Nutrition-reproduction interaction in poultry

[1]Jiwuba, P. C., [1]Ugwu, D. O., [1]Azodo, N. L. and [2]Ilo, S. U

[1]*Department of Animal Production Technology, Federal College of Agriculture, P.M.B.7008, Ishiagu, Ebonyi State, Nigeria.*

[2]*Department of Animal Science, University of Nigeria, Nsukka, Enugu State, Nigeria.*

Corresponding author: jiwubapc@gmail.com

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Abstract

Recent research regarding nutrition-reproduction interaction in poultry is very limited. Nutrition is science that interprets the interaction of nutrients and other substances in feed in relation to maintenance, growth, reproduction, health and disease of an animal. The performance of poultry therefore is largely dependent on their reproductive performance, and there are interactions between reproductive performance and nutrient status. For optimal reproductive performance in poultry, all the nutrients which include protein, energy, minerals, fat and oil and vitamins must be met and fed to the birds using the appropriate feeding method. Previous studies have shown the effects of nutrition on male and female fertility, spermatogenesis, sperm motility and concentration, egg production, shell quality, hatchability, internal egg quality and progeny performances etc. Therefore this paper was an attempt to review the interaction between nutrition and poultry reproduction. The work also reviewed the positive and negative effects of feeding methods, over-feeding and under-feeding of nutrients on poultry reproduction. Furthermore, this review could also serve as a ready source of literature for researchers in animal nutrition and nutritional reproductive physiology.

Key words: poultry, male fertility, spermatogenesis, progeny, nutrition and reproduction.

Introduction

Reproduction is an important physiological function in the body of farm animals as well as poultry and has precedence in nutrient partitioning. Appropriate nutrient intake, associated with desirable concentrations of blood metabolites, especially glucose, is needed for a normal reproductive cyclicity. The interaction between reproduction and nutrition becomes critical during fertilization and egg formation in hen and spermatogenesis in cockerels when most of the nutrients are utilized for supporting reproductive activities in poultry (Lutwak-Mann, 1958). Good nutrition increases productivity and reproductive efficiency of animals. Genetic, biological, environmental and nutritional factors tend to affect the reproductive performance of animals. The relationship between nutrition and reproduction is a topic of increasing importance and concern among poultry farmers, feed manufacturers, nutritionists and physiologists. Maximization of reproductive performance (fertility in both male and female, egg number, egg weight and egg mass, survival of the progenies) and henceforth profits depends majorly on the genetic component and nutrition of the birds (Arscott and Parker, 1967; Pana et al., 2000).

Nutrition in poultry involves providing a balance of nutrients that best meets the animals' need for maintenance, reproduction and any other productive function. Hence, poultry require the presence of at least 38 dietary nutrients in appropriate concentrations and balance (Klasing,

1995) to enhance its reproductive and productive performances. Earlier findings have reported the positive influences of minerals, (Ogbuewu et al., 2015), protein (Alagawany et al., 2016), amino acids (Todd, 2008), energy (Bramwell et al., 1996) and vitamins (Yaun et al., 2014) in poultry reproduction. Nutrition was identified as an essential factor for male and female reproduction in poultry. Although nutrition in its totality has a broad range of functions in the body, it is primarily crucial for fertility in poultry. Generally, it has been shown that poor nutrition causes abnormal spermatogenesis in males and poor fertility and hatchability in females. Nutrition-reproduction interaction is crucial for healthy offspring and species survival of all animals (Hocking, 1987), especially poultry. In recent year, there is a paucity of review works on nutrition-reproduction interaction in poultry, hence lies the objective of this paper.

Male fertility and spermatogenesis in poultry

Sperm concentration and maturity are vital for reproductive potential of cockerels. In poultry, male fertility is predominantly related to semen and sperm qualities, which includes the volume of semen per ejaculate, sperm viability, sperm motility, concentration of sperms in the semen and the sperm fertilizing capacity. The sperm qualities can be chiefly influenced by dietary manipulations and other factors which can be genetic or environmental. Feeds and feeding methods have been implicated as one of the factors known to affect spermatogenesis and semen quality among the male birds. Severe feed restrictions and underfeeding have detrimental effect on male fertility and delays sexual maturity in female and male broiler breeders. Boone and Hughes (1969) demonstrated that starvation of cocks for a period of six days adversely affected semen production, but was reversed after fourteen days of resumption to normal feeding regime. In another experiment by Pana et al. (2000) they reported that Cornish broiler cocks whose daily feed consumption was limited to 130 g/day produced ejaculates whose concentration did not differ from their full-fed counterparts. Ezekwe et al. (2003) reported decreased semen volume, motility and concentration by severe underfeeding while moderate underfeeding did not influence semen production and semen quality. The effects of underfeeding on semen quality traits appeared to be more severe on the physical rather than biochemical characteristics, which implies that the spermatogenic functions of the testes are more responsive to underfeeding than the secretory activities of the reproductive tract, the authors conclude. Similarly, Kabir et al. (2007) in their experiment to determine the effects of underfeeding on semen quality of Rhode Island cocks found that cocks that were severely underfed had significantly longer time to ejaculate, in addition to ejaculation failure. Ejaculate volume, progressive sperm motility and sperm concentration were significantly decreased in the severely underfed cocks than in the moderately underfed cocks. Fertility may be negatively affected by male broiler breeder flocks fed *ad libitum* because they have a reduced success rate in natural mating (McGovern, 2002).

The improvement of poultry production depends partly on synergy between crude protein and amino acids. Dietary crude protein (CP) requirements are somewhat of a contradiction as the requirement is based on the amino acids content of the protein. Crude protein and amino acids are one of major factor in the effectiveness of reproductive function in poultry. They may affect the efficiency of related hormone production and the growth of reproductive organs. Dietary crude protein has been reported (Hocking and Bernard, 1997 a) to affect semen production of broiler breeder (BB) males. In poultry, crude protein and amino acids serve not only as nutrients but can also be used to manipulate the reproductive performance of birds. Optimal crude protein is shown to be important in maintaining high productive and reproductive performances of male birds. Cerolini et al. (1995) reported that the optimal daily feed supply for the best reproductive performance was 15.6 g of CP for Ross breeder males. However, Wilson et al. (1987) observed that level of dietary protein intake (12 or

14%) had no adverse effects on semen volume or fertilizing capacity in broiler breeder males. Zhang et al. (1999) reported a significant lower level of fertility in male BB when CP requirements were not met. Crude protein and their effects on fertility of both male and female BB, has been researched with conflicting results. Wilson et al. (1987 a) reported no significant effect of CP intake on factors determining semen quality and fertility (semen volume, concentration, number of fertile eggs at candling at 18 days of incubation and activity of sperm). Hocking and Bernard (1997 a) however reported the effects of CP (110 or 160 g CP/kg) on overall fertility of BB males of a particular strain. They observed lower fertility rate among the group of strains receiving 160 g CP/kg, which they attributed to heavier breast muscling, less frequent copulations and a high number of incomplete matings, possibly due to unsuccessful cloacal contact. Hocking and Bernard (1997 b) in a similar experiment also showed that the sperm concentration was lower in males fed a diet containing 16% compared to 12% CP. They also observed that males on the high protein diet had a smaller average testes size and spermatogenesis in the testes was absent in a large proportion of the males. In another experiment, Fontana et al. (1990) reported that when naturally-mated commercial BB males and females were fed separately, with males on a 12% CP diet and females on a 14% CP diet, egg fertility was significantly higher when compared to the control diet, where both males and females were fed 14% CP. Semen concentration was the same in birds fed separately and birds fed from the same feeder, thus the increased egg fertility was attributed to the size and weight of the males, allowing them to copulate more successfully and not to semen concentration. Borges et al. (2006 a) in their experiment with differing CP (12.0, 14.2, 16.4, 18.6 and 20.8 g CP/bird/day) fed to BB males between 27 and 61 weeks observed that fertility (vigour, mobility, quality and quantity of semen) responded to dietary CP, where birds on extreme deficient or excess CP diets had decreased reproductive efficiency. Wilson et al. (1987 a) found no undesirable effects on semen quality, testes weight or sexual maturity, of BB males on a restricted isocaloric diet (containing 12 to 14% CP; 15.6 and 18.2 g CP/day respectively) from 20–52 weeks of age. A ration containing 16% CP (20.8 g CP/day) was used as a control feed. It was found that males receiving the 15.6 g CP/day diet produced higher concentrations of semen than those receiving 18.2 or 20.8 g CP/day. Zhang et al. (1999) showed that sperm concentration, volume, number of spermatozoa per ejaculate and testes weight tested at 50 weeks of age were unaffected by CP levels (9, 12, and 15%) in the diet (isocaloric intake) before sexual maturity.

Energy requirements of cockerels are more complex than those of CP requirements in that energy is required for maintenance as well as for reproduction in the breeder. Attia et al. (1995) reported that BB males fed low metabolizable energy (ME) diets were unable to maintain body weight (BW) with little or no excess ME for body weight (BW) gain. However, concern arose that the sperm maturation process was altered, where motility was affected, resulting in fewer spermatozoa reaching the sperm storage tubules (SST's). Brown and McCartney (1983) found that BW gain and mating performance was not satisfactory in males receiving restricted diets and stated that 1.92 MJ ME/bird/day was necessary to maintain BW and optimal breeding performance. Borges et al. (2006 b) in an experiment, fed diets differing in ME (1.21, 1.30, 1.38, 1.47 and 1.55 MJ ME/bird/day) to BB males and observed that fertility (vigour, mobility, quality and quantity of semen) was highest at 1.47 MJ ME/bird/day suggesting that the intake of ME is sufficient to meet the energy requirements of the birds during breeding. Sexton et al. (1989) reported that increasing the daily metabolizable energy of the diet increased fertility.

The importance of minerals in production efficiency, reproductive performance and their interactions between reproductive performances in poultry cannot be over emphasized. Minerals are inorganic nutrients, usually required in small amounts and play a significant role in metabolic processes and diverse functions. Several mineral elements have been shown to be essential for testicular development and spermatogenesis. Zinc is crucial in male reproductive system of poultry; one of them is its participation of ribonuclease activity, which is highly active during the mitosis of spermatogonia and meiosis of spermatocytes. Zinc deficiency results to gonadal dysfunction, decrease in testicular weight, and causes shrinkage of seminiferous tubules (Underwood, 1977), hence leading to lower fertility. Dietary zinc deficiency (less than 5 ppm) has been reported to impair reproduction in males and females (Underwood and Somers, 1969). However, high zinc concentrations have been reported to depress oxygen uptake in the sperm cell and albumin induced acrosome reaction (Foresta et al., 1990). Hazim and Mahmood (2012) in their experiment observed that adding supplementary zinc to the diet of roosters resulted in significant increase in absolute and relative weights of testes, seminiferous tubules diameter, germinal cells thickness, volume density and relative weight of spermatogonia, spermatocytes, spermatids, sperms, total spermatogenic cells, sertoli cells, total seminiferous tubules components, leydig cells, total interstitial tissue components and the ratio of total seminiferous tubules components to total interstitial tissue components and significant decrease in seminiferous tubules lumen diameter, vacuoles, lumen and interstitial spaces in comparison to control group. Sodium and potassium function to maintain and regulate osmolarity and action of spermatozoa, sperm motility and the acrosome reaction. Tumenbaevish et al. (2012) revealed that the S-containing compounds increased mobility and survivability of the absolute rate of cryopreserved spermatozoa. Magnesium is needed for hyperactivation, capacitation and acrosome reaction of spermatozoa (Semczuk and Kurpisz, 2006). The level of magnesium in the seminal plasma increases with sperm concentration but shows no significant relationship with sperm motility (Wong et al., 2001). However, Marzec-Wróblewska et al. (2012) reported a positive effect of Mg on sperm motility, morphology and spermatozoa concentration. Phosphorus plays a vital metabolic role and has more physiological functions than any other mineral (Marzec-Wróblewska et al., 2012). Phosphorus is generally needed for the maintenance of glycolysis and motility of sperm cells (Flerchinger and Erb, 1955). Ogbuewu et al. (2015) stated that calcium (Ca) is the most abundant mineral in the body and 99% is found in the skeleton. Nevertheless, calcium is required in many physiological processes as a regulator in all living cells, including sperm cells. Spermatozoa are highly differentiated cells with the plasma membrane being the major cellular component, involved in diverse and complex functioning of the sperm cell to achieve fertilization. Many of these functional processes are made effective by the transport of ions across the plasma membrane through ion channels, with various types of Ca channels. Selenium plays important roles in avian reproduction by maintaining antioxidant defences of the spermatozoa and embryonic tissues. Deficiency of selenium (Se) deficiency has been associated to reproductive problems in poultry. Edens (2002) reported that, cockerels fed basal diet containing 0.28 ppm Se without dietary supplementation of Se had 57.9% normal spermatozoa with two major abnormalities as bent midpiece (18.7%) and corkscrew head (15.4%). Perhaps, when the diet was supplemented with an additional 0.2 ppm Se in the form of selenite, the percentage of normal spermatozoa increased to 89.4% and abnormalities in the form of bent midpiece and corkscrew head were decreased down to 6.2 and 1.8% respectively. However, when organic Se was included in the cockerel's diet in the same amount, semen quality was further improved and those abnormalities decreased down to 0.7 and 0.2% and the percentage of normal spermatozoa increased up to 98.7%. In all instances, selenium added to the basic diet restored both growth and reproductive capability (Underwood, 1977). Copper deficiency impairs reproductive efficiency in animals. Abnormal levels of copper may affect spermatocytogenesis with regard to the sperm production, maturation and fertilizing capacity (Wong et al., 2001; Yunsang and Wanxi, 2011). Copper rich diets enhance sperm motility (Yunsang and Wanxi, 2011) and it may also act on the pituitary receptors which control the release of luteinizing hormones (LH). Generally poultry semen contains some amounts of iron (Fe), as its physiological level is required for a normal spermatozoa production and functions. The Fe contained in the seminal plasma is significant for the maintenance of sperm motility and viability; thus helps the spermatozoa to maintain their functions. According to Knazicka et al. (2012) lower concentrations of iron (II) sulphate (≤ 250 μmol/dm^3) sustained the spermatozoa motility and energy metabolism, which are key factors supporting the spermatozoa function. High Fe concentration, however can negatively affect the morphology and DNA integrity of spermatozoa (Perrera et al., 2002). Low intake of dietary phosphorus (P) has been associated with decreased fertility rate and delayed sexual maturity (Cromwell, 1997). The presence of Mg is necessary for capacitation, hyperactivation and acrosome reaction of spermatozoa (Semczuk and Kurpisz, 2006) in poultry. It was reported by Wong et al. (2001) that the Mg level in the seminal plasma increases with sperm concentration but has no significant relationship with sperm motility. However, positive effects of Mg on the motility, morphology and concentration of spermatozoa have also been reported by Marzec-Wróblewska et al. (2012).

There are thirteen vitamins named alphabetically from vitamin A to vitamin K. Vitamin E is a generic term for a group of tocopherols and tocotrienols that have some amount of vitamin activity (Rengaraj and Hong, 2015) which function chiefly in protecting cells from oxidative damage. Vitamin E deficiency results to a disease condition known as encephalomalacia, which occurs in birds fed diets high in polyunsaturated fatty acids of the linoleic acids with a low supplementation of vitamin E. In an experiment by Arscott and Parker (1967) fed male chickens with a diet high in linoleic acid (7.3%) and low in vitamin E (4.3 mg/kg diet) from hatch to 28 weeks of age, and high in both linoleic acid (7.3%) and vitamin E (166.3 mg/kg diet) from 28 to 40 weeks. As a result, the adverse effects on fertility and semen concentration were restored in chickens fed on the diet high in vitamin E. However, this explains that the adverse effects of high dietary linoleic acid on male fertility are not permanent, thus can be remedied by vitamin E supplementation. A compound, dilauryl succinate, similar to linoleic acid, induces encephalomalacia in chickens (Rengaraj and Hong, 2015). In a study by Yoshida and Hoshii (1976), fertility of roosters fed diet containing 12% dilauryl succinate for 16 weeks was significantly low, but when the roosters were fed a diet containing 12% dilauryl succinate and 200 mg/kg *dl*-α-tocopheryl acetate, the sperm fertilizing capacity was significantly high. Avian sperms are rich in polyunsaturated fatty acid which provide membrane flexibility and enhances sperm motility (Rengaraj and Hong, 2015). However, due to the high levels of polyunsaturated fatty acids, avian sperms are very sensitive to reactive oxygen species, causing male infertility (Surai et al., 2000). Hence, an increased antioxidant status in semen or spermatozoa is a prerequisite for the prevention of male infertility. In a study by Surai et al. (1997) six-month-old male Rhode Island Red chickens were fed with a diet containing 0, 20, 200, or 1000 mg/kg α-tocopheryl acetate for eight weeks. During the final two weeks, they observed that the concentration of vitamin E in semen and sperms had doubled, and the susceptibility of the semen to lipid peroxidation was decreased, particular in birds fed with 200 mg/kg of vitamin E. Another vitamin of great influence on reproductive performance in male breeder birds is vitamin A and vitamin C. Vitamin A is a fat-soluble vitamin and involved in a number of physiological processes including differentiation and maintenance of epithelial cells, structural development, reproduction and vision. Vitamin A deficiency is implicated for infertility and impaired reproduction in poultry (Clagett-Dame and DeLuca, 2002). Vitamin C plays very important role in improving and maintaining health and fertility status of breeder males (Iftikhar et al., 2015). The beneficial effects of vitamin C on heat stressed male BB birds have been studied. McDaniel et al. (1996) observed poor semen quality from BB males heat stressed at 27 °C for 12 hours where the number of sperm penetrating the egg was reduced by 48% as compared to results obtained when hens were inseminated with semen from males maintained at 21 °C. In another experiment, McDaniel et al. (1995) found that fertility declines by 42% when the male broiler breeder was heat stressed at 32 °C. Vitamin C have been reported to improve performance associated with the suppressed stress responses indicated by lowering of the plasma corticosterone level and adrenocorticotropic hormone (Lin et al., 2006). Many reports documented the beneficial effect (Ahmadu et al., 2016) of supplementing the diet with vitamin C for stressed mature poultry males. Such benefits are improved spermatozoa production and fertility in male poultry birds. However, a contradictory report was given by McDaniel et al. (2004) stating that dietary ascorbic acid did not improve the reproductive performance of broiler breeder males under normal or heat stress conditions.

Pullets and hens

Feeding method has a strong influence on the reproductive performance of pullets and hens. Feed restriction is an essential management technique employed in BB hens to maintain the body weight of the animals to improve performance. Feed restriction is very important to limit the formation of excessive numbers of ovarian yellow follicles arranged in multiple hierarchies (Leksrisompong, 2010). Low egg production during early lay in broiler breeder hens fed *ad libitum* is associated with multiple ovulations caused by the presence of at least two hierarchies of ovarian yellow follicles. Restricting the quantity of feed during early lay period limits, the maturation of yellow follicles and in turn reduces the incidence of double ovulations as well as internal laying, these impacts lead to overall increase in the number of eggs laid (Hocking et al., 1987). Madnurkar et al. (2014) in their experiment to determine the effect of dietary phytoestrogens, feed restriction and their interaction on reproductive status of broiler pullets, observed that feed restriction delayed the age of sexual maturity but helped in the reduction of ovary weight, number of yellow follicle, number of atretic yellow follicle, incidence of double hierarchy, and internal ovulation. Similarly, Tesfaye et al. (2009) observed that feed restriction at 35 to 84 days of age resulted in higher egg weight, heavier uterus weight and longer length in absolute term than the control; thus an indication of good consistency for the subsequent egg production. Feed restriction during rearing and breeding to limit body weight had resulted to reduced mortality, enhanced feed efficiency, egg fertility, shell quality, and egg production (Oosterhoff, 1998), delayed sexual maturity, leading to higher egg weight.

Optimum reproductive performance of hens can be achieved by controlling body weights of birds throughout the entire production cycle by providing the required nutrients in the right amount and form. Protein is one of the most important nutrients in poultry nutrition (Alagawany et al., 2016) especially for it role in reproductive and productive performance in birds. Shim et al. (2013) in an experiment to determine the effects of balanced dietary protein levels on egg production and egg quality parameters of individual commercial layers, observed that feeding layers with low levels of crude protein resulted in lower hen day egg production (90.33% peak production) and more feed per kilogram of eggs compared with the high or medium levels (HDEP; 93.23 and 95.68% peak production, monthly basis). Egg weight responded in a linear way to balanced dietary protein level (58.78, 55.94, and 52.73 g for high, medium, and low CP, respectively). Egg production and egg weight were however, significantly increased with the levels of 16 and 18% CP compared to the low level 14.3% (McDonald, 1979). Harms and Russell. (1996) also noted that birds that consumed 13.8 g of CP per day had significantly reduced egg weight compared with birds that consumed 14.6 or 16.3 g of CP through 44–63 weeks-old. Calderon and Jensen (1990) reported significant increase in egg number and egg weight with increased dietary protein level from 13–19% in diets of layers. This agrees with the findings of Bunchasak et al. (2005) who observed that birds on 14% CP diet had poor egg production, egg weight and egg mass than those on 16 or 18% CP treatments through peak period for layers**.** However**,** De Mendonca and Lima (1999) reported no effect of dietary CP level on egg albumen, but during the second production stage, eggshell quality of layers fed 14.5% CP was improved than those fed diets with 16.5% CP. These was corroborated by Novak et al. (2006) who reported that the percentages of dry and wet albumen, albumen solids as well as percentages of yolk and albumen protein were decreased with feeding low-CP diets. However, protein intake is not seen to be a factor in low fertility (Lopez and Leeson, 1994) as fertility of BB hens is basically affected by BB male performance. However, in an experiment by Pearson and Herron (1982) they reported low hatchability between 26 and 36 weeks on birds fed high protein (27 g/bird/day) and low energy (363 kcal ME/bird/day) as a result of an increase in the percentage of dead embryos in the second week of incubation and an increase in the number of pipped eggs at the end of incubation. They suggested that embryo mortality at this age is likely to be attributed to nutritional deficiency in the egg and that hatchability could be depressed when daily allowances of protein and energy exceeded 15 g: 239 kcal/bird.

Energy is crucial in breeder hen performance for maintenance and egg production purposes. Severe decline in egg production of BB hens following energy restriction to 368 kcal/bird/day was reported by Blair et al. (1976), and energy intake above 370 kcal/bird/day was reported to be adequate for both maintenance and egg production (Balnnve et al., 1978). Fertility may show a decreasing trend with increasing energy intake (Hocking, 1987). The hen becomes heavier and fatter because of higher energy intake and may result to mating difficulties. A physiological mechanism may be involved, since McDaniel et al. (1981) observed poor fertility using artificial insemination in caged broiler breeders fed on high levels of energy. Increased fatness may have made insemination more difficult, or fat may block the sperm storage organs or inhibit sperm transport. Alternatively, a combination of two or more of these effects may combine to reduce fertility. Pearson and Herron (1981) observed a highly significant decrease in fertility associated with an energy intake of 450 kcal/bird/day in the last trimester of the laying circle. At that, time hens and cockerels were significantly heavier than birds fed 363 kcal/bid/day. However, the effect of high energy intake and its consequence on body weight has been described as the main cause of low fertility associated with BB hens (Lopez and Leeson, 1994). Nahashon et al. (2007) in their research to determine the effect of varying concentrations of dietary crude protein and metabolizable energy on laying performance of pearl grey guinea fowl hens, observed that the mean hen-day egg production, egg mass, egg weight and shell thickness were significantly higher in hens receiving diet with 2,800 kcal of ME/kg of feed than those fed diet containing 2,900 kcal of ME/kg. Similarly, Pearson and Herron (2008) on the effects of energy and protein allowances during lay on the reproductive performance of broiler breeder hens observed that body-weight gain and carcass fat and water content increased and fertility decreased with increasing energy allowance.

Minerals are inorganic substances, which are required for maintenance of physiological processes such as growth and reproduction in poultry. A deficiency of calcium and/or phosphorus in poultry results to abnormal bone development, normal skeletal calcification, reduced shell quality, cage layer fatigue and osteoporosis. Cage layer fatigue is caused by an impaired calcium flux related to the high output of calcium in the eggshell (Leeson, 2016). A high incidence of cage layer fatigue can be prevented by ensuring the normal weight-for-age of pullets at sexual maturity and by giving pullets a high-calcium diet (minimum 4% calcium) for at least 7 days before first oviposition (Leeson, 2016). Selenium improves fertility and, more importantly, increase the duration of fertility (Agate et al., 2000). Improved antioxidant (Se) defenses during embryonic development may increase hatchability; thus antioxidants (vitamin E, carotenoids and Se) could be transferred from the diet to the egg and consequently to the developing embryo (Surai, 2002). In hens, selenium deficiency results to reduced egg production and hatchability. Zinc serves not only as a nutrient in poultry but can also be used as a dietary supplement to manipulate the reproductive system of the bird (Park et al., 2004). In breeder hens, Zn is important as a component of carbonic anhydrase, which is involved in the supply of carbonate ions during eggshell formation (Nys et al., 1999). Breeder diets deficient in Zn can lead to a decrease in egg production and eggshell quality, as well as in hatchability (Kienholz et al., 1961). Essential for formation of the bone cartilage, Mn plays a significant role in the formation of chondroitin sulfate. Perosis and chondrodystrophy in young birds and production of thin-shelled eggs and poor hatchability in mature birds have been attributed to deficiency of manganese in the diet. Manganese deficiency on egg production is corrected by feeding a diet that contains at least 30–40 mg of manganese/kg, provided the diet does not contain excess calcium and/or phosphorus (Leeson, 2016). Iron and copper deficiencies can result to anemia. Moreover, Cu is closely associated with iron metabolism because it is a part of ceruloplasmin. Copper plays an important role in eggshell membrane formation, which in turn influences eggshell structure, texture, and shape (Baumgartner et al., 1978). Iodine deficiency can lead to a lower output of thyroxine from the thyroid gland, which in turn stimulates the anterior pituitary to produce and release increased amounts of thyroid stimulating hormone (TSH), which eventually results to goiter. Inhibition of the thyroid by administration of thiouracil or thiourea results to stoppage in lay and obesity in breeder hens (Leeson, 2016). Administration of thyroxine or iodinated casein can remedy the effects of iodine deficiency on egg production and eggshell quality. Iodine deficiency can also result to reduced hatchability and delayed yolk sac absorption in breeder hen (Leeson, 2016) and thus could be corrected by supplementing the feed with as little as 0.5 mg of iodine/kg, although a level of 2–3 mg/kg is more commonly provided to sustain good feathering in fast-growing birds. Naturally occurring feedstuffs are usually rich in magnesium; hence, deficiencies are rare. However, magnesium deficiency in laying hens results in a rapid decline in egg production, hypomagnesemia, egg size, shell weight, decrease in the magnesium content of yolk and shell and a marked withdrawal of magnesium from bones. Increasing the dietary calcium of laying hens accentuates these effects. Potassium, sodium and chloride are termed body electrolytes. The effects of deficiency of any one element are often a consequence of alteration of the body acid-base balance. A deficiency of chloride causes ataxia with classic signs of nervousness, often induced by sudden noise or fright. Birds deficient in dietary potassium show poor growth rate. A deficiency of sodium leads to a lowering of osmotic pressure and a change in acid-base balance in the body. Cardiac output and blood pressure both decrease, PCV increases, elasticity of subcutaneous tissues decreases, and adrenal function is impaired. This leads to an increase in blood uric acid levels, which can result in shock and death (Leeson, 2016). A less severe sodium deficiency in chicks can result in retarded growth, soft bones, corneal keratinization, impaired food utilization, and a decrease in plasma volume. In layers, reduced egg production, poor growth, and cannibalism can result (Leeson, 2016).

Requirements for vitamins A, D, and E are expressed in IU. The main role of vitamin E as an antioxidant is to prevent lipid oxidation which largely affects the deterioration of food products, and has adverse effects on colour, flavour, nutritive value and even safety of food products (Moak and Christensen, 2001). The requirement for vitamin E in poultry is highly variable and depended on the concentration and type of fat in the diet, the concentration of Se, the presence of prooxidants and antioxidants. NRC recommended 5 IU/kg of feed for a Leghorn-type laying hen consuming 100 g/d (NRC, 1994). In laying hens, the role of vitamin E on vitelline membrane strength (VMS), egg production, quality parameters and deposition in the egg are well documented. In a study by Monsalve et al. (2004), high dietary amounts of vitamin E (150 IU/kg) significantly improved VMS of fresh eggs. In another study by Kirunda et al. (2001) on the effect of vitamin E on egg quality during heat stress, found that VMS declined in birds receiving the lowest vitamin E level of 20 IU/kg compared to 60 and 120 IU/kg. Vitamin E as a fat-soluble vitamin is accumulated in the vitelline membrane and therefore responsible for its strengthening by functioning as an antioxidant (Halliwell and Gutteridge, 1989). In an experiment by Canan et al. (2007), egg production in laying hens in a heat stressed group and a non-heat stressed group both increased significantly with the supplementation of dietary vitamin E. These results agreed with the findings of Puthpongsiriporn et al. (2001) who also showed that supplementation of vitamin E significantly increased egg production in laying hens exposed to heat stress. A change in egg quality can be affected by many factors, including stress, age, and diet of the bird; hence vitamin E supplementation could be an effective way to alleviate the negative effects of stress on laying hens. Vitamin E accumulation in egg yolk reflected its level in the breeder diet and varied with Se supplementation (Surai, 2000). Dietary organic Se significantly increased the vitamin E level in the yolk, but no further increase in vitamin E accumulation in the egg yolk was noticed when a combination of Se and increased vitamin E were supplemented. Previous studies on animals have shown that inadequate amounts of vitamin E result in anemia, reproductive failure, muscular dystrophy, and neurological disease (Leonhardt et al., 1997). Earlier study by Zulkifli et al. (2000) reported favourable influence of the supplementation of vitamin C either to drink or feed on poultry production results. The role of vitamin C in the improvement of egg laying has not been sufficiently elucidated although various researchers indicate its involvement in the process of maturation of egg vesicles (Kolb and Seehawer, 2001). The beneficial effect on egg production of vitamin C added to feeds for laying hens was particularly evident when the birds were exposed to stress caused by high air temperature or increased stocking rate of birds per unit area (Njoku and Nwazota, 1989). Vitamin A is necessary for support of growth, health and life of all major animal species. Supplementation of vitamin A at doses of 45,000 IU/kg and above significantly decreased egg weight, yolk color, eggshell thickness and strength, and reproductive performance (Yuan et al., 2014).

Progeny performance in Poultry

The fertility functions of females, like those of males, are crucial for successful production of healthy offspring. More specifically, in poultry species the daily egg production, egg quality, including egg weight and components of the yolk and albumin, the egg fertility and hatchability are the most important factors that determine healthy offspring (Rengaraj and Hong, 2015). Managing the reproduction efficiency of the hen and rooster is therefore the basis of broiler breeder production. A fertile egg will provide a closed environment within which all nutritional needs of the embryo have to be met, with the notable exception of gaseous exchange (Lopez and Leeson, 1994); thus the physiological condition of the hen and the egg are related to normal embryo development. A high positive relationship between egg weight and chick size has been reported by Pinchasov (1991), and chick weight is usually 62–76% of egg weight (Pinchasov, 1991). Most of the differences in chick weight at hatch is accounted for by differences in the fresh weight of the egg, weight loss during incubation, and the weight of the shell and other residues at hatch (Lopez and Leeson, 1994). However, it is worthy to note that egg size increases with the age of the bird consequently**,** it would be expected that the age of the hen would also affect chick weight. However, in an experiment by Shanawany (1984), he observed no significant effect on flock age and hatching weight. He perhaps attributed the effect to increased shell porosity, more efficient utilization of nutrients by embryos from older birds, and more efficient deposition of nutrients for embryonic development in the eggs from older birds.

It has been demonstrated that chick weight at hatching affects subsequent growth of the broiler (Goodwin, 1961), while others have reported residual effect of chick weight to quickly disappear (Pinchasov, 1991). Goodwin, (1961) reported that 1 g difference in egg weight results in some 10–12 g difference in body weight at 8 to 9 weeks. The study of the effect of egg size on chicken mortality has shown inconsistent results. Some researcher reported no significant effect (Proudfoot and Hulan, 1981), while high mortality has been reported in chicks coming from small eggs (McNaughton et al., 1978; Wyatt et al., 1985). The high mortality has been attributed to maternal age, where higher mortality is seen in chicks from young breeders (McNaughton et al., 1978). McNaughton et al. (1978) suggested that this viability could be explained by the fact that older breeders produce chicks with significantly more body fat at hatching.

While better feed efficiency of broiler chicks has been related to larger egg size (Proudfoot et al., 1982), results are not always convincing (Wyatt et al., 1985). Obviously, effect egg size has on feed efficiency may be confounded with age of the breeder flock. Pone et al. (1985) reported that maternal age had a significant effect on live body weight of broilers, reporting less feed consumption with broilers from younger parents. This effect was also observed by Pinchasov (1991) who reported heavier body weight of birds from older breeders due to higher feed intake. Because chick size is positively correlated with egg size, it seems reasonable to assume that changes in the diet which influence egg weight will also influence the size of the chick at hatch. However, whether or not breeder nutrition modifies subsequent broiler performance is still not clear.

Conclusion

There is paucity of recent information on the interactions between nutrition and reproduction in male, female and progeny birds. Some of the information is contradictory because we are dealing with a biological system that is prone to intrinsic variability. Although there are gaps in our knowledge about the nature of interactions, we have sufficient data on important positive interactions. These need to better exploited to enhance reproductive efficiency of poultry. On the other hand, excessive energy before lay will tend to induce multiple ovulations with attendant consequences for egg-shell quality and usable egg production. Delaying the onset of maturity by feed restriction may improve the synchronization of the onset of lay and energy supply in a flock of birds. Low hatchability in broiler breeders reared on an *ad libitum* diet is probably due to poor shell quality caused by multiple ovulation. Increasing knowledge in this area may permit more efficient modelling and prediction of nutrient responses and reduce our dependency on empirical experimentation.

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