pathogenic bacteria proliferation. Moreover, accurate energy bioassays are required to provide values of dietary energy and true availability of energy to the birds. Currently, metabolisable energy (ME) systems are commonly used to evaluate poultry energetics. However, ME does not represent the total energy available to the birds, as it cannot measure the proportion of dietary energy that is lost as heat during feed ingestion, absorption and metabolism. In fact, the ME system can underestimate energy provided by fat by 13% and overestimate energy from proteins by 20% in chicken feeds. As net energy (NE)/ME ratio can vary from 59% to 77% depending on dietary composition, the NE systems are suggested as alternative, more accurate energy measurement methods, as they provide energy values corrected for heat increment. This paper reviews energy sources for poultry and addresses the potential to use NE measurements as a tool to evaluate the ability of feeds and feed additives to improve the exploitation of energy utilisation.

KEYWORDS

Net energy; metabolisable energy; metabolisable energy efficiency for net energy; carbohydrases; indirect calorimetry system; heat production

Introduction

Feed accounts for approximately 70% of the poultry production costs, of which as much as 75% comes from dietary energy (van der Klis and Kwakernaak 2008; Noblet 2015). Therefore, strategies for enhancing dietary energy utilisation are important and con-

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stantly under investigation. One strategy is the application of feed additives, including exogenous carbohydrases, prebiotics and probiotics, to improve feed efficiency and weight gain (Rinttilä and Apajalahti 2013), gut health and maintenance of gut microbial balance, and resilience against enteric diseases in broiler chickens (Chiang and Hsieh 1995; Jin *et al.* 1997; Panda *et al.* 2003; Collett 2005). On the other hand, accurate determination of dietary energy content is vital for feed formulation, especially as all nutrients must be formulated proportionate to the dietary energy content, and energy dictates feed intake (FI) (Leeson and Summers 2001; Choct 2004). The evaluation of poultry dietary energy is currently based on the metabolisable energy (ME) system. This system encompasses energy required for catabolism related to diet-induced thermogenesis or heat increment of feeding (HI_f), and for anabolism, or the energy needed for growth and/or egg production (Vohra 1972). It can be described as a balance between gross energy (GE) in feed consumed and GE lost in excreta (Rivera-Torres *et al.* 2010). However, more accurate values of energy utilisation by the birds can be obtained from net energy (NE) measurements, as these take into consideration HI_f (Noblet *et al.* 2015). Although this system can provide a closer estimate of available energy for birds (Pirgozliev and Rose 1999; Latshaw and Moritz 2009), it requires specialised equipment able to measure gas exchanges, meaning there is limited repeatability and high costs associated with NE bioassay. Therefore, analysis of ME is currently still the default system in the evaluation of feed energy in poultry feed formulation. The present review focusses on energy substrates, the positive and negative attributes of different poultry feed energy systems, and proposes the way forward in this field. It also addresses the potential to use NE measurements as an accurate evaluation tool to optimise poultry energetic estimates.

Energy sources in poultry nutrition

The dietary energy level is the starting point in feed formulation. Arguably, feed energy determines FI, because birds are assumed to eat until their energy requirements are satisfied (NRC 1994; Kleyn 2013). Birds acquire energy from metabolisable nutrients, such as carbohydrates, fats and proteins, which are regarded as the major nutrients to yield energy in the animals (NRC 1994).

Fats and oils

Fats (a solid state at room temperature) and oils (a liquid state at room temperature) are triglycerides containing differing levels of fatty acids. The term 'lipids' denotes all ether-soluble substances, and in most cases crude fat is expressed as the assayed value for ether extract (EE) (Leeson and Summers 2001). Lipids can be provided by animal sources (tallow and lard) or vegetal sources (soybean oil, sunflower oil, canola oil, cottonseed oil, palm oil and so on) (Lu *et al.* 2014). The inclusion of lipids in diets for growing animals can improve the utilisation efficiency of energy intake, as HI_f is lower in fat-rich diets, because fatty acids are deposited in the body with minimal metabolism (Leeson and Summers 2001). In fact, lipids can provide twice as much energy (approximately 9.4 kcal/g) as the energy provided by digestible carbohydrates or protein (about 4.1 kcal/g each). However, fat digestion is affected by the viscous environment that interferes with proper emulsification into micelles (Choct and Annison 1992; Bedford 2002; Ravindran *et al.*

2016). The digestibility problem associated with high digesta viscosity is more apparent for tallow (saturated fats) than soybean oil (unsaturated fats). It was shown that xylanase supplementation in broilers fed the rye/tallow-based diet and rye/soybean oil-based diet increased fat digestibility by 33.3% and 5.7%, respectively (Danicke *et al.* 1995; Bedford 1997). In addition, the energy:protein ratio needs to be maintained at about 13.2 (kcal:g) to maximise energy utilisation from lipids (Leeson and Summers 2001).

Carbohydrates

Carbohydrates represent approximately 70% of poultry feeds and they are mostly provided by cereal grains, such as corn, sorghum and wheat (NRC 1994; Leeson and Summers 2001; Kleyn 2013). They can be divided into three main groups: simple sugars (monosaccharides and disaccharides), oligosaccharide (3 to 10 units of monosaccharides) and polysaccharides (more than 10 units of monosaccharides) (Medeiros and Wildman 2013). Monosaccharides, including single glucose, galactose, mannose and fructose, are well digested by birds. Disaccharides that are digestible by birds include maltose (glucose + glucose) and sucrose (glucose + fructose). The overall utilisation of energy from cereals in chickens results in efficient utilisation of these small sugars (monosaccharides and disaccharides). Oligosaccharides, such as raffinose, stachyose and verbacose from pulses and oilseed meals, are poorly digested by birds (NRC 1994; Leeson and Summers 2001; Bedford 2002). Starch is a form of plant energy reserve mostly stored in seeds, grains and tubers. Naturally, starch exists as insoluble granules, which resist digestion but can be broken down by cooking. They are also disrupted when they are soaked in water, which explains how the initial soaking of feed in the crop facilitates starch digestion in chickens. Starch is mainly composed of amylopectin that is insoluble in hot water, representing 80% to 90% of total starch, and the remaining is amylose, which is soluble in hot water (Leeson and Summers 2001). Starch and sugars (also known as nitrogen-free extract) are easily digested by birds (Bedford 2002).

Birds lack endogenous enzymes to digest other types of carbohydrates, such as non-starch polysaccharides (NSP) and resistant starches (resulting from processing), meaning these are excreted and the chemical energy they store is wasted (Bedford 2002; Choct 2002). The term NSP encompasses non-digestible fibre excluding lignin (Medeiros and Wildman 2013). NSP represents the main component of dietary fibres in poultry diets (Slominski 2011) and, based on their capacity for water-solubility, they can be classified as insoluble and partially soluble fibres (Choct 2002). Insoluble NSP constitutes the bulky fraction of diets, with nutrient dilution effect, and may act as a physical barrier for digestive enzymes, thereby reducing dietary energy content (Noblet and Le Goff 2001; Morgan *et al.* 2018). However, the inclusion of moderate amounts of insoluble NSP can improve gut and gizzard development, as well as maintaining excreta consistency through absorbing excess water and ensuring normal gut motility (Choct 2002; Kheravii *et al.* 2017).

Soluble NSP (sNSP) act as anti-nutritional factors (ANF) by increasing digesta viscosity because of the high weight of their molecules and their solubility in the intestinal environment (Bedford 2002). The main water-sNSP in rye, wheat and triticale are pentosans (xylans and arabinoxylans), whilst those of oats and barley are β-glucans. The presence of these water-sNSP in cereals has a direct negative impact on energy

utilisation in chickens and all monogastric species (Choct and Annison 1990; Marquardt 1997). For instance, the addition of water-soluble pentosan in sorghum/soybean meal-based diets decreased protein and lipid ileal digestibility by 18.7% and 25.8%, respectively (Choct and Annison 1991). High digesta viscosity interferes with enzymatic activity, increases digesta transit time and decreases nutrient digestion and absorption (Annison 1993; Choct 2002; Yegani and Korver 2008). Cozannet *et al.* (2017) also demonstrated that the application of multi-carbohydrases in the diet with high digesta viscosity increased 3.2% protein digestibility and 3.8% energy utilisation. In terms of enzyme activity interference, Almirall *et al.* (1995) noted significantly decreased activities of endogenous amylase and lipase in young chickens fed high viscous diets and concluded that digesta viscosity is the most limiting factor for nutrient digestibility in chicks.

Proteins

Dietary protein content is often described as crude proteins (CP), which are estimated as 6.25 fold of feedstuff nitrogen. Proteins can be supplied by vegetable (mostly oilseed meals) or animal sources (Ravindran 2013b). In poultry feed formulation, lysine, methionine and threonine are mostly considered as limiting essential amino acids (AA) (Ravindran 2013c). However, non-essential AA are also physiologically essential and need to be provided in diets, as it is not economical if they are synthesised by the host animal from essential AA rather than being provided by feed CP (NRC 1994). Leeson and Summers (2001) stated that there is minimal loss of heat when dietary proteins are well balanced, but any excess or deficit of proteins in a diet can induce energy wastage in the form of heat. Moquet (2020) reported that an imbalanced AA profile can induce HI_f resulting from energy costs associated with either N excretion or poor N retention. The energy-to-protein ratio is crucial in growing broilers to optimise AA and energy utilisation (Kleyn 2013). The lower energy-to-protein ratio in a diet can be followed by increased FI to increase energy intake, and this can result in lean muscle, whereas excessive energy relative to protein can reduce FI, coupled with the increased energy retained as fat (Leeson *et al.* 1996; Swennen *et al.* 2004; Kleyn 2013).

Feed additives

Supplementing broiler diets with feed additives, such as exogenous enzymes, probiotics and prebiotics, can contribute to gut health and nutrient utilisation efficiency. Probiotics, which are direct-fed microbial additives, are used to promote gut health of the host through balancing intestinal microbiota (Fuller 1989; Prabakaran 2003). This can lead to improved growth rate, FCR, nutrient digestibility and absorption of birds (Jin *et al.* 1997; Panda *et al.* 2003). However, these improvements are rather contradictory, as some studies did not observe benefits of probiotic use (Knap *et al.* 2011; Zhao *et al.* 2013). This is probably due to a number of factors, including dietary fibre content and immune stimulation. Prebiotics, such as xylo-oligosaccharides, arabinoxylo-oligosaccharides and fructo-oligosaccharides, are carbohydrates that are not digested by the host, but are selectively utilised by beneficial gut commensals to grow and produce short-chain fatty acid that act as an energy source for animal host (Gibson and Roberfroid 1995; Lan *et al.* 2005; Morgan *et al.* 2017).

Exogenous enzymes are biological components derived from bacteria, fungi and industrial production. These enzymes are used as feed additives for enhancing the digestion of specific substrates that are not adequately hydrolysed by the hosts' endogenous enzymes. They are able to reduce the effect of ANF, such as NSP, and to improve nutrient digestion and absorption (Kiarie *et al.* 2013), whilst leaving fewer nutrients to the hindgut, where they would be used by microbiomes to proliferate and subsequently disrupt ecosystem balance (Yegani and Korver 2008; Kiarie *et al.* 2013). Exogenous enzymes fall into three main categories: carbohydrases, microbial phytases and proteases (Bedford 2002; Ravindran 2013a). The most dominant enzyme on the global market is phytase, accounting for 60%, followed by carbohydrases at 30% and the remaining enzymes, such as lipases and proteases among others, sharing 10% of the market (Kiarie *et al.* 2013). The use of microbial phytase can hydrolyse phytates which bind not only P, Ca and other trace minerals, but also carbohydrates and protein (Simons *et al.* 1990; Schöner and Hoppe 2002). Protease enzymes are used for protein digestion in grain legumes, such as peas and soybean meal.

Carbohydrases are involved in hydrolysing an array of carbohydrates, and include glucanases and xylanases targeting viscous cereals (barley, wheat, rye, etc.), and other enzymes, such as amylases, that degrade non-viscous grains (sorghum, corn, etc.) (Bedford 2002; Ravindran 2013a). The use of carbohydrases in broiler diets can modulate gut ecology by enhancing the rate of nutrient utilisation by the bird, thereby decreasing the presence of undigested nutrients in the hindgut, which can act as fuel for pathogenic bacteria. These enzymes can also improve gut health by hydrolysing complex polysaccharides into small oligosaccharides, which have prebiotic properties and are utilised by colonic and caecal flora to produce volatile fatty acids, used by birds as an energy source and to control harmful bacteria, such as *Salmonella* (Bedford 2000, 2002; Yang *et al.* 2009).

Factors influencing carbohydrase activities

Improvements associated with feed enzyme use may not always be presented as direct increases in performance, because a number of different factors dictate the response to enzymes. These include (a) quality and quantity of NSP substrates present in a diet, (b) dietary fat content, as fat with poor quality and saturation can lead to poor carbohydrase responses, (c) status of the gut microbial community, with microbial challenged birds responding better to enzymes, (d) technological methods used for feed manufacturing, based on how thermolabile enzymes are, (e) storage time, with NSP adverse effects declining as cereals are stored for a longer period, (f) age of birds, with bird response to enzymes decreasing with age, because the hindgut microbiota depolymerising NSP increases as bird ages, thus adult chickens are less relying on exogenous NSP degrading enzymes (Leeson and Summers 2001; Bedford 2002; Yang *et al.* 2009; Bautil *et al.* 2019). Furthermore, when the quality of cereals is high, based on the environmental origin, variety, drying or processing conditions, the improvements induced by supplemental carbohydrases will be low. In contrast, the use of carbohydrases in poor quality grains will substantially improve energy availability from undigestible substrates (Bedford 2002). Overall, the extent of hydrolysis effect of exogenous enzymes is based on the availability of dietary substrates left undegraded by endogenously secreted enzymes. Therefore, the

knowledge of undigested feed substrates is potentially needed for selecting suitable exogenous enzymes (Vieira *et al.* 2014).

Combination of exogenous enzymes to enhance their activities

It is evidenced that the simultaneous application of different enzymes with multiple activities can enhance dietary nutrient utilisation by birds (Cowieson *et al.* 2006; Ravindran 2013a). Combining multiple enzymes can lead to synergistic, additive or sub-additive effects, thereby providing a greater response, such as growth performance and bone mineralisation, than applying separate enzymatic components (Zyla *et al.* 1999). In addition, nutrients are not individually present in feed ingredients but in an array of structures with complex bonds. Thus, the activity of one enzyme can be facilitated by the other, either by decreasing dietary ANF or by increasing access to its dietary substrates (Ravindran 2013a). Therefore, a complex blend of phytases, proteases and multiple carbohydrases (β-glucanase, xylanase, amylase, etc.) may be applied in poultry diets to achieve viable and consistent bird performance and economic returns (Cowieson and Adeola 2005; Slominski 2011; Abdallh *et al.* 2020). It has been found that the use of enzyme blends (xylanase, amylase, protease and phytase) increased 12.3% weight gain and reduced 10.4% FCR in corn/soybean meal-based diets with marginal nutrients (Cowieson and Adeola 2005).

Dietary energy partitioning and ME system for poultry feed bioassay

Dietary energy partitioning

Dietary energy in poultry feeds is partitioned into three components based on energy lost during the process of feed digestion. These include GE, ME and NE (Kong and Adeola 2014). Gross energy is the total energy content in feed or feedstuffs and does not represent the energy digested and absorbed by birds. Part of it is lost in faeces and the remaining part called 'digestible energy' is absorbed by the bird. Of this energy, other losses occur in the urine, mainly in the form of nitrogenous compounds oxidised or lost as gas. At this point, the energy obtained after correction for these losses is termed ME. As faeces and urine (collectively termed droppings or excreta) are excreted together by birds, ME is preferred in poultry nutrition over digestible energy (Farrell 1974; Leeson and Summers 2001; Carré *et al.* 2013). However, ME is not fully available for the bird, as there is further energy lost as HI_f owing to protein retention (from digestible proteins) and fat retention (from digestible carbohydrates and fats). The ME corrected for HI_f results in NE ultimately used by birds for maintenance (NEm) and production (NEp) (Farrell 1974; Leeson and Summers 2001; MacLeod 2002; Noblet 2015).

Gross energy system in poultry feed bioassay

Gross energy in feed and in excreta are directly evaluated by burning samples within an adiabatic bomb calorimeter. However, apart from being a starting point of dietary energy evaluation, the GE values are meaningless for animal feeding values, as they do not

consider energy losses occurring after FI. For instance, one unit of a fibrous feedstuff can provide the same GE value as one unit of starch (Moehn *et al.* 2005), but their available energy for poultry differs greatly due to very little digestible carbohydrates in fibre. The ME and NE are, therefore, two systems used to evaluate feed energetics in the poultry industry.

Metabolisable energy system in poultry feed bioassay

Details on ME bioassay for poultry are described in a review by Wu *et al.* (2020) and Mateos *et al.* (2019). The ME system was first adopted in the 1960s after a number of studies concluded it to be more accurate and simpler to determine ME compared to NEp previously recommended by Fraps (Fraps 1946; De Groote 1974). Subsequent studies also concluded that NE bioassay is complex and expensive to conduct (NRC 1994; Noblet *et al.* 2010). Therefore, ME has become a generally accepted system of choice to evaluate energy content of feeds or raw materials and to formulate poultry diets in most countries; tables listing ME values of raw materials for poultry are popular to nutritionists (Miller 1974; NRC 1994; MacLeod 2002; Choct 2004).

However, the values provided by the ME system do not fully reflect the energy utilised by birds for production or maintenance. It has been reported that 15%, 22% and 32% of ME from fat, carbohydrate and protein, respectively, are lost as HI_f in growing chicks (Carré *et al.* 2014; Wu *et al.* 2019). De Groote (1974) also indicated that AME values underestimate energy provided by fat by 13% and overestimate proteins by 20% in chicken feeds. Ning *et al.* (2014) also found that the NE system provided the closest estimates of the energy value of feed ingredients in laying hens, whereas with the ME system, the energy value of corn was 12.1% and 7.3% higher than that of wheat bran and distillers dried grains (DDGS), respectively. However, Pirgozliev and Rose (1999) reported that the ME system overestimates the energy value of protein-rich feedstuffs from animal origin but not vegetable protein, such as high-protein vegetable feedstuff, cereals and cereal by-products. Therefore, NE system has been recommended, as it allows energy lost as HI_f to be accounted for (Ning *et al.* 2013).

Net energy system and its bioassay

Net energy intake in growing animals is calculated by adding together the values of fasting heat production (FHP) and retained energy (RE) (Noblet *et al.* 1994; Ning *et al.* 2014). This system is commonly used in pig and ruminant feeding, because it can better predict performance in these animals. This is based on the fact that AME efficiency for NE utilisation or NE/ME ratio varies greatly with dietary nutrient or chemical composition for these animals. For instance, NE/ME value in pigs is about 90% for fat, 80% for starch and 60% for protein and fibre (Noblet *et al.* 2010).

Metabolisable energy efficiency for NE utilisation

Efficiency of ME utilisation for NE – a subject of debate for poultry NE system

Despite the promising potential of NE systems as a tool to predict poultry energy requirements, there is an ongoing debate regarding its value. De Lange and Birkett

(2005) stated that NE systems only marginally improve the accuracy of predicted RE values compared with an ME system. These authors explained that this is because nutrient digestibility varies very little between ingredients used in broiler diets compared with those used in pigs, meaning there is a lack of variation in efficiency to derive NE from ME, i.e., NE/ME. Similarly, van der Klis *et al.* (2010) questioned the significance of NE to broilers, given the lack of a significant difference in NE/ME observed between different poultry diets, despite a large variation in their nutrient composition. This argument was supported by Zuidhof (2019), who claimed that NE systems provide no advantage over ME systems, because NEp is identical to ME used for production (MEp). This author argued that HP (termed ME for maintenance or MEm) is easier to estimate empirically, and can be used to calculate RE, via subtraction. However, this concept seems flawed, as HP measured through slaughter method or using calorimetry systems is used to determine NE rather than ME value. In addition, the ME system is unable to estimate MEm, as only GE of feed and excreta can be produced from ME bioassay. Another review conducted by van der Klis and Jansman (2019) based on three studies, suggested that dietary protein and fat have little effect on HI_f. This consequently implies that NE/ME is also not influenced by dietary CP and EE levels, as NE/AME increases with decreasing HI_f. However, one of these studies, published by Carré *et al.* (2014), was performed in 1996, so it is likely that birds used were quite different to modern broilers, meaning this data might be outdated.

On the other hand, earlier studies showed that HI_f in poultry feeds is affected by dietary composition, such as EE, CP and fibres (Leeson and Summers 2001; MacLeod 2002), but this was overlooked in the reviews by Zuidhof (2019) and van der Klis and Jansman (2019). In addition, a study examining NE responses to dietary compositions in broilers (Wu *et al.* 2019) and layers (Barzegar et al., 2020) showed significant positive effects of dietary fat level and negative effect of dietary protein level on NE/ME. A recent report in layers by Barzegar *et al.* (2020) suggests that birds fed diets containing higher NE with the same AME collected for nitrogen (AMEn) level (with 75.2% NE/AME) performed better compared to their counterpart fed a lower net energy diet (73.5% NE/AME). Moreover, Noblet *et al.* (2010) initially detected no dietary EE nor CP effects on NE/AME, but later observed a significant EE effect on the NE/ME ratio, as discussed in Wu *et al.* (2019).

Does NE/ME not vary across broiler diets?

Mateos *et al.* (2019) reviewed the work of Schiemann (1972), De Groote (1974) and Carré *et al.* (2014), and commented that NE/ME ratio in commercial diets ranges only from 73% to 76%. However, Wu *et al.* (2019) demonstrated that changing dietary CP and EE can vary NE/ME ratio from 71% to 76%, and Cerrate *et al.* (2019) observed a 59.0% to 77.4% variation in NE/ME by changing dietary CP, EE and fibre levels. In addition, data in Table 1 show that NE/AME can provide significant responses depending on the dietary ingredient, such as DDGS, and dietary composition, such as CP and NSP (Barekatain *et al.* 2013; Swick *et al.* 2013b). For instance, Swick *et al.* (2013b) observed that NE/ME values can range from 69% to 76% depending on dietary composition, with the lowest value recorded in a diet containing 16.8% CP and 11.9% sNSP/total NSP (tNSP), and the highest value noted in a diet with 21.9% CP and 5.9% sNSP/tNSP. Moreover, data in Table 2 illustrate that NE/ME

Table 1. Impact of AME efficiency for NE on dietary nutrient composition.

Dietary treatments	AME, MJ/kg DM	NE, MJ/kg DM	NE:AME, %	Reference
Control	12.95[a]	9.07[a]	70.0[a]	(Barekatain *et al.* 2014)
DDGS	12.39[b]	8.42[b]	68.0[b]	
Control + enzymes[a]	13.02[a]	9.42[a]	72.4[a]	
DDGS + enzymes	12.41[b]	8.52[b]	68.5[b]	
Negative control	13.36[c]	9.41[b]	70.4	(Yang *et al.* 2008)
Low mannanoligosaccharide	13.60[b]	9.50[b]	69.9	
High mannanoligosaccharide	13.62[b]	9.57[ab]	70.3	
Positive control (zinc bacitracin)	13.96[a]	9.98[a]	71.5	
16.8% CP, 7.7% EE, 11.9% sNSP/tNSP	12.90[bc]	8.84[bc]	69[d]	(Swick *et al.* 2013b)
20.1% CP, 5.0% EE, 8.5% sNSP/tNSP	12.56[bc]	9.23[b]	73[abc]	
21.1% CP, 7.5% EE, 5.9% sNSP/tNSP	12.32[c]	9.13[b]	74[abc]	
21.9% CP, 6.1% EE, 5.9% sNSP/tNSP	14.32[a]	10.85[a]	76[a]	
22.2% CP, 5.6% EE, 13.2% sNSP/tNSP	12.13[c]	8.89[bc]	73[abc]	
23.1% CP, 9.2% EE, 9.3% sNSP/tNSP	12.50[bc]	9.34[b]	75[ab]	
23.5% CP, 7.4% EE, 2.5% sNSP/tNSP	11.14[d]	8.08[cd]	72[abcd]	
23.6% CP, 8.0% EE, 8.1% sNSP/tNSP	11.29[d]	7.91[d]	70[cd]	
24.0% CP, 6.1% EE, 12.2% sNSP/tNSP	12.40[bc]	8.95[bc]	72[abcd]	
24.2% CP, 6.7% EE, 5.2% sNSP/tNSP	13.18[b]	9.53[b]	72[abcd]	
28.3% CP, 8.2% EE, 9.0% sNSP/tNSP	10.51[d]	7.40[d]	70[bcd]	
30.0% CP, 4.5% EE, 1.6% sNSP/tNSP	11.03[d]	8.07[cd]	73[abc]	

Abbreviations: AME, apparent metabolisable energy; DM, dry matter; NE, net energy; NE:AME, AME efficiency for NE; DDGS, distillers dried grains; CP, crude protein; EE, ether extract; NSP, non-starch polysaccharide; sNSP, soluble NSP; tNSP, total NSP.

[a]Enzymes used were based on carbohydrases plus protease

[a-d]Means within a column for each reference, followed by a different letter are significantly different.

Table 2. Effect of exogenous enzymes on AME, NE and NE/AME.

Dietary treatments	AME, MJ/kg DM	NE, MJ/kg DM	NE:AME, %	Reference
Control	13.87	9.80[b]	70.7	(Wu *et al.* 2015)
Phytase A	14.26	10.35[a]	72.6	
Phytase B	14.23	10.30[a]	72.3	
Phytase C	13.65	9.86[b]	72.3	
12.2% sAX/tAX	14.57[ab]	10.87[bc]	74.7	Musigwa (unpublished)
17.1% sAX/tAX	14.39[abc]	10.67[c]	74.1	
20.3% sAX/tAX	13.96[c]	10.53[c]	75.4	
12.2% sAX/tAX + carbohydrases	14.93[a]	11.34[a]	75.9	
17.1% sAX/tAX + MC	14.31[bc]	10.80[bc]	74.1	
20.3% sAX/tAX + MC	14.93[a]	11.23[ab]	75.1	

Abbreviations: AME, apparent metabolisable energy; MJ, mega joule; DM, dry matter; NE, net energy; NE:AME, efficiency of AME utilisation for NE; AX, arabinoxylan; sAX, soluble AX, tAX, total AX

[a-c]Means within a column for each reference, followed by a different letter are significantly different

responses may not show a significant difference, yet the NE system can still detect a more significant difference in energy values compared to the ME system. This occurs particularly when microbial phytases are supplemented in broiler feeds, or when exogenous carbohydrases are supplemented in diets rich in insoluble NSP (Olukosi *et al.* 2008; Pirgozliev *et al.* 2011; Wu *et al.* 2015). In other cases, values may be similar between AME and NE (Yang *et al.* 2008), but this does not contradict the accuracy of the NE system outputs, as commented by Mateos *et al.* (2019); it is likely a reflection of the specific diets being tested. Additionally, given the high energy densities required by modern broilers, coupled with the cost of energy supply, even a small difference in NE/ME of feed can be economically significant (Pirgozliev and Rose 1999). Furthermore, it is likely that diet formulated with

NE instead of ME may not always provide an advantage, as long as NE values of the ingredients can be predicted using available equations, there will be no harm to include NE values in the formulation to fine-tune the energy values. Essentially, more research is warranted for more accurate assessment of NE values in the poultry ingredients and for large-scale evaluation of values of NE system in the field for its potential advantages.

Respiration and heat production in animals

Respiration quotient

The respiration quotient (RQ) is a term used in a calorimetric system equivalent to the ratio between the volume of CO_2 exhaled to O_2 consumed. This ratio reflects the type of dietary energy substrate oxidised and oxidation level of test diets (Choct 2004; Nienaber *et al.* 2009). The normal values of RQ range from 1 to 0.7, the latter value being equivalent to fat or protein oxidation and the former value to carbohydrate degradation (Noblet *et al.* 1999). As dietary nutrients are not independently catabolised, the composite RQ value should be within the above range (Leeson and Summers 2001). Oxidation of proteins gives an RQ value of 0.81 for mammals and 0.74 for fowls, and mixed fat provides RQ of 0.71 for both mammals and birds (Brody 1945; Walsberg and Hoffman 2005). However, RQ values out of range may occur; the synthesis of fats from carbohydrates may increase RQ values (1.0 to 1.2) (Matarese 1997), whereas the synthesis of carbohydrates from fat or protein or incomplete oxidation can lower the values of RQ. A study done by Nian *et al.* (2011) demonstrated that RQ was 5.7% greater in broilers fed the wheat-based diet supplemented with xylanase than birds fed the non-enzyme diet (with RQ value of 1.087 and 1.025, respectively). This implies that the xylanase-fed birds could have deposited more energy retained as fat than the unsupplemented birds. In addition, the low RQ value may be observed in birds resulting from protein catabolism and formation of uric acid, whilst the RQ value above the optimum can occur in growing animals due to the feeding level exceeding the maintenance requirements (Noblet *et al.* 1999; Leeson and Summers 2001).

Heat production

The animal can produce heat from diet-induced thermogenesis and from metabolic processes, such as production, homoeostasis, maintenance and physical activities (Van Milgen *et al.* 1997). Therefore, heat production (HP) can be divided into three components including HI_f related to the thermic effect of feeding (about 31% of total HP), FHP (around 52%) and HP associated with physical activities (17%) (van Milgen *et al.* 2001; Lopez and Leeson 2008). The HP associated with physical activities is beyond the scope of the present review.

Diet-related heat is produced when energy substrates undergo oxidation leading to CO_2 and H_2O production (Farrell 1974); thus oxygen and carbon dioxide are used to determine animal HP (Cueva 2015), according to the following chemical equation proposed by Leeson and Summers (2001).

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + heat\ (equivalent\ to\ 673\ kcal\ per\ mole) \quad (1)$$

However, there is no complete combustion of proteins, as N can be released as uric acid (Farrell 1974). But Brody (1945) stated that the correction of proteins for N is not needed

when HP is calculated using the measured values of O_2 consumed; thus different studies have determined HP without correcting for N retention (Spratt *et al.* 1990; Ning *et al.* 2013, 2014). Therefore, the basic principle of the indirect calorimeter is that HP in birds can be determined from the respiratory gaseous exchange without N correction (Spratt *et al.* 1990), using a modified equation proposed by Brouwer (1965):

$$HP = 3.866\ O_2 + 1.200\ CO_2 \quad (2)$$

where HP is expressed in kcal kg^{-1}, O_2 and CO_2 represent volumes in L of gas consumed and produced, respectively.

Equilibrium fasting heat production

Fasting HP, or basal metabolism, expresses the rate of HP of an unfed animal resulting from body lipid or protein catabolism after carbohydrate stock is exhausted (Emmans 1994). It is an indicator of the basal metabolic rate of animals, and it is expressed in NEm (Noblet *et al.* 2015). Its estimate can be obtained from literature or by fasting birds (Noblet *et al.* 2010), but the standard fasting period is difficult to determine (Ning *et al.* 2014). Previously, FHP estimates in meat-type chickens were proportionate to the concept of metabolic BW of $BW^{0.75}$ that is conventionally used in all mature animals (Sakomura 2004). However, a 0.70 exponent value was suggested to be used in growing modern broilers rather than 0.75, as this may bias FHP values in those chickens (Ferrell and Oltjen 2008; Noblet *et al.* 2015). Therefore, FHP for broiler chickens with 0.5 to 3.0 kg BW was suggested to be proportional to $BW^{0.70}$ with FHP at zero activity accounting for 420 to 450 kJ kg^{-1} $BW^{0.70}$ over 24 h and under thermoneutral conditions (Noblet *et al.* 2010; Noblet 2015).

Heat increment of feeding

Heat increment of feeding is mainly attributed to the post-absorptive energy cost of feeding. It represents animal heat loss in excess to the FHP (Swick *et al.* 2013b), and can be obtained by subtracting FHP from HP, which is related to ME intake in fed animals (Noblet 2015). It varies with different factors, such as FI, with HI_f rising with increased FI and ambient temperature (Zhou and Yamamoto 1997; Koh and Macleod 1999), and dietary chemical composition in which proteins promote more HI_f than carbohydrates and fats (Shannon and Brown 1969; Noblet 2006). Heat loss due to protein retention is by far the largest with about 8.72 kcal/g, followed by lipid retention (from digestible carbohydrates), with approximately 3.92 kcal/g, and lastly fat retention (from digestible fats) amounting to about 1.05 kcal/g (Leeson and Summers 2001).

Bioassay for NE determination

Since the development of the equation NE = ME – HI_f by Armsby and Fries (1915), NE evaluation methods have been developed based on this equation. As described in detail below, these include HP estimation using data obtained from comparative slaughter analysis, NE estimation using prediction equations based on nutrient components or ME content of feed ingredients, as well as determining HP using the calorimetric method (Pirgozliev and Rose 1999; Sakomura 2004; Ramirez 2014).

Estimation of NE values using slaughter techniques

The comparative slaughter method partitions ME consumed by birds into RE and HP (where HP combines HI_f and FHP) based on the equation ME = RE + HP (Olukosi *et al.* 2008; Nienaber *et al.* 2009). However, the slaughter method measures RE and calculates HP as the difference between ME and RE, whereas the calorimetric system measures HP and obtains RE by subtracting HP from ME (Nienaber *et al.* 2009). The RE estimates in the comparative slaughter method are obtained by determining the energy content in the carcase of representative test animals before and after running a feeding trial. The difference between the final and initial average values per animal gives the RE (Farrell 1974; Sakomura 2004; Nienaber *et al.* 2009). However, Barekatain *et al.* (2014) demonstrated that RE values obtained using the slaughter method were overestimated by more than 20% in all test diets compared with RE measured in the indirect calorimeter. Similarly, Liu *et al.* (2016) showed 4.2% numerical increased in RE obtained using comparative slaughter method compared with RE from indirect calorimetry. The comparative slaughter method was also questioned by MacLeod (2002) for lacking precision, as the ranges of NEp values of the same feedstuff may amount to an error of up to 20%.

Prediction equations for NE values

Net energy bioassay can be complex and expensive to undertake. Therefore, the use of prediction equations derived from reliable NE bioassays and chemical characteristics of feedstuffs can potentially be a good alternative (Noblet *et al.* 2010). NE prediction equations are widely used in the pig industry; HI_f values measured on 61 pig diets by Noblet *et al.* (1994) were used to develop prediction equations for NE calculations. These equations, combined with feed consumption data and digestible CP, carbohydrates and fat values, are extensively used in the pig industry to calculate NE values of feedstuffs for pigs (Moehn *et al.* 2005; Choct 2012). The values obtained from these calculations are assumed to be closer to the true energy values of feeds, and accurately match with measured NE values and energy requirements of animal (Noblet *et al.* 1994; Noblet 2006, 2007).

In poultry, four equations were suggested to predict NE values from the chemical composition of poultry feeds but their application for poultry energetics are limited by their reliability (Noblet 2015). The first two equations are based on digestibility coefficients of nutrients, whereas the last two equations employ ME as a starting point. These include, respectively,

$$NE = 13.4\ dCP + 35.3\ dEE + 13.0\ dNFE \tag{3}$$

(De Groote 1974)

$$NE = 10.80\ dCP + 33.5\ dEE + 13.4\ (dNFE + dCF) \tag{4}$$

(Hoffmann and Schiemann 1980)

$$NE = ME + 4.0\ dEE - 3.80\ FOM - 4.672\ dCP \tag{5}$$

$$NE = 1.17\ ME - 4.2\ CP - 2.44 \tag{6}$$

(Emmans 1994)

where NE, net energy (MJ/kg); CP, crude protein; dCP, digestible CP; dEE, digestible ether extract; dNFE, digestible nitrogen-free extract; dCF, digestible crude fibre (all nutrients are expressed as kg/kg); FOM, faecal organic matter (Pirgozliev and Rose 1999).

Pirgozliev and Rose (1999) used these four prediction equations and suggested that ME collected for nitrogen (MEn) was linearly associated with NEp, but there was an overestimation of NEp by MEn for feedstuffs with high protein content. Noblet (2015) also stated that none of the above predictive equations can accurately predict NE values for poultry, with the biggest discrepancy noted in equations suggested by Emmans (1994).

Carré *et al.* (2014) proposed other prediction equations, in which NE values could be predicted with feed MEn, with

$$NE = 0.80\,MEn \tag{7}$$

or with equations combining MEn values and the ratio CP:MEn but not with ME system. This implies that NE is not related to dietary nutrients or diet characteristics. Noblet (2015) questioned these equations, as the result interpretation might have been biased.

Recently, Wu *et al.* (2019) found that NE is positively correlated to EE and ME or MEn and negatively correlated with dietary CP. The NE prediction was therefore developed by the study, with

$$NE = 0.781\,ME - 0.028\,CP + 0.029\,EE \tag{8}$$

$$NE = 0.808\,MEn - 0.017\,CP + 0.031\,EE \tag{9}$$

However, the application of these equations in feed formulation is yet to be validated.

Calorimetric hp measurement

The heat produced by birds owing to the thermic effect of feeding can be measured using direct or indirect calorimetry, based on respiratory gas exchange. Both methods were developed by Lavoisier in 1777 (Brody 1945). Direct calorimeter quantifies the heat lost in the environment. This system can provide rapid responses and accounts for fluctuations in heat loss caused by different bird activities. However, it is unable to provide an indication of the proportion of oxidised dietary nutrients (Farrell 1974). The indirect calorimetric method determines HP based on quantitative measurement of gaseous exchange of animals in respiration chambers (Feddes and McDermott 1992; Ramirez 2014). This method is mostly used because it is easy to operate and it can also provide accurate values of ME, HP and NE (Feddes and McDermott 1992; Swick *et al.* 2013a). Indirect calorimeters are subdivided into open – and closed-circuit calorimeters.

Open-circuit system

The open-air circuit calorimetric type is a system in which outside air can constantly flow through the chamber (Brody 1945). The amounts of consumed and produced gases is quantified using values obtained by measuring the composition and flow rate of outlet and inlet air (McLean 1972; Ramirez 2014). The concentration of respiratory gas exchange can also be measured using gas sensors (Farrell 1974). This system allows for HP calculation based on the measured gas exchange (O_2 consumed and CO_2 produced) without hampering animal behaviour, and gas analysers can provide results in a short

period of time. However, variations in RQ and HP values may occur because of a large volume of the respiratory chamber, short measurement interval, as well as limited sensitivity for gas analysers (McLean and Watts 1976; Van Milgen *et al.* 1997; Kuhla *et al.* 2015). In addition, HP measurement using the open system requires a higher level of accuracy, as 1% error occurring during system calibration may generate a minimum of 21% error in the calculation of consumed O_2 (Choct 2012). Therefore, the open-circuit system may pose risk in accuracy of the measurements.

Closed-circuit system

Chambers in the closed-circuit calorimetric system differ from open-air calorimetric chambers in that, as the name suggests, they are hermetically closed to avoid contact with fresh air from the ambient environment. Animals housed in this system continue to breathe the air circulated in the chamber with CO_2 removed by chemical reaction and O_2 replenished by a controlled oxygen supply (Brody 1945; Farrell 1974; Choct 2012). Historically, the design of the calorimetric system as a method for determining animal HP was founded by Lavoisier in 1777 (Brody 1945). More than seven decades later (in 1850) Regnault and Reiset adopted this system and developed the first closed-circuit metabolism apparatus for small animals. Since then, a number of modifications of this system have been performed to improve its utilisation for respiratory gas exchange measurement (Brody 1945; Farrell 1974). In 1972, Farrell described a sealed chamber constructed of Perspex, modified from that described by Waring and Brown (1965), which provided HP measurement over a 24-h period (Farrell 1972). A modification of this metabolism apparatus was developed at the University of New England with the ability to generate HP results over a 3-d period. More details of the modifications and mode of operation are detailed in Swick *et al.* (2013b) and Wu *et al.* (2019). The main disadvantages associated with the closed system is that the temperature within the system needs to be stable during the trial to avoid pressure changes (Farrell 1974). However, this system was reported to be a reliable method for accurately measuring poultry energetics (Choct 2012).

Challenges associated with NE and the way forward

The ME system is still preferred over NE system because of the difficulties associated with obtaining NE results, coupled with variations of its values because of experimental conditions (Pirgozliev and Rose 1999; Latshaw and Moritz 2009). In fact, values for dietary NE are influenced by many factors. These include the level of FI, type of production (carcase content in terms of fats or proteins, or egg output), dietary chemical composition and ambient temperature (Farrell 1974; Pirgozliev and Rose 1999; Sarmiento-Franco *et al.* 2000). Dietary heat increment, which is used to determine NE, can vary with a wide range of ME intake (Noblet *et al.* 2010; Choct 2012). There is a linear decrease in energy intake over an increasing range of ambient temperatures, which can have an effect on energy requirements and expenditure (MacLeod 1992). The NEm can also vary in response to environmental factors, particularly ambient temperature. Birds in ambient temperature below a critical point increase HP for maintaining homeothermy (Sakomura 2004). However, these variation factors are also common in the ME system.

Therefore, it is imperative to evaluate dietary NE values under conditions that minimise calculation biases. The measurements should be done on animals of identical physiological conditions, such as a similar BW range, same sex, age, FI and similar genetic background. Fortunately, some of these variation factors, such as FI and genetics, may not be a problem during NE measurement using modern broilers (Swick *et al.* 2013b). The current broiler strains can have identical *ad libitum* FI with positive N balance from d 20 to 30, which makes them suitable for NE evaluation (Choct 2012). In addition, birds should be fed an identical and balanced diet of similar levels of energy for achieving their growth or production potential. They should also be reared under their thermoneutral zone within an environment where the temperature is well controlled. Under such conditions, although errors resulting from FHP estimates may affect NE absolute values, the ranking of feeds or feedstuffs according to their energy content will remain unaffected (Emmans 1994; Noblet *et al.* 2010; Choct 2012; Noblet 2015).

Conclusion

Exogenous enzymes, such as carbohydrases can be used to attenuate dietary ANF effect, facilitate access of other enzymes to dietary substrates and improve intestinal health and functioning, to maximise nutrient digestion and absorption. It is well established that carbohydrases improve feed energy utilisation in poultry, but accurate bioassay method is needed to be able to measure this effect. Although the ME system is currently a default method used for poultry energetic bioassay, its values are not fully available for birds to meet their energy requirements for maintenance and production. The NE system was, therefore, recommended as a sensitive and precise method to predict bird energetics, as it allows correction of energy lost as HI_f. The energy values provided by this system can be used in feed formulation and promote optimal bird performance in economical and effective way. An accurate and reliable method to measure NE is indirect calorimetry system, especially the closed-circuit calorimeter. Although this method is costly and labour intensive, it may provide a more accurate assessment of energy efficiency produced by supplementing feed additives in broiler diets. Further study on the cost-effectiveness of using ME or NE system to predict poultry energetics is needed.

Disclosure statement

The authors declare the absence of conflict of interest.

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