THE EFFECTS OF MATERNAL DIETARY LYSINE INTAKE ON BROILER BREEDER OFFSPRING PERFORMANCE

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THESIS

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ABSTRACT

The aim of this study was to evaluate the effects of broiler maternal dietary lysine intake on progeny performance. Three experiments were conducted with chicks hatched from Cobb 500 breeders at 38, 48, and 60 weeks of age. Breeder hens received six dietary treatments (T1-T6) from 26 to 60 weeks of age, which allowed an intake of 800, 930, 1070, and 1200 mg lysine/bird/d (T1-T4) respectively. An intake of 800 mg/bird/d at 26 weeks was increased by 25 mg every two weeks to provide 1225 mg lysine/bird/d at 60 weeks (T5). An intake of 1200 mg/bird/d at 26 weeks was reduced by 25 mg every two weeks to supply 775 mg lysine/bird/d at 60 weeks (T6). A total of 320, 401, and 390 chicks were hatched from breeder hens at 38, 48, and 60 weeks of age respectively. Immediately after hatching, 270, 384, and 384 unsexed chicks from breeder hens at 38, 48 and 60 weeks of age respectively, were placed in an environmentally controlled room and randomly allocated (within a treatment) to single-tier cages (80 × 50 cm). Nine chicks from breeders at 38 weeks of age and 8 chicks from breeders at 48 and 60 weeks of age were placed in each pen, keeping chicks from the same treatment group together for 21 d. Chicks were fed *ad libitum* with a commercial broiler starter crumble for 21 d and water was provided *ad libitum* throughout the duration of each trial. Feed intakes (FI), body weight gain (BWG) and feed conversion ratio (FCR) were measured weekly. Data were subjected to analysis of variance using a generalized linear model of GenStat 12th edition. Simple linear regression model of GenStat 12th edition was used where appropriate. Significant improvements in offspring feed intake and body weight gain from 7-21 d were observed in chicks hatched from young breeder flocks (38 weeks) with low dietary lysine intakes (800, 930 and 950 mg/bird/d). The effect of maternal dietary lysine intake on offspring performance disappeared with the aging of the breeder flock (60 weeks). It was concluded that lower maternal dietary lysine intakes (800, 930 and 950 mg/bird/d) may improve feed intake and body weight gain from 7-21 d of broiler chicks hatched from younger breeder flocks (38 weeks).

DEDICATION

This thesis is dedicated to my two late elder brothers, Vuyile (aka Ntsunde) Khetani and Mlungisi (aka Koko/Master) Ketani and to my best friend, Ayanda (aka Gilbert) Blekiwe. I know for certain that given the opportunity that I have had to reach this far with my studies, they would have gone even further than the level that I have achieved.

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PREFACE

The experimental work described in this dissertation was carried out at Ukulinga Research Farm, University of KwaZulu-Natal, Pietermaritzburg, from July 2008 to January 2009, under the supervision of Dr. Mariana Ciacciariello.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.

DECLARATION 1 - PLAGIARISM

I, THAMSANQA LUCKY KHETANI, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain the data, pictures, graphs or other information of other persons, unless specifically acknowledged as being so-sourced.

4. This thesis does not contain the writing other persons, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
   a. Their words have been re-written but the general information attributed to them has been referenced
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5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged and with the source being detailed in the thesis and in the References sections.

Signed by:

T.L. Khetani

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1. GENERAL INTRODUCTION

The introduction of genetic selection programs for increased growth rate and body weight gain has had a positive impact on broiler performance over the years. However, the effects of broiler-breeder genetic selection techniques on egg composition and embryonic development have not been widely investigated. The continued genetic selection for increased growth rate and other traits of economic importance is a constant challenge against the production maximization of broiler-breeder settable eggs (Robinson *et al*., 2007; Zuidhof *et al.*, 2007). This is seen through reduction in the number of broiler-breeder fertile hatching eggs produced following intensive selection for increased growth and body weight gain. This further leads to a reduction in the number of high quality saleable chicks produced. Therefore, it would be better for a balanced selection to aim more at improving key life performance traits whilst maintaining reproductive potential of broiler-breeders (Wolc *et al.*, 2009). In the near future, it is likely that selection criteria will change in a way that allows more balance between growth and production traits in meat-type birds (Leeson, 2008). It is also believed that with some form of maternal dietary nutrient manipulation, broiler-breeder reproductive challenges can be successfully tackled in order to effectively keep up with the needs of these continually changing genotypes (Leeson, 2005; de Beer, 2009; Gous, 2010). Gous (2010) recommended an extensive review of ways in which modern broiler-breeders are fed in order to successfully maximise their growth and reproductive potential.

Since poultry embryos, unlike those of mammals, grow and develop outside the maternal body (Schaible, 1970; Speake *et al.*, 1998a, b), they rely entirely on nutrients deposited within the egg for their normal embryonic growth and development (Romanoff & Romanoff, 1949; Wilson, 1997; Perić *et al*., 2007). All these nutrients are derived from the maternal diet and maternal metabolism (Ewing, 1963; Freeman & Vince, 1974; Wilson, 1997). Amounts, forms, balance and efficiency with which nutrients are deposited by breeder hens into the egg, are important for the potential embryonic growth and development to be attained (Wilson, 1997). The immune and digestive systems of broiler chicks are not well-developed or fully functional immediately after hatching (Sell, 1996; Maiorka *et al.*, 2006); thus the yolk-sac is the lone provider of all nutrients required to support the physiological status and performance of these chicks throughout their transition period to self-sufficiency (Noy & Sklan, 1999; Koutsos *et al*., 2003; Moran, 2007; Perić *et al*., 2007). Therefore, maternal nutrition plays an important role in ensuring that all the nutrients required for supporting the potential growth and development of the embryo, as well as hatchling performance shortly post-hatch, are available within the egg.

Minimal attention has been given to the role played by maternal nutrition on offspring performance. However, there are conflicting views in the literature about the effects of maternal nutrition on offspring performance. There are researchers who believe that regardless of egg size or breeder-hen nutrition, hens deposit the same proportion of available nutrients into the egg (Lopez & Leeson, 1994a, b; Etches, 1996). Fisher (1998) as well as Gous & Nonis (2010) also made an assumption that regardless of age and strain, egg amino acid composition is expected to be constant. In contrast to these claims, Schaible (1970) reported that maternal nutrition does affect composition and hatchability of fertile eggs. Therefore, it is worth investigating whether egg composition could be manipulated through maternal nutrition, in an attempt to maximize broiler embryonic growth and post-hatch performance. The objective of this study was to evaluate the effects of broiler maternal dietary lysine intake on offspring performance. Lysine was chosen as the testing amino acid in this research specifically due to the scarcity of experiments conducted in broiler breeder production where lysine is investigated. It was also chosen because of its economic importance and that it is often the first limiting nutrient in poultry feeds.

2. LITERATURE REVIEW

2.1 INTRODUCTION

There is currently some level of complexity encountered in deciding upon further broiler-breeder selection objectives. However, these birds have been successfully selected for a number of economically important traits over the past years. Broiler-breeders have undergone intensive genetic selection for increased growth rate and body weight gain for many years and this has resulted in considerable improvements in broiler performance (Deeb & Lamont, 2002). Such improvements in broiler performance are seen in decreased durations to market age, reduced amount of food required per unit of body weight gain (Havestein *et al.* 2003a, b; Dozier *et al*., 2008b) and an increase in the efficiency with which birds convert feed into body tissues (Skinner-Noble & Teeter, 2003; Schmidt *et al*., 2009). However, there has been little attention dedicated to determining whether there is any correlated change in broiler-breeder egg composition and embryonic growth, with genetic selection for the above-mentioned traits.

Success in a broiler-breeder enterprise depends upon the proper combination of feeding-management, diet composition, flock uniformity and production management (Fisher, 2008). Broiler-breeder reproductive efficiency is determined by the number of saleable chicks produced (Zuidhof *et al.*, 2007). High-quality day-old-chicks form a significant starting material for an improved broiler flock at slaughter (Tona *et al.*, 2003, 2005). Therefore, it is important to ensure that breeder hens lay eggs which produce high-quality day-old-chicks. This could be achieved through successful manipulation of maternal dietary nutrient composition and metabolic transformation (Leeson, 2005). This Chapter reviews aspects related to the advances made in broiler-breeder genetic selection programmes, free access versus restricted feeding, broiler-breeder nutrition and production and most importantly, the effects of maternal broiler-breeder dietary nutrient intake on offspring performance with regards to growth and development. This is done in an attempt to get a clear understanding of any possible changes that could have taken place in the way in which broiler-breeders invest nutrients to support offspring performance, following the advent of genetic selection techniques for increased growth rate and weight gain.

2.2 BROILER-BREEDER GENETIC SELECTION

The worldwide poultry industry has shown a phenomenal growth over the past 50 to 60 years and this growth is forecast to continue (De Koning *et al*., 2004; Hoffmann, 2005; Havestein, 2006; Berri *et al*., 2007; De Oliveira *et al*., 2008; Muir *et al*., 2008; Gous, 2010). Evolution from Jungle Fowl to modern broiler has taken approximately 5000 years. However, the greatest improvement in meat-type birds took place in the last two centuries, particularly in the last 50 years (Howie *et al*., 2009). Most developments seen in broiler-breeder production have been associated with advances made in the science of genetics (Havestein *et al.* 2003a, b; Howie *et al*., 2009), which is supported by technological improvements (Hoffmann, 2005), and nutritional-management (Havestein *et al*., 2003a, b). With retained genetic diversity and management, there could be a large number of benefits in poultry production carried out under different environmental conditions (Notter, 1999; Muir *et al*., 2008). Therefore, if continued growth of the poultry industry is to be maintained, sufficient genetic diversity must exist within breeding companies, in order to sustain further genetic improvements and facilitate rapid adaptation of poultry to continually changing breeding objectives (Notter, 1999; Fulton, 2006; Muir *et al*., 2008; Tixier-Boichard *et al*., 2009).

2.2.1 Advancements in broiler breeder selection

The employment of genetic selection techniques over the past 50 years has resulted in the improvements seen in broiler performance (Cheema *et al*., 2003; Havestein, 2006; Muir *et al*., 2008; Howie *et al*., 2009). Selection in broiler breeder operations has mainly been based on traits such as rapid early growth and enhanced muscle mass (Berri *et al*., 2007; Schmidt *et al*., 2009), which led to increased broiler body weight gain (Beumont *et al*., 1998), and high breast-meat yield (Scheuermann *et al*., 2003; MacRae *et al*., 2007; Schmidt *et al*., 2009). Decreased days to market age are the result of such developments (Skinner-Noble & Teeter, 2003; Schmidt *et al*., 2009). The entire selection program, based on the above-mentioned and other traits of economic importance, has resulted in the development of broiler-breeder birds which are different from egg-type hybrids.

Schmidt *et al*. (2009) conducted a study in which growth and feed-efficiency of a modern broiler line (Ross 708) were compared to that of a heritage broiler line (UIUC) which was not selected since the 1950s. Birds were grown under the same environmental conditions for 5 weeks post-hatch. In this study, modern birds appeared to deposit body mass more efficiently than their heritage counterparts (Figure 2.1). Significantly improved breast-meat deposition was also reported in Ross 308 strain of 2001, when fed diets representative of commercial broiler feeds fed in 2001, than in Athens-Canadian Randombred Control strain of 1957, when fed diets representing those fed in 1957 (Havestein *et al.*, 2003a, b). This improvement in breast-meat deposition of modern birds was mainly attributed to genetic selection advances achieved over time (Havestein *et al.*, 2003a, b; Schmidt *et al.*, 2009). Improved breast weight and yield were also reported in broiler strains selected for body weight and breast yield but not in their unselected counterparts grown under the same environmental conditions (Berri *et al.*, 2001).

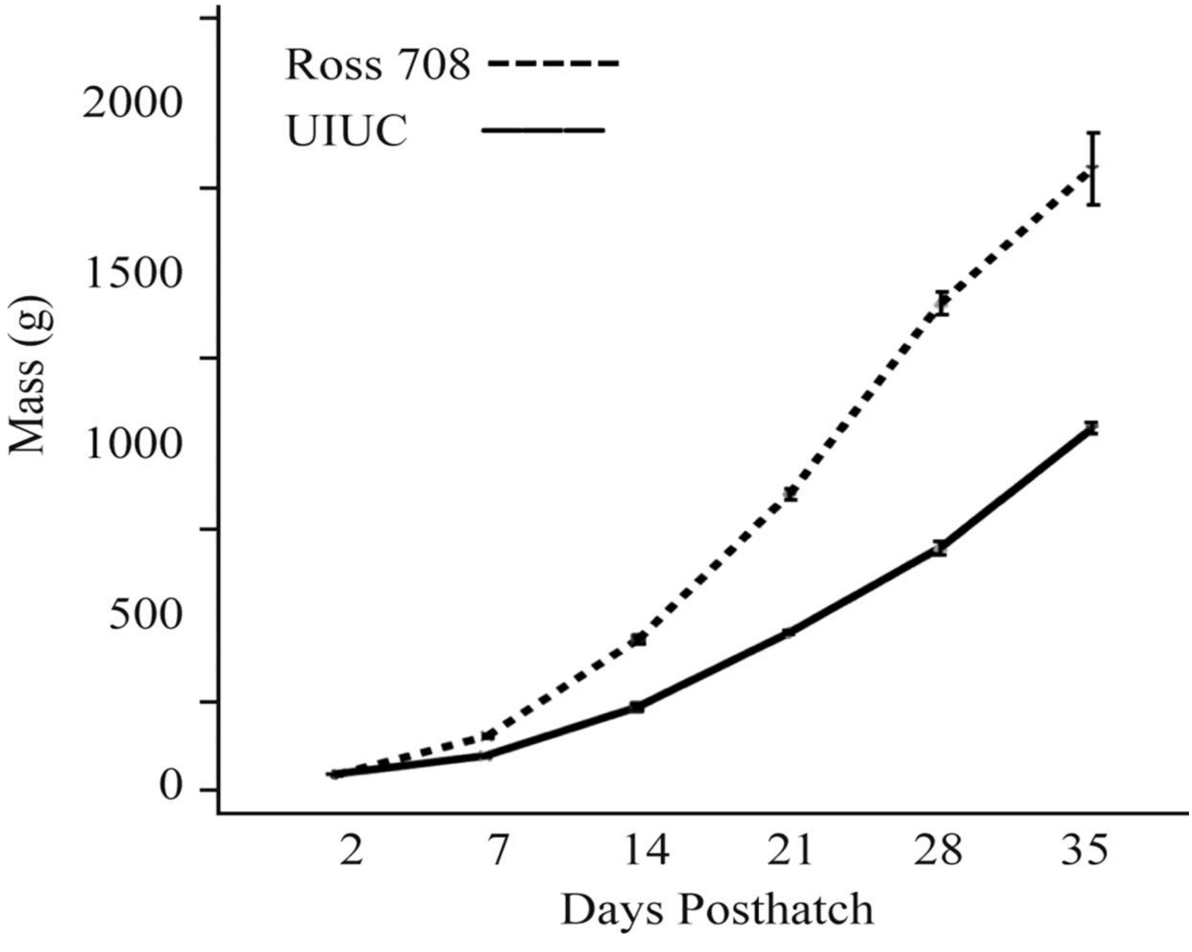

Figure 2.1 Body mass versus day post-hatch for modern (Ross 708) and heritage (UIUC) broiler lines. Bars indicate SE of the measurements (adapted from Schmidt *et al.*, 2009).

With feed representing around 50 to 70 percent of the total cost of broiler production, efficiency of feed utilization becomes one of the most important traits in broiler operations (Bottje *et al*., 2002). The amount of food required per unit of body weight gain has decreased markedly with increasing efficiency of birds to convert feed into body tissues (Figure 2.2 & 2.3). This is mainly attributed to the development made in technologies such as DNA markers and selection indices (Deeb & Lamont, 2002). Modern birds converted feed nutrients into body tissues more efficiently than heritage birds grown under the same environmental conditions for 5 weeks after the hatching process (Figure 2.2). Reduced levels of feed intake and maximum conversion of feed into body mass were also reported in male broiler chicks compared to their male egg-laying counterparts, when fed the same amount and composition of feed from 0 to 21 d of age (Morris & Njuru, 1990).

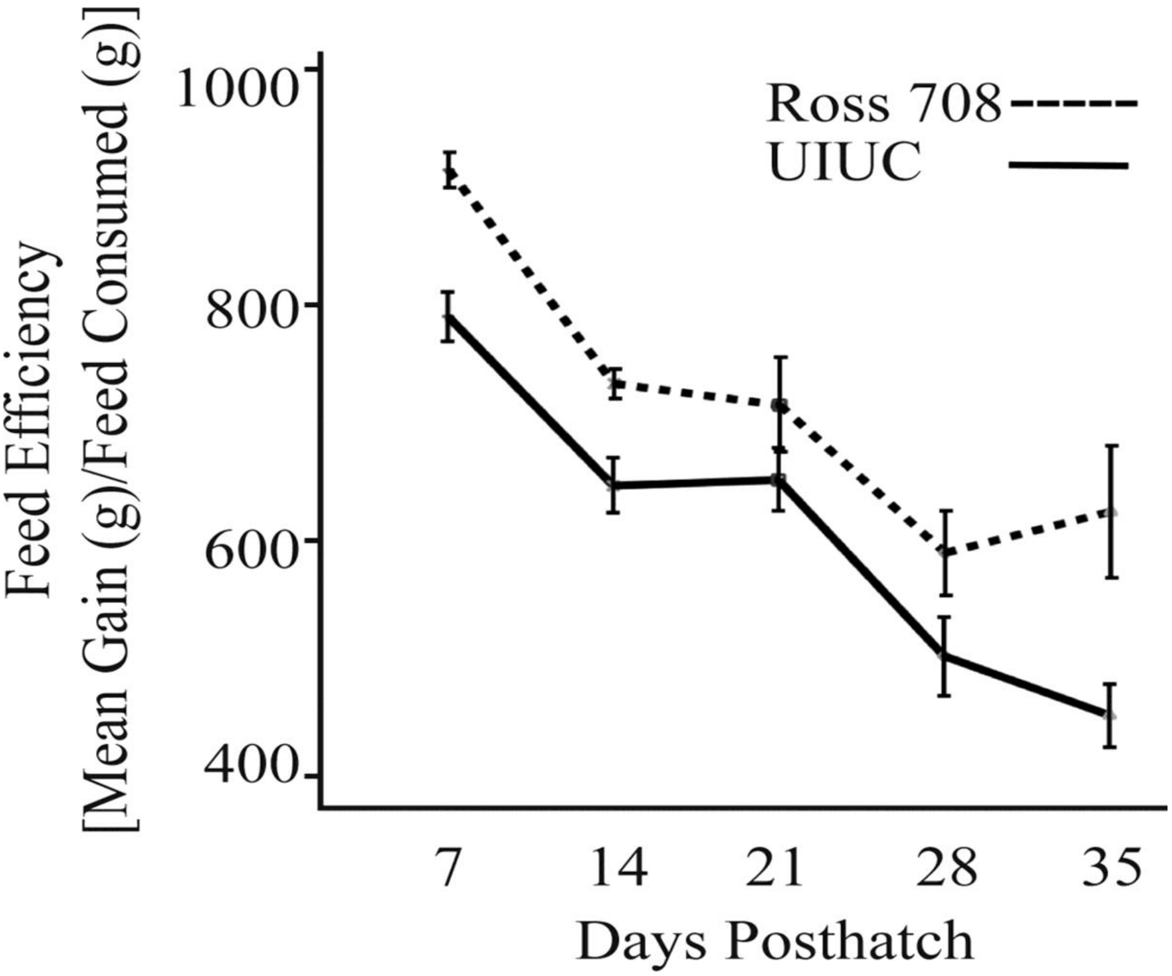

Figure 2.2 Feed efficiency as measured by the amount of body mass gain per unit of feed consumed with values determined for each cage and averaged. Bars indicate SE of the measurements (adapted from Schmidt *et al*., 2009).

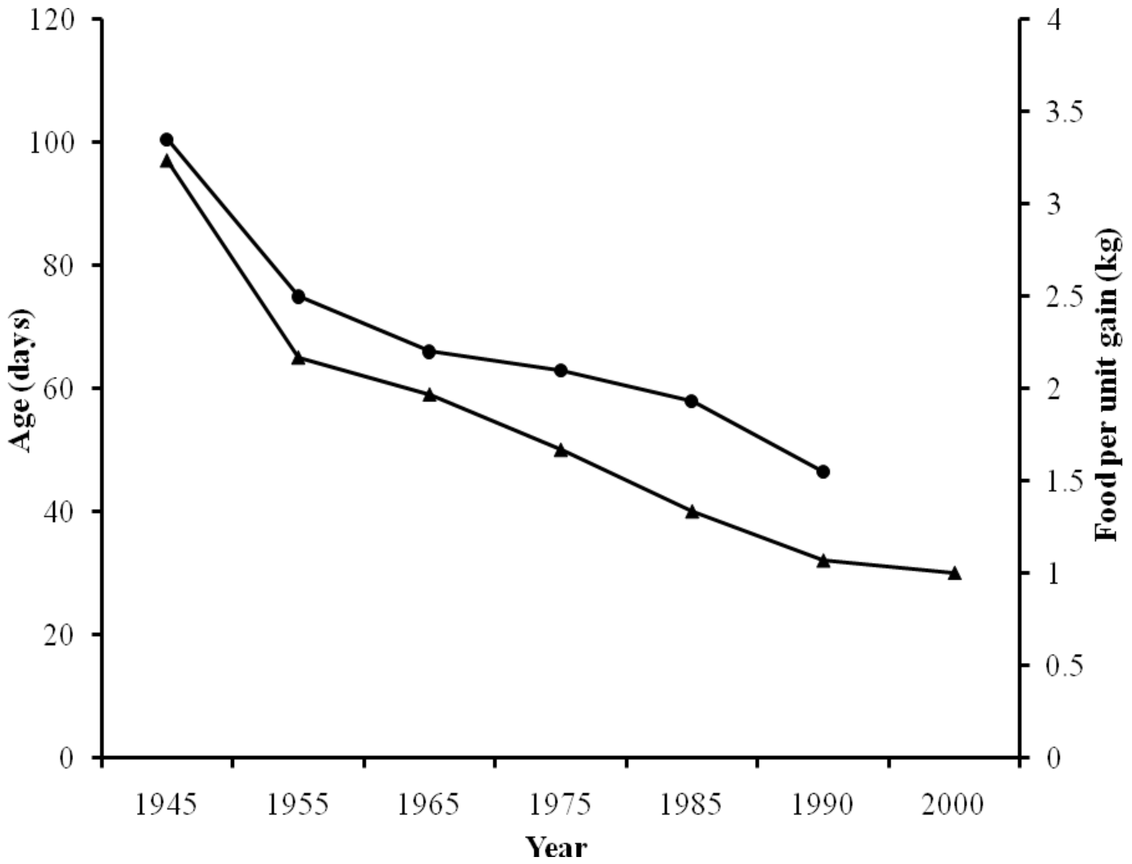

Figure 2.3 Age in days (▲) and the amount of food required per unit of body weight gain (●) to reach 1.5 kg live weight of broiler birds over the past 55 years. Data from Barbato (1994).

Even though there have been considerable improvements in broiler performance brought about by broiler-breeder genetic selection for increased growth rate and other traits of economic importance, such improvements have come at a cost (Rauw *et al*., 1998; Cheema *et al.*, 2003). This is seen through an increase in birds' appetite and voluntary feed intake following breeder selection for increased growth rate and body weight, thus resulting in birds that do not adequately regulate their feed intake in order to achieve a proper energy balance when exposed to free access feeding (Richards, 2003; Renema & Robinson, 2004; Chen *et al*., 2006; Rajman *et al.*, 2006). This becomes the main cause of birds' susceptibility to obesity, lowered production and reduced fertility and hatchability of broiler-breeder settable eggs (Richards, 2003; Richards *et al.*, 2003).

Broiler-breeder genetic selection for increased growth rate necessitated the development of new management practices (Peebles *et al.*, 1998; de Beer, 2009). Improved broiler-breeder management programs are needed to help improve the cost efficiency of production since these birds are expected to maintain high growth rates while performing well reproductively. Therefore, in order to sufficiently meet demands of these constantly changing genotypes, breeder nutrition programs need to be continuously modified (Peebles *et al.*, 1998; Gous, 2010). A better understanding of genotype, nutrition and environmental interactions are also needed in order to best channel such information towards improving broiler-breeder performance, health and welfare even further in a global spectrum (Douglas & Buddiger, 2002).

Despite decades of successful broiler-breeder selection for faster growth, increased meat yield, and better feed utilization efficiency, differences still exist among different strains of chicken due to specific selection criteria employed by various breeding companies (Melnychuk *et al.*, 2004; Marcato *et al.*, 2008). Chickens selected for different traits have different nutritional requirements for their optimal performance (Marcato *et al.*, 2008). This is caused by differences in body weight, feed conversion efficiency, meat yield, and carcass conformation, leading to differences in growth curves of thesebirds (Gous *et al.*, 1999).

2.2.2 Inclusion of various breeding traits in selection programs

The criteria used to select for different broiler-breeder traits has undergone a great deal of amelioration over time. It shifted from selecting for very few traits, such as increased live weight, which was the case in early 1960s, to selection for a variety of traits, which is the case nowadays (Figure 2.4). Biological sciences have provided the rationale and measurement tools essential for the inclusion of more complex traits into the breeder selection programs. This has resulted in breeding-companies, which evolved through specialization, to develop complementary lines that provide hybrid crosses at the commercial level.

Identifying the best breeder candidates by way of phenotype and mating these to produce the next generation has been the most commonly used selection and breeding method over the past centuries (Havestein, 2006). Even though this method of selection is still used, a number of more advanced selection techniques have gained popularity over the years (Havestein, 2006). Among many of these techniques are: selection for quantitative trait loci (QTL) (Morris & Pillot, 1997; De Koning *et al*., 2004), selection by estimating breeding values using the Best Linear Unbiased Prediction (BLUP) (Danbaro *et al*., 1995) and the use of a selection index (SI) (Morris & Pillot, 1997).

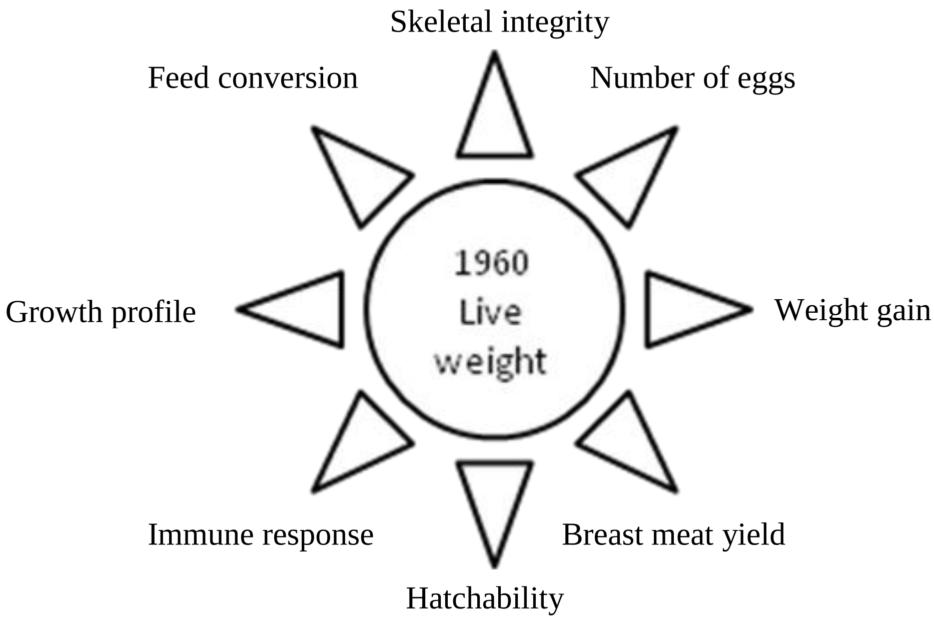

Figure 2.4 Schematic outline of the developments attained through inclusion of more traits into the modern broiler breeding programs. From Emmerson (1997).

Some of the traits considered for selection purposes are correlated either in a positive or negative manner. For example, selection for rapid weight gain is negatively correlated with increased levels of egg production (Bruggeman *et al.*, 1997; Melnychuk *et al.*, 2004) and selection for increased efficiency of feed utilization is positively correlated with improved carcass lean-tissue accretion (Geraert *et al.*, 1993).

2.3 BROILER BREEDER AMINO ACID REQUIREMENTS

An adequate amount of nutrient intake is required for optimum broiler-breeder production to be attained (Harms & Ivey, 1992). Therefore, a sufficient intake of all required nutrients is necessary to ensure that animals produce to their full potential. High-intake levels of broiler-breeder digestible nutrients are essential to obtain higher rates of growth and reproduction (Enting *et al*., 2007) and nutrient digestibility is known to increase with age (Batal & Parsons, 2002). Broiler breeder nutrient requirements are likely to change with the advances made in improving their genetic potential and through changes in egg production with age. Therefore, nutritionists should consider advances made over the years to improve the genetic potential of modern broiler breeders when formulating feeds, to sufficiently meet the requirements of these continually changing genotypes.

Broiler-breeder nutrient requirements, including amino acids, are based mainly on the minimum dietary concentrations of that particular nutrient required for maximum performance (Sterling *et al.*, 2005). Dietary protein and amino acid requirements are known to vary with physiological and production status of the bird (Garcia *et al.*, 2005; Fakhraei *et al*., 2010). Sterling *et al.* (2003) reported that amino acid requirement estimates may vary, depending on the dietary protein source and quality, dietary energy level, genetic strain, sex, experimental conditions and the method of statistical evaluation used. Therefore, poultry feeding programs need to be continuously adjusted according to the above-mentioned attributes, in order to ensure sufficient supply of nutrients required for maintenance, growth, and egg production.

Commercial poultry diets are mostly formulated on the basis of digestible amino acids rather than total amino acids (Rostagno *et al*., 1995, Farrell *et al*., 1999; Lemme *et al*., 2004; Dozier *et al*., 2008a; Adedokun *et al*., 2009; Khaksar & Golian, 2009). The level of feed intake and feed composition are the most important determinants of amino acid supply in broiler-breeder feed, since feed intake of such birds is often controlled (Fisher, 1998). Nutrient requirements of individual birds within a flock may differ, due to variations in body weight, body composition and potential egg output (Gous & Nonis, 2010). Variations in broiler-breeder feed intake within a flock could have a direct effect on the correct dietary level of all amino acids, at a given level of intake requirement (Fisher, 1998). Therefore, it is important to supply an adequate amount of nutrients and accurately estimate the response of broiler-breeders to dietary amino acids, when formulating feeds for such birds. Description of expected egg output; egg-output composition with respect to amino acids; efficiency of utilization of amino acids for egg production and estimate of the amino acid requirement for maintenance, is all potential information for accurately determining the amino acid requirement for maintenance, tissue growth and egg production (Fisher, 2008).

Broiler-breeders require a continuous supply of amino acids, mainly for maintenance, tissue growth and egg production (Fisher, 1998; de Beer, 2009; Gous & Nonis, 2010). Fisher (1998) presented amino acid requirements in a factorial equation as follows:

$$Raai = aE + bW^n \pm c\Delta W$$

Where: Raai = amino acid intake requirement (mg/bird d);

aE = the requirement for egg production as a function of E (egg output g/d);

bW^n = tissue requirement for maintenance as a function of body or tissue weight;

and $c\Delta W$ = the requirement for tissue growth as a function of weight change (g/d).

2.3.1 Amino acid requirements for maintenance

Maintenance requirements are the needs that persist throughout an animal's life, regardless of whether the animal is growing, reproducing or neither (Fuller, 1994; Gous & Nonis, 2010). However, in relation to amino acid requirements, maintenance is normally defined as nitrogen equilibrium, referring to the state in which nitrogen intake exactly equals the sum of nitrogen losses, so that the nitrogen content of the body remains constant (Fuller, 1994). Since maintenance accounts for about one-third of the broiler-breeder hen requirements for amino acids, a proper supply of nutrients necessary to sustain maintenance of such birds, is needed throughout their lifespan (Fisher, 2008; Gous & Nonis, 2010). The main problem encountered when predicting birds' nutrient requirements for maintenance, is to quantify the rate at which that particular nutrient should be supplied to the bird, considering its current state and genotype (Gous & Nonis, 2010). However, body protein and maintenance requirements are assumed to be constant during the laying period (Gous & Nonis, 2010). Fisher (1998) represented protein requirements for maintenance in a factorial equation as expressed below:

$$MPr = BP_m^{-0.27} \times BP \times X$$

$$= BP_m^{-0.27} \times X\ BP$$

Where: MPr = maintenance protein requirement (g/d), expressed as ideal protein;

BP_m = feather-free body protein mass at maturity (the figure was found to be 0.836 kg);

BP = feather-free body protein mass; and

X = a constant, with a value of 8 g/kg.

2.3.2 Amino acid requirements for tissue growth

Breast-meat and feathers are among tissues that need consideration with regards to amino acid requirements when poultry feeds are formulated (Gous *et al.*, 1999; Wylie *et al.*, 2003). Breast meat yield is more important in most markets than meat from other body parts (Gous *et al.*, 1999; Scheuermann *et al.*, 2003). High dietary amino acid concentrations improve breast meat development to a certain extent, but may also increase mortality (Kidd *et al*., 1998; Kerr *et al*., 1999; Dozier *et al*., 2008b). This is most commonly seen in lysine and such mortality is attributed to a bird's rapid growth rate, which is caused by relatively high dietary lysine concentrations (Kidd *et al*., 1998). D'Mello & Lewis (1970) reported that an excess consumption of an essential amino acid may limit the efficiency of nutrient utilisation relative to the optimum balance.

Body weight (BW) of Hy-Line laying-hens fed differing dietary protein levels from 44 to 60 weeks of age, was reported to decrease with a decrease in dietary protein intake (Novak *et al*., 2006). Similar results were reported in commercial crossbred pullets fed different levels of dietary protein from 23 to 63 weeks of age (Fisher & Morris 1967). Harms & Ivey (1992) and Harms & Russell (1995) reported an increase in broiler-breeder body weight with an increase in dietary protein and lysine intake. Significant improvements were also reported in body weight gain, feed conversion ratio and efficiency of male broiler birds fed low-protein diets supplemented with essential amino acids from 1 to 18 days of age (Abdel-Maksoud *et al*., 2010). Dozier *et al*. (2008a) observed significant improvements in BW, BW gain, carcass weight, breast-meat weight and yield of male broilers, when progressive levels of lysine were added onto a dose-response diet deficient in digestible lysine, from 49 to 63 weeks of age. However, there were no improvements observed in performance, with regards to the above mentioned traits of female broilers of the same age fed the same diets during the same time period (Dozier *et al*., 2008a). The lack of protein or amino acid effects on broiler breeder body weight gain was also reported in other studies (Joseph *et al*., 2000; Fakhraei *et al*., 2010; Kingori *et al*., 2010).

There may be differences in nutrient requirements for tissue growth among different bird strains, due to variations in body weight, feed conversion efficiency, carcass conformation and meat yield (Romanoff & Romanoff, 1949). Broiler-breeder strains exhibiting rapid muscle growth and strains with low feed intake are more likely to have high amino acid requirements, than strains with slow muscle growth and high feed intake (Bornstein, 1970; Sterling *et al*., 2006). Therefore, nutritionists should account for genetic-strain differences when formulating feeds, to provide adequate amino acids needed to meet the differing requirements of different bird strains (Sterling *et al*., 2006; Dozier *et al*., 2008b).

2.3.3 Amino acid requirements for egg production

Amino acid utilization for egg production varies in a complex manner with the rate of lay, thus making it difficult to be directly measured (Bowmaker & Gous, 1991). The irregular pattern of egg production observed in broiler-breeders is as a result of some birds feeding while not producing eggs, resulting in a zero utilization-efficiency of amino acid for egg production (Fisher, 2008). This is difficult to determine in a flock due to the variation among individuals. However, responses from a number of individual birds were simulated over time and such information was integrated for each day of the laying period, to get the mean requirement for the flock (Gous & Nonis, 2010). Fisher (1998) also proposed that broiler-breeder amino acid utilization-efficiency can be estimated from feeding experiments, as the ratio of amino acid in the egg to the amino acid used for egg production, excluding maintenance requirements. Bowmaker & Gous (1991) suggested that an understanding of the expected variation in rate-of-lay between individuals within a broiler-breeder flock is an important requirement. This could allow for better estimates of the optimum amino acid amounts to be made (Bowmaker & Gous, 1991). Fakhraei *et al*. (2010) pointed out a need to accurately predict egg mass changes, rather than isolated responses to egg production and egg weight, for broiler-breeder lysine intakes to be successfully established.

Significant improvements in egg production and egg weight with an increase in dietary lysine intake were reported in seven commercial brown laying-hen strains, from 21 to 36 weeks of age (Gunawardana *et al*., 2008b). Increasing egg production with an increase in dietary protein intake was also reported in other studies, conducted with both meat-type (Cave, 1984; Harms & Russell, 1995; Joseph *et al*., 2000; Fakhraei *et al*., 2010) and egg-laying strains (Liu *et al*., 2005; Gunawardana *et al*., 2008a). Fakhraei *et al*. (2010) reported significant improvements in egg production; the factors of egg mass, egg content, and percentages of settable eggs collected from breeder hens fed dietary lysine levels ranging from 0.5 to 0.85%, being positively affected. These parameters showed improvement with an increase in dietary lysine levels, up to a point where there were no further improvements obtained from increasing dietary lysine concentrations. Therefore, egg weight and rate-of-lay decreases to a certain point with a decrease in dietary amino acid and protein intake (Fisher & Morris, 1967; Morris & Gous, 1988; Bowmaker & Gous, 1991; Harms & Ivey, 1992; Harms & Russell, 1995). Amino acid requirements were reported to diminish in cases where egg production decreases with breeder age (Gous & Nonis, 2010). However, other studies reported no improvement in egg weight (Cave, 1984; Novak *et al*., 2006; Fakhraei *et al*., 2010) and egg production with an increase in hens' dietary protein intake (Wu *et al*., 2005; Kingori *et al*., 2010). Fakhraei *et al*. (2010) also observed no improvements in body weight gain, egg weight, and percentage hatch of breeder hens fed differing dietary lysine levels at 52 and 62 weeks of age. Gous & Nonis (2010) reported a more likely increase in amino acid requirements with time for high-producing broiler-breeders, due to an increased amino acid deposition in the egg.

2.4 LYSINE IN BROILER BREEDER PRODUCTION

Lysine is an essential amino acid which is used almost exclusively for protein synthesis. It is responsible for the greater part of white meat deposition in the body of broilers and broiler breeder hens (Kidd *et al*., 1998 Leclercq, 1998). Lysine levels higher than the requirement may increase feed conversion ratio of birds (Leclercq, 1998). However, birds' mortality rate may be increased, when fed excessive quantities of lysine (Kidd *et al*., 1998). Improvements in broiler breeder performance are often reported when birds are fed on an amino acid diet supplemented with lysine (Harms & Ivey, 1992).

Lysine is the most extensively researched amino acid; therefore, it is often used as a basis for setting requirements of other essential amino acids. However, this is true in broiler production but not in broiler breeder production. Because of its economic importance and limited research in broiler breeder production, lysine was then chosen to be the testing amino acid for experiments reported in this dissertation.

2.5 RESTRICTED VS. *AD LIBITUM* FEEDING IN MEAT-TYPE BIRDS

2.5.1 *Ad libitum* feeding

Broiler-breeder birds exposed to free-access feeding tend to consume more feed than required to reach their potential performance (Etches, 1996). These birds often show signs of reproductive unfitness through reduced egg production, which is mainly attributed to layers of adipose tissue enveloping the reproductive organs (Gowe *et al*., 1960; Bruggeman *et al.*, 1997, 1999; Richards, 2003; Richards *et al.*, 2003; Taherkhani *et al*., 2010) and multiple ovulations (Hocking *et al*., 1987, 1989). *Ad libitum* feeding is also associated with the likelihood of producing eggs with shell defects and/or multiple yolks (Chen *et al*., 2006), as well as decreased fertility and hatchability (Hocking *et al*., 2002). Increased body-fat deposition of breeder birds is mostly accompanied by a high susceptibility to metabolic and skeletal disorders (Robinson *et al*., 1992; Julian, 1998; Richards, 2003; Angel, 2007).

Broiler-breeder birds with free-access feeding consumed significantly higher levels of feed and gained more weight than their restricted counterparts, in a study where Cobb 500 hens were subjected to *ad libitum* feeding (ALF); once-a-day feed restriction (R1D); twice-a-day feed restriction (R2D) and three-times-a-day feed restriction (R3D), from 27 to 39 weeks of age (Taherkhani *et al*., 2010). It is clear that without any form of feed restriction, birds become overweight and obese. Breeder hens fed twice and three times a day, showed significantly lower levels of body weight than birds fed once a day from 35 weeks onwards, except for birds fed twice a day at 37 weeks of age. Feed-restricted birds from all groups, displayed significantly lower percentages of double-yolk and soft-shelled eggs than *ad libitum* fed birds. Feed consumption of broiler-breeder hens during lay becomes higher than it should, due mainly to greater maintenance requirements of heavy birds. Mortality of *ad libitum*-fed birds tends to be higher than normal (Hocking *et al*., 2002). Therefore, a program of controlling feed intake is essential during the rearing period, in order to produce pullets at point-of-lay in a physical condition that will allow them to start producing at a desired age and weight and also achieve reproductive potential of the genotype.

2.5.2 Controlled feeding

Broiler-breeder genetic selection for increased growth rate and body weight gain, has led to the production of birds that are unable to control their feed intake and resultantly gain more weight. Higher body weights negatively impact the reproductive efficiency of these birds. Broiler-breeder birds need to be fed so as to consume a given amount of nutrients within a given period of time, to produce a bird whose weight, body condition and frame allows for the reproductive organs to mature and function optimally. Therefore, attempts have been made to minimize problems associated with rapid growth and weight gain of these birds and feed restriction programs are the most-preferred managerial tools used to tackle such problems (Bruggeman *et al.*, 2005; Sandilands *et al.*, 2005, 2006; Vakili & Akbarogli, 2006).

Feed-restriction is defined as denying fast-growing birds a full access to nutrients required for potential growth and development and this can be achieved through quantitative or qualitative feed restriction (Gous, 1978). In quantitative feed-restriction, birds are physically deprived access to the feed and water during certain times of the day (Bullock *et al*., 1963; Gous, 1978; Crouch *et al*., 2002; Urdaneta-Rincon & Leeson, 2002; Nielsen *et al.*, 2003) while, in qualitative feed-restriction, birds are only deprived of full access to certain nutrients in the diet through provision of a low-density diet or a diet with amino acid imbalances (Bullock *et al*., 1963; Gous, 1978; Robinson *et al*., 1992; Savory & Lariviere, 2000; Nielsen *et al.*, 2003; Sandilands *et al.*, 2005; Tolkamp *et al.*, 2005; Sandilands *et al.*, 2006). There are different methods used to feed-restrict birds, such as skip-a-day feed restriction (SK), once-a-day feed restriction (R1D), twice-a-day feed restriction (R2D), and three-times-a-day feed restriction (R3D) (Vakili & Akbarogli, 2006; Spradley *et al*., 2008; Taherkhani *et al*., 2010).

Feed-restriction reduces rapid growth, incidents of skeletal and metabolic disorders and ovulation-rate of meat-type birds, while increasing egg production (Gowe *et al*., 1960; Hocking *et al*., 1987, 1989; Robinson *et al*., 1992; Bruggeman *et al*., 1999; Hocking *et al*., 2002; Spradley *et al*., 2008; Taherkhani *et al*., 2010). It also brings about improvements seen in the efficiency with which feed is utilized by broiler-breeders, through reduced overall maintenance requirements (Robinson *et al*., 1992; Urdaneta-Rincon & Leeson, 2002). Taherkhani *et al*. (2010) reported significantly lower levels of egg production in *ad libitum*-fed birds than in their feed-restricted counterparts from 27 to 39 weeks of age. On the other hand, birds fed twice-a-day displayed significantly higher levels of egg production than birds fed using other methods of feed allotment. Similar results were reported by Spradley *et al*. (2008), who observed significantly higher percentages of total hatching eggs in breeder hens fed twice-a-day, than in hens fed once-a-day from 21 to 60 weeks of age. These results were mainly attributed to the significantly lower number of dirty eggs produced by breeder hens fed twice-a-day, than those produced by birds fed once-a-day. However, there were no differences observed in fertility of eggs collected from hens subjected to either of these feed-restriction methods (Spradley *et al*., 2008). Therefore, benefits of feed-restriction differ with the method of feed allotment used (de Beer, 2009).

The degree and timing of feed-restriction are the two most important determinants of broiler-breeder reproductive performance (Bruggeman *et al*., 1997, 1999). The more severe the feed-restriction, the lower is the chance for birds' to recover from feed-restriction stress. Severity and duration of feed-restriction have raised concerns about the welfare of broiler-breeders (Heck *et al.*, 2004, Tona *et al.*, 2004) and there have always been imbalances in producing broiler-breeders which exhibit rapid growth, whilst maintaining optimal reproductive performance and good welfare status (Hocking *et al*., 2002; Renema & Robinson, 2004). Dwarf broiler-breeders which maintain a relatively good reproductive performance, even under *ad libitum* feeding conditions during growth, have been suggested as suitable alternatives in tackling broiler-breeder welfare-related matters (Hocking *et al*., 1987; Heck *et al.*, 2004; Tona *et al.*, 2004; Decuypere *et al.*, 2006; Puterflam *et al.*, 2006). However, this may negatively impact the progress made in selection. Therefore, broiler-breeder feed-restriction severity and duration of feed-restriction, needs to be continuously adjusted according to the changing selection goals and genotype of the birds (Bruggeman *et al.*, 2005). However, even with the use of feed-restriction programs, broiler-breeders do not lay at the same rate as commercial laying-hens (Robinson & Wilson, 1996; Spradley *et al*., 2008; Taherkhani *et al*., 2010). This is mainly due to the fact that broiler-breeders have been bred specifically for increased growth rate and body weight gain and these traits are negatively correlated with egg production, the trait for which laying-hens have been selected.

2.6 BROILER-BREEDER REPRODUCTIVE EFFICIENCY

Broiler-breeder reproductive efficiency is determined by the number of saleable chicks produced (Zuidhof *et al.*, 2007). Successful broiler-breeder productivity results from good combinations of feeding management, diet composition and flock uniformity (Fisher, 2008). Brake *et al*. (1985) reported that broiler-breeder nutrient consumption, during the pre-breeder period, plays an important role in determining the subsequent performance of the birds. Animals are unable to perform to their genetic potential when nutritional requirements are not met (Hocking, 1987). Therefore, it is important to have a clear understanding of the relationship that exists between mechanisms controlling efficiency of feed utilization, for maintenance, growth and development and egg production, in order to successfully achieve an optimum broiler breeder reproductive efficiency (Romero *et al*., 2009).

Breeder hens undergo a number of physiological changes just before sexual maturity (Renema *et al*., 2007). Therefore, in order to successfully optimize broiler-breeder reproductive fitness, sexual maturation must be properly managed, especially during the rearing period (Robinson *et al.*, 2007). The continual genetic selection for improved broiler growth and increased breast-meat-yield, poses a challenge toward attempts made at maximizing production of broiler-breeder settable eggs (Robinson *et al*., 2007; Zuidhof *et al.*, 2007). Therefore, it was proposed that understanding the effects of genetic selection for broiler rapid growth rate and weight gain, on breeder nutritional requirements, may be a key solution to maximise breeder reproductive performance (de Beer, 2009).

2.7 BROILER-BREEDER EGG COMPOSITION

Benefits brought about by genetic selection techniques for increased growth rate and body weight gain are well documented; however, whether there is a correlated response in egg composition still remains a matter of uncertainty. It was reported that genetic selection results for increased egg size, exhibited production of larger eggs containing smaller yolk and yolk-fat percentages (Tharrington *et al*. 1999). In contrast, Sainz *et al*. (1983) reported that the content of egg components is determined by genetic factors, not egg size. Internal weight and composition of egg contents were also reported as being affected by age and bird strain (Wolanski *et al*., 2007). Egg contains an excess of fat and moisture but not protein (Al-Murrani, 1978). Al-Murrani (1978) and Kingori *et al*. (2010) reported egg protein-content as the main factor affecting embryonic growth within the egg, rather than space. Production and hatchability of fertile eggs can be affected by mineral dietary status of the breeder hen (Dibner, 2005). However, most minerals within the egg may not be affected by maternal diet (Angel, 2007). Egg is made up of three different components namely; eggshell, albumen (egg white) and egg yolk.

2.7.1 Eggshell

Eggshell is the outer covering of the egg which protects the egg contents from both microbial and physical environmental contaminations and further, controls gaseous and water exchange into and out of the egg (Romanoff & Romanoff, 1949; Freeman & Vince, 1974; Board & Scott, 1980; Narushin & Romanov, 2002; Karlsson & Lilja, 2008; Chien *et al*., 2009). It acts as a primary source of calcium for the developing embryo (Romanoff & Romanoff, 1949; Tuan, 1983; Karlsson & Lilja, 2008; Chien *et al*., 2009) and also provides minimal amounts of other nutrients such as magnesium, phosphorus, iron, and sulphur (Romanoff & Romanoff, 1949). Eggshell supplies the developing embryo with calcium through dissolution of certain interior shell regions during the process of incubation (Moran, 2007; Chien *et al*., 2009). It also regulates and maintains suitable temperatures required to support potential embryonic growth and development within the egg (Chien *et al*., 2009). Therefore, production of eggs with good shell quality is essential for incubation purposes (Narushin & Romanov, 2002).

Eggshell strength and porosity are fundamental for embryonic metabolism, development and resistance to bacterial infections. However, an increase in shell thickness is often associated with an increase in early embryonic deaths (Romanoff & Romanoff, 1949; Peebles *et al*., 2001). Therefore, the shell should be sufficiently thin and fragile to allow hatching while maintaining moderate strength for the prevention of cracking before hatching (Romanoff & Romanoff, 1949; Ewing, 1963; Narushin & Romanov, 2002). Eggshell thinning as a way of allowing embryonic pipping for emergence, normally occurs during the process of shell dissolution, which in turn occurs to supply the developing embryo with calcium (Moran, 2007; Chien *et al*., 2009). Chien *et al*. (2008, 2009) proposed that an occluded protein network within the eggshell may facilitate the calcium-release needed to support embryonic skeletal growth.

Poorly-calcified eggs increase shell-porosity and egg weight losses during incubation and this subsequently increases the incidence of embryonic mortalities (Bennett, 1992; Novo *et al*., 1997). Appreciable pre-hatch losses in the laying environment are mainly attributed to weak and poor eggshell quality. Therefore, poor eggshell quality is a hidden cost to egg producers and every effort should be directed towards improving shell quality and reducing egg breakages. At the same time, sufficient porosity to allow suitable gaseous and water exchange to promote successful hatching process, must be maintained. Karlsson & Lilja (2008) proposed and proved that fast- and slow-growing birds lay eggs with different shell structures designed to support different embryonic calcium removal-rates. Extensive shell-calcium removal was observed in slow- as opposed to fast-growing birds (Karlsson & Lilja, 2008). Tharrington *et al*. (1999) and Anderson *et al*. (2004) reported that, following genetic selection for increased egg size, eggshell quality traits of modern birds have improved or been maintained at a high level.

2.7.2 Albumen

Avian albumen is a complex multifunctional egg medium which promotes growth and development of the embryo. The major part of albumen is made up of water (Romanoff & Romanoff, 1949; Etches, 1996) and protein is the second-largest component while other nutrients are present in minimal fractions (Romanoff & Romanoff, 1949; Freeman & Vince, 1974; Vieira & Moran, 1999). Egg albumen is rapidly consumed during the incubation process to supply amino acids required for body-protein synthesis (Muramatsu *et al*., 1990). Therefore, albumen content regulates embryonic body protein synthesis during the incubation process (Muramatsu *et al*., 1990). Albumen proteins have an antimicrobial effect that helps to protect the developing embryo against any harmful microorganism (Wellman-Labadie *et al*., 2008). This is made possible mainly by lysozyme, the major protective enzyme, especially against Gram-positive bacteria, found in the egg-albumen (Cegielska-Radziejewska *et al*., 2009). Proteins from the egg albumen move into the amniotic fluid where they are absorbed by the embryo before the hatching process takes place (Tona *et al.*, 2002, 2003; Nelson *et al*., 2010; Tona *et al*., 2010a, b).

The egg-albumen amino acid profile contains high concentrations of valine and leucine and relatively low levels of tryptophan, methionine and cysteine (Hank *et al*., 2001). Albumen pH increases with an increase in egg storage duration, and may lead to reduced hatchability of eggs (Lapão *et al*., 1999; Tona *et al*., 2002). Manson *et al*. (1993) associated the higher incidences of embryonic mortality observed during mid- and late-incubation period, with low albumen potassium concentrations which normally occur during these stages. These embryonic deaths were also linked alternatively to increasing sodium concentrations within the egg assuming that potassium: sodium ratio is maintained (Manson *et al*., 1993). Manson *et al*. (1993) proposed that a proper balance of albumen potassium with other minerals within the egg, may improve hatchability.

2.7.3 Egg yolk

Egg yolk is the richest nutrient fraction of the egg (Romanoff & Romanoff, 1949; Yilmaz-Dikmen & Sahan, 2009; Milisits *et al*., 2010) which serves as the primary storage site for minerals (Romanoff & Romanoff, 1949). It is known as the fuel of embryo development and is also considered rich in the antioxidant pigment carotenoid (Romanoff & Romanoff, 1949; Hartmann *et al*., 2003; Hall *et al*., 2007; Yilmaz-Dikmen & Sahan, 2009). Yolk lipids of an avian egg provide a wide range of components that are essential for embryonic tissue development and functioning (Romanoff & Romanoff, 1949; Brand *et al.*, 2003; Hall *et al*., 2007; Cherian *et al*., 2009). The larger part of embryonic energy needs are supported by the oxidation of yolk-derived fatty acids and metabolic features are mainly represented by transport and transformation of yolk lipids (Yilmaz-Dikmen & Sahan, 2009). Lipids are actively transferred from the yolk to the embryo during the second half of avian embryonic development (Noble & Connor, 1983). An avian embryo metabolizes yolk lipids through oxidation pathways, to obtain energy necessary for its growth and development (Romanoff, 1960; Speake *et al.*, 1998a, b; O'Dea *et al.*, 2004). It is during the process of egg incubation, mainly during the final week, when fat-soluble antioxidants are transferred from the egg to the developing tissues of the embryo (Noble & Cocchi, 1990; Surai *et al*., 1996). Therefore, egg yolk and its fatty acid content are essential for meeting nutritional requirements of the developing embryo (Brand *et al.*, 2003; Hall *et al*., 2007; Cherian *et al*., 2009; Milisits *et al*., 2010).

The amount of nutrient resources available within the egg increases with an increase in egg mass and albumen mass increases at a greater rate than yolk mass (Finkler *et al*., 1998; Nelson *et al*., 2010). However, yolk contains more solids and therefore becomes richer with energy than albumen (Nelson *et al.*, 2010). At hatch and a few days thereafter, the chick continues to utilize yolk material while going through transitional stages from depending on embryonic reserves for nutritional requirements, to relying entirely on dietary extracts (Noy & Sklan, 1999; Vieira & Moran, 1999; Yadgary *et al*., 2010).

2.8 BROILER-BREEDER REPRODUCTIVE PHYSIOLOGY

A fertile broiler-breeder egg has a biological function of producing an embryo with all the features required to produce a healthy chick (Manson *et al*., 1993; Lopez & Leeson, 1994b; Narushin & Romanov, 2002) and the general consensus, is that each egg is designed with a complete capacity to produce a new organism (Romanoff & Romanoff, 1949). However, this appears not always to be the case due to various reasons, including poor egg-fertility and hatchability. Egg quality has a direct effect on: successful embryogenesis, embryonic ability to access nutrients, resources necessary to support embryonic emergence, chick transition to self-sufficiency, chick quality and growth and it further determines the potential performance of birds in production (Tona *et al.*, 2003, 2005). Poor and prolonged egg storage conditions have a negative effect on egg quality and embryonic development, resulting in longer incubation time, embryonic mortalities, and production of poor quality hatchlings (Byng & Nash, 1962; Tona *et al.*, 2003; Reijrink *et al*., 2010).

Poultry embryos grow and develop from nutrients deposited and stored in the egg (Romanoff & Romanoff, 1949; Brand *et al.*, 2003) and these nutrients are mainly derived from the maternal diet (Wilson, 1997). The quantities and quality of nutrients, including minerals and water, available within the avian egg to support embryonic development, are predetermined by physiological processes taking place in the dam during egg formation (Manson *et al*., 1993). Egg composition influences not only embryonic mortality, chick body weight and composition at hatch, but also the weight at slaughter (Milisits *et al*., 2010). However, metabolic rates of the embryo, dry body mass and internal-organ mass were reported as independent of egg composition (Finkler *et al*., 1998).

Broiler-breeder embryonic mortalities at each transitional phase of development may be indicative of a deficiency or toxicity of certain nutrients within the egg (Moran, 2007). Embryonic mineral uptake can be improved mainly by a proper selection of dietary mineral sources (Angel, 2007). Al-Murrani (1982) suggested that breeder hens laying eggs for broiler production may be in need of additional protein sources. However, increasing nutritional content of the egg does not necessarily mean that nutrients will be efficiently incorporated into the embryonic body mass but a certain level of improvement is more likely to be attained (Finkler *et al*., 1998). It takes a fertile egg to undergo incubation and attain a successful hatching process.

2.8.1 Fertility of broiler-breeder eggs

Egg fertility is affected by both male and female breeding birds (Wolc *et al*., 2009). In breeder hens, fertility refers to the proportion of fertilized eggs, regardless of whether they hatch or not (Romanoff, 1960). Because of its effects on chick output and its importance in attaining a successful production, fertility is a trait of major interest in broiler-breeder production (Wolc *et al.*, 2009). Broiler-breeder egg fertility and hatchability are known to increase with breeder age (Kirk *et al*., 1980; Pedroso *et al.*, 2005; Ulmer-Franco *et al*., 2010) up to a point, after which they start decreasing (Novo *et al*., 1997). Therefore, young breeders produce less fertile eggs, with significantly lower percentage of hatching during, their early laying stages than older breeders (Pedroso *et al.*, 2005). In contrast to this, higher percentages of infertile eggs and total embryo mortality, which resulted in reduced hatchability percentages, were reported in eggs from older as opposed to younger breeders (Almeida *et al*., 2008).

A pattern of feed allocation during the rearing period may affect broiler-breeder hen fertility (Walsh & Brake, 1999). Lopez & Leeson (1995) reported that broiler-breeder egg fertility and hatchability can be improved by feeding low-protein diets. Contrarily, Walsh & Brake (1997, 1999) observed significantly higher fertility percentages in broiler-breeder hens fed diets containing higher levels of crude protein during the rearing period, than hens fed on lower dietary crude protein levels. Hocking *et al*. (2002) reported no improvements in fertility and hatchability of broiler-breeder hens fed on high and low levels of dietary protein during the rearing period. It was proposed that the reduction in broiler-breeder fertility which is observed in eggs from modern breeder birds and often associated with genetic selection for rapid growth, may be a result of increased nutrient requirements (Walsh & Brake, 1997). Therefore, a feeding program designed to take into account all the developments made over the years to improve broiler breeder genetic potential, is needed in order to adequately supply nutrients required to maximize fertility and hatchability of these frequently-changing genotypes. Walsh & Brake (1997) proposed that adequate amounts of crude protein are needed during the rearing period in order to support optimum development of the oviduct and enhance breeder hens' spermatozoal storage capacity.

2.8.2 Incubation of broiler-breeder eggs

Intensive selection for increased broiler growth rate and improved weight gain has resulted in decreased days to slaughter but not in incubation time, thus resulting in an increase in the proportional time in overall growth spent in incubation (Hulet, 2007; De Oliveira *et al*., 2008). With the dramatic changes brought about by genetic selection programs in growth potential of broilers, poultry incubation techniques have remained relatively unchanged, with eggs from different strains still incubated under the same setting conditions (O'Dea *et al.*, 2004; Joseph & Moran, 2005). Therefore, in order to improve production of high-quality chicks, current egg-management and incubation procedures may need to be modulated (Decuypere *et al.*, 2001; Wolanski *et al.,* 2006; Hulet, 2007; Abudabos, 2010; Tona *et al*., 2010a, b). Without any form of transformation, the current-egg management and incubation procedures may lead to a decrease in hatchability of broiler-breeder eggs (Hulet, 2007), mostly due to a the highly increased embryonic growth-rate that has taken place as a results of genetic selection over the years.

Incubator environment plays a decisive role in growth and development of chicken embryos (French, 1997; Yildirim & Yetisir, 2004; Decuypere & Bruggeman, 2007; Shafey *et al*., 2007; De Oliveira *et al*., 2008) and any alteration in incubation environment can influence embryonic metabolism and growth with a consequent impact on post-hatch performance of the growing chick (Shafey *et al*., 2007, Willemsen *et al*., 2010). Modern broiler embryonic heat production is expected to increase, following genetic selection for increased growth rate. Broiler and layer genetic selection for different traits appears to have affected not only production parameters but also the pattern of development and metabolic characteristics of the embryo (Everaert *et al*., 2008; Druyan, 2010). Higher levels of embryonic heat production were reported in egg-type chickens than their meat-type counterparts (Sato *et al*., 2006, 2007). Chwalibog *et al*. (2007) reported lower metabolic rates and fat oxidation in embryos of the slow-growing as opposed to the modern fast-growing broiler strains. Layer embryos showed slower growth and development (Sato *et al*., 2006, 2007; Everaert *et al*., 2008), which caused them to start hatching a day later than broiler embryos set under the same incubation conditions (Druyan, 2010). Layer embryos were thought to have delayed hatch so they could consume additional yolk to reach a relative yolk-weight similar to that of broiler embryos at hatch (Druyan, 2010). Sato *et al*. (2006) observed faster yolk-sac consumption, which is used as a lipid source, in broilers than in layer embryos. Therefore, Druyan (2010) and Tona *at al*. (2010a, b) proposed that incubation environment needs to be adjusted according to the line of birds being used. However, Yildirim & Yetisir (2004) reported that the modern hatching broiler eggs exhibit almost similar patterns of heat production and temperature to that of the past generations during, the last five days in the hatcher.

Overheating of embryos during the incubation process, has raised concerns about the survival of broiler embryos, as this leads to lowered hatchability, increased embryonic mortalities and reduced chick-quality post-hatch (Hulet, 2007; Willemsen *et al*., 2010). Excessive egg water-losses which result from overheating, could lead to embryonic mortalities by dehydration, while below-optimum reduction in egg water-loss may, on the other hand, cause embryo hydration thus resulting in impaired gaseous exchange. Leksrisompong *et al*., (2007) reported negative effects of higher (40.0 to 40.3°C) than optimum (38.2 to 38.4°C) incubation temperatures which were applied to broiler eggs during later stages of the incubation process. Embryonic body weight was reduced in eggs set in higher incubating temperatures compared to eggs placed under normal incubating temperatures (Leksrisompong *et al*., 2007). This reduction in embryonic weight observed in eggs incubated under high temperatures, was attributed to a reduction in yolk-sac absorption which might have led to reduced levels of available nutrients required for potential embryonic growth and development (Leksrisompong *et al*., 2007). Egg sizes, airflow, age of the embryo and breeder-flock fertility are factors contributing to an increase in heat stress of the developing embryo (Hulet, 2007). Therefore, in order to attain a successful incubation process, it is important to maintain favourable conditions for the fertile hatching egg (Decuypere & Bruggeman, 2007; Hulet, 2007; Shafey *et al*., 2007).

2.8.3 Hatchability of broiler-breeder eggs

Most hatcheries aim at obtaining higher egg hatchabilities (large numbers of marketable chicks) while farmers are in need of high quality chicks with best growth performances (Tona *et al*., 2005; Decuypere & Bruggeman, 2007; Willemsen *et al*, 2008). Good hatchability does not necessarily correlate positively with high percentages of good quality chicks and maximal hatchability is known not to be the best indicator of high post-hatch broiler growth and viability (Tona *et al*., 2005). Therefore, incubation of fertile eggs should always aim at producing chicks of superior quality that are highly competent, rather than producing many low quality chicks (Decuypere & Bruggeman, 2007).

The success of broiler-breeder hatchery management is determined by the percentage of hatched eggs from those set and the number of high quality day-old chicks produced (Yassin *et al.*, 2008). It was reported that better hatchability is attained from broiler-breeder eggs laid during the period between 40 and 42 weeks of age (Tona *et al*., 2001). Lopez & Leeson (1995) reported an increase in hatchability (in terms of total eggs set and fertile eggs) of eggs from breeder hens fed on low dietary protein levels. Similar results were reported by Brake *et al*. (1985), who observed a significantly better hatch of fertile eggs in breeder hens fed low dietary protein, when compared to hens fed high dietary protein. They attributed their results to the significant increases they observed in late embryonic deaths of breeder hens fed high dietary protein. In contrast, Kingori *et al*. (2010) reported no effects of maternal dietary protein on hatchability of eggs laid by 52-week-old indigenous laying hens fed different dietary protein levels. The extension of egg storage prior to incubation is known to delay the hatching process (Kirk *et al*., 1980; Tona *et al.*, 2003; Reijrink *et al*., 2010) and such a delay is often associated with a delay in the initiation of embryogenesis, with a subsequent decrease in embryo development (Byng & Nash, 1962; Tona *et al.*, 2003). This delay adversely affects day-old-chick quality and performance of the newly hatched chick (Tona *et al.*, 2003). Two of the most important factors affecting hatchability of broiler-breeder eggs, are fertility and embryonic mortality (Kirk *et al*., 1980; Yassin *et al.*, 2008). Other reasons for lowered hatchability of breeder eggs could be improper breeder-flock management and the use of incorrect incubation procedures (Yassin *et al.*, 2008; Abudabos, 2010).

2.9 EFFECTS OF BREEDER HEN NUTRITION ON OFFSPRING PERFORMANCE

Broiler-breeder nutrition has a direct effect on the production of high quality and fertile hatching eggs that are able to provide the balanced supply of nutrients essential to attain potential embryonic growth and development (Schaible, 1970; Dibner, 2005; Leeson, 2005). Powell & Bowman (1964) reported that nutrient deficiencies in the maternal diet may be manifested in the composition of the egg, which may further affect embryonic development and offspring post-hatch growth. Maternal investments, in the form of albumen, yolk and mechanisms by which the embryo utilizes energy and nutrients, have significant effects on embryo and hatchling phenotype (Nelson *et al.,* 2010). Protein and energy intake variations of the individual broiler-breeders within a flock may have a direct effect on the carcass quality of broilers at market weight (Spratt & Leeson, 1987). Pappas *et al*. (2008) reported that health and performance of the progeny is affected by maternal nutrition. Effects of dam nutrition on the immune status and chick quality during the first few weeks post-hatch, becomes increasingly important as days to slaughter-weight get shorter (Hocking, 2007). Sufficient maternal nutrition is crucial for the effective transfer of adequately balanced nutrients, which are necessary for normal growth and development of the embryo, into the egg (Ewing, 1963; Rol'nik, 1970; Freeman & Vince, 1974; Wilson, 1997). Therefore, success of potential embryonic development and hatching of a healthy chick is determined by the amounts and forms of nutrients deposited by the breeder hen into the egg (Brand *et al.*, 2003).

Powell & Bowman (1964) and de Beer (2009) reported that vitamin and trace mineral nutrition play an important role, not only in breeder performance but in progeny performance as well. Virden *et al*. (2003) attributed to maternal nutrition, all the improvements observed on the livability of chicks hatched from 37-week-old breeder hens, fed a diet supplemented with zinc and manganese from amino acid complexes. Supplementing broiler-breeder diets with zinc and manganese from 21 to 43 weeks of age, may improve offspring cardiac output and immune system endpoints (Virden *et al*., 2004). However, Hudson *et al*. (2004) observed little to no effects of zinc source on the physiological status, of chicks hatched from breeder hens fed diets supplemented with various zinc sources, from hatch till 65 weeks (eggs were collected for incubation at 29, 41, 53, and 65 weeks of age).

de Beer (2009) reported that the impact of maternal nutrition on progeny performance may be most significant, in cases where low vitamin diets are fed to breeder hens or in times of stress in the breeder house. Chicks hatched from breeder hens fed diets supplemented with higher levels of vitamin D_3 at different ages, showed improvements in body weight compared to chicks hatched from breeder hens fed diets supplemented with low vitamin D_3 levels (Atencio *et al*., 2005). However, Kingori *et al*. (2010) observed no effects of maternal dietary nutrition on offspring performance for chicks hatched from 52-week-old indigenous laying hens fed different levels of dietary crude protein.

Breeder nutrition is mainly evaluated in terms of egg numbers and hatchability, with little attention paid to progeny performance (Spratt & Leeson, 1987; Leeson, 2005). Hocking (2007) cautioned, that due to the interaction of many maternal nutrition factors on chick quality, determining optimum maternal nutrition which improves chick quality is likely to be complex. The fact that chick quality is mainly assessed based on chick performance under different environments, also adds to the complexity of finding the optimum maternal nutrition required to maximise chick quality (Hocking, 2007). The complexity of measuring chick performance, as affected by maternal nutrition, was also reported by Kidd (2006) and de Beer (2009).

2.10 EFFECTS OF BREEDER HEN AGE ON PROGENY PERFORMANCE

Tona *et al*. (2001) proposed that, for hatchability to be improved, attention needs to be paid to breeder hen age during the incubation period, since hatchability varies between eggs produced by young, intermediate and old breeder flocks. Ahn *et al*. (1997) observed a low egg solid contents from young (28-week-old) and old hens (97-week-old) compared to higher egg solid contents of the intermediate aged hens (55- to 78-week-old). A clear understanding of boiler breeder age and nutrient intake effects on the offspring performance may help to improve the quality and performance of broiler chicks (Hudson *et al*., 2004). Hudson *et al*. (2004) reported that inadequacies observed in the performance of chicks hatched from young breeder hens, may be successfully managed by evaluating the physiological differences that exist among chicks from breeder hens of varying ages. Broiler chicks from young breeder flocks, with small egg-yolks, exhibit low performances when grown in the same environmental conditions as chicks from older breeder flocks, with larger egg-yolks (Ulmer-Franco *et al*., 2010).

Different conflicting results about the effects of breeder age on progeny performance, are found in the literature. Early hatch was reported in chicks from 59-week-old hens than in chicks from 29-week-old broiler breeder hens (Ulmer-Franco *et al*., 2010). Hudson *et al*. (2004) observed a significantly greater body weight in broiler chicks hatched from 48-week-old breeder hens, when compared to broiler chicks hatched from 29-week-old breeder hens. Similar results were reported by Ulmer-Franco *et al*. (2010), who observed higher body weight in chicks hatched from 59-week-old breeder hens than in chicks from 29-week-old hens. In contrast to this, Peebles *et al*. (1999a) reported a better performance, from 0 to 21 d, in chicks hatched from 35-week-old breeder hens, when compared to chicks hatched from 51- and 65-week-old hens. Chicks from 51-week-old broiler breeder hens, showed a significantly better performance, from 22 to 42 d, than chicks hatched from 35- and 65-week-old breeders (Peebles *et al*., 1999a). A significantly higher body weight was also reported in chicks hatched from 65-week-old breeder hens, when compared to chicks hatched from 48-week-old breeder hens (Hudson *et al*., 2004). A greater number of yolk-free chicks at hatch were also observed in chicks from 65-week-old breeder hens than in chicks from 29- and 41-week-old breeder hens (Hudson *et al*., 2004). Broiler chicks hatched from 63-week-old breeder hens were reported to have greater slaughter yields than chicks hatched from 35- and 51-week-old breeder hens (Peebles *et al*., 1999b). Hudson *et al*. (2004) stated that chicks hatched from young breeder hens tend to have a relatively low yolk-sac and heart weight, which are factors likely to reduce post-hatch performance of these chicks. However, Peebles *et al*. (1999a) observed lower mortality rates in chicks from 35- and 51-week-old breeder hens, when compared to chicks from 63-week-old breeder hens. Tona *et al*. (2001) also reported a decrease in embryonic mortality for breeder hens from 27 to 40 weeks of age, than those from breeder hens older than 40 weeks. Therefore, broiler breeder hen age has no predictable effect on offspring performance throughout the growing period.

2.11 CHICK QUALITY AND PERFORMANCE

Chick quality is an area of utmost importance in broiler production (Decuypere *et al.*, 2001; Willemsen *et al.*, 2008; Yassin *et al.*, 2009). A day-old-chick of good quality can be defined as a chick of high performance potential (Tona *et al.*, 2003). High quality day-old-chicks form a significant starting material for improved feed-conversion efficiency and low mortality rates of broiler-flock at slaughter (Tona *et al.*, 2003, 2005; Decuypere & Bruggeman, 2007). Greater survivability and better growth potential during broiler's early life stages are realised through high quality day-old-chicks (Tona *et al*., 2005; Kidd, 2006; Yassin *et al.*, 2009). Day-old-chick quality is related to incubation conditions and egg characteristics, including embryonic reserves in the form of yolk (Tona *et al*., 2005; Decuypere & Bruggeman, 2007). Both these factors influence embryonic development, particularly physiological and hatching parameters (Tona *et al*., 2005). Establishing an independent chick depends on embryonic reserves in place to fuel its transition to feed-utilization, post-hatch (Moran, 2007).

Chick quality is determined using subjective methods which vary from one hatchery manager to the other and these methods are mostly based on chick appearance (Tona *et al*., 2005; Willemsen *et al*, 2008). However, the majority of hatchery managers tend to use almost similar grading scores for chick quality, with much consideration placed on chick activity, down appearance, retracted yolk, eyes, legs, navel, remaining membrane, and remaining yolk (Tona *et al.*, 2003, 2005). Navel condition appears to be the parameter of most importance in determining day-old-chick quality (Tona *et al.*, 2005; Fasenko & O'Dea, 2008). Therefore, much attention and effort needs to be directed towards implementing all the precautions required to attain a high quality day-old-chick, which attains better yields at slaughter.

2.12 DISCUSSION

It is clear from the review that genetic selection techniques have made a major contribution to the improvements observed in increased growth rate, feed conversion efficiency, body weight gain and breast-meat yield of the modern broiler. These improvements are mainly reflected by a decrease in days to market age and an increase in the efficiency with which modern birds convert feed into body tissues. However, such developments have not come without a cost. There are side effects pertaining to the introduction of broiler-breeder genetic selection for increased growth rate and body weight gain. Such side effects include an increase in bird's appetite and voluntary feed intake, resulting in birds that do not adequately regulate feed intake to achieve a proper energy balance when exposed to free-access feeding. This becomes the main cause of broiler-breeder susceptibility to obesity, lowered egg production, reduced fertility and hatchability of settable eggs produced and susceptibility to metabolic and skeletal disorders. Since further developments are likely to take place in genetic selection, this may cause major concerns to the entire field of broiler-breeder production, by putting bird's welfare at stake. Therefore, serious measures need to be taken in order to successfully tackle such problems. Modifying genetic selection objectives to create a balance between growth and reproductive traits, and manipulating maternal diet in order to improve egg composition to support optimum embryonic growth and offspring performance post-hatch, could be few of the solutions to this matter.

Because of their growth taking place outside the maternal body, avian embryos rely entirely on nutrients deposited and stored within the egg for their potential growth and development (Romanoff & Romanoff, 1949; Schaible, 1970). These nutrients are mainly derived from the maternal diet and maternal metabolism. However, what appears to be of most importance, are the amounts, forms, balance, and efficiency with which nutrients are deposited by the breeder hen into the egg, to fully support the potential embryonic growth and development. Since the immune system of the chick is not well developed or fully functional during the first few days post-hatch, it is the responsibility of yolk reserves to support the physiological status and performance of these chicks throughout the transition period to self-sufficiency. Composition of the broiler maternal diet is known to affect production of high quality and fertile hatching eggs (Schaible, 1970). Therefore, adequate maternal nutrition needs to be provided if production of high quality and well performing offspring is to be attained.

Broiler breeder age effects on progeny performance are inconsistent throughout the growing period. Effects of maternal nutrition on offspring performance have not been widely studied. However, conflicting views regarding the effects of maternal nutrition on offspring performance are found in the literature. Lopez & Leeson (1994a, b) and Etches (1996), believe that regardless of egg size or breeder-hen nutrition, hens deposit the same proportion of available nutrients into the egg. Fisher (1998) and Gous & Nonis (2010) assumed that regardless of age or strain, egg amino acid composition is expected to be constant. Contrarily, Schaible (1970) reported that maternal nutrition affects composition and hatchability of fertile eggs. Therefore, there is a research-need to evaluate whether the maternal diet can be used to manipulate egg composition, in order to increase embryonic growth and subsequently improve day-old-chick quality. This dissertation aims to investigate whether broiler-breeder nutrition has any effect on offspring performance, through possible changes in egg composition caused by different maternal dietary amino acid intakes.

3. THE EFFECTS OF BROILER-BREEDER DIETARY LYSINE INTAKE AT 38, 48, AND 60 WEEKS OF AGE ON OFFSPRING PERFORMANCE

3.1 INTRODUCTION

Broiler embryonic growth and development is determined, to a large extent, by the supply of all required nutrients within the egg (Wilson, 1997). This supply of nutrients originates in the maternal diet and maternal metabolism and is further determined by the effective deposition and storage of these nutrients into the egg (Wilson, 1997). Amount and forms of nutrients deposited in the egg determine embryonic development and hatching ability of a healthy chick (Brand *et al.*, 2003). Broiler-breeder diet composition affects the production of fertile hatching eggs. Therefore, adequate maternal nutrition is important for the effective transfer of adequately balanced nutrients into the egg and for maintaining egg production (Ewing, 1963; Rol'nik, 1970; Freeman & Vince, 1974; Wilson, 1997).

Not much research has been conducted on the effects of maternal nutrition on offspring performance. Fisher (1998) and Gous & Nonis (2010) assume that regardless of age or strain, amino acid composition of the egg will remain constant. This assumption is supported by the findings of Lunven *et al*. (1973), which showed no effects of breed or diet on amino acid composition of egg-protein, for eggs collected from laying hens fed on diets containing differing protein levels, from 4 to 48 weeks of age. Lopez & Leeson (1994a, b) and Etches (1996) also reported that hens deposit the same proportion of nutrients in an egg and that an egg would not be produced if the required nutrients were not available in adequate amounts. However, in contrast to this, Schaible (1970) stated that maternal nutrition affects composition and hatchability of fertile eggs. Therefore, it is worth investigating the possible effects of broiler-breeder maternal nutrition on offspring performance through a change in egg composition. The present study was conducted at three different breeder-hen ages, in an attempt to evaluate the effects of maternal dietary lysine intake on offspring performance. Lysine was chosen as it is often used as a basis for setting requirements of other essential amino acids and it is also used exclusively for protein accretion. Lysine is most often the first limiting nutrient in broiler feeds.

3.2 MATERIALS AND METHODS

3.2.1 Parental birds and management

Ethical approval by the University of KwaZulu-Natal Ethics Committee was obtained (reference 051/09/Animal) prior to the start of the experiment, and the code of conduct was adhered to throughout. Nine hundred Cobb 500 broiler-breeder hens and 90 males (22 weeks of age) were bought from a local chicken farm in Pietermaritzburg, and housed in an open-sided house at Ukulinga Research farm, University of KwaZulu-Natal. Fifty females and five males were kept in each of the 18 floor-pens used throughout the duration of the study. Each pen was provided with 10 nest-boxes filled with wood shavings. Separate-sex feeding was performed, with two female and one male feed-trough placed on the floor in each pen. Birds were exposed to 16 hours of artificial light.

3.2.2 Dietary treatments

From 22 to 26 weeks of age, breeders were fed on the same commercial diet (Table 3.3) which they received at the local chicken farm, Pietermaritzburg. Two basal feeds (A & B) were formulated to provide isocaloric diets differing in lysine (Table 3.1). These basal feeds were blended to provide six different treatments in the mash form from 26 to 60 weeks of age. The first four treatments had fixed levels of basal feed A and B, blended as shown in Table 3.2 throughout the duration of the study. The last two treatments (T5 & T6) had different combinations of basal feed A and B, which kept changing with breeder age. At 38 weeks of age, T5 contained 37% basal feed A and 63% basal feed B, while T6 consisted of 63% basal feed A and 37% basal feed B. At 48 weeks of age, T5 contained 69% basal feed A and 31% basal feed B, while T6 consisted of 31% basal feed A and 69% basal feed B. At 60 weeks of age, T5 contained 100% basal feed A and 0% basal feed B, while T6 consisted of 0% basal feed A and 100% basal feed B. Amino acids were modified to provide a balanced amino acid mixture for each diet and each hen was allocated 160 g feed/d. Treatments allowed an intake of 800, 930, 1070, 1200 mg of lysine/bird/d (T1-T4) respectively. An intake of 800 mg/bird/d at 26 weeks increased by 25 mg every two weeks, to provide 1225 mg lysine/bird/d at 60 weeks (T5). An intake of 1200 mg/bird/d at 26 weeks reduced by 25 mg every two weeks, to supply 775 mg of lysine/bird/d at 60 weeks (T6). Each treatment provided 1.9 MJ ME/d and these treatments were fed to the birds from 26 to 60 weeks of age.

Table 3.1 Composition and nutrient content of the experimental feeds (g/kg feed)

Ingredient	Basal A		Basal B	
Maize	57.06		67.47	
Wheat bran	9.18		9.12	
Soybean full fat	24.83		14.31	
L-Lysine HCl	0.07			
DL-Methionine	0.11		0.03	
L-Threonine			0.55	
Vit + min premix	0.25		0.25	
Limestone	6.85		6.92	
Salt	0.17		0.28	
Monocalcium phosphate	0.49		0.50	
Sodium bicarbonate	0.49		0.19	
Potassium carbonate	0.52		0.39	
Nutrients	**Total**	**digestible**	**Total**	**digestible**
AMEn Adult (MJ/kg)	11.88		11.88	
EE	10.79		10.92	
Lysine	0.85	0.75	0.57	0.50
Methionine	0.36	0.33	0.24	0.22
Methionine + cystine	0.66	0.56	0.51	0.43
Threonine	0.59	0.50	1.00	0.93
Tryptophan	0.17	0.15	0.12	0.11
Arginine	1.01	0.91	0.76	0.69
Isoleucine	0.66	0.57	0.50	0.43
Leucine	1.45	1.31	1.26	1.16
Histidine	0.44	0.39	0.36	0.32
Phenyl + tyrosine	1.26	1.10	1.00	0.88
Valine	0.78	0.67	0.63	0.55
Ash	10.07		9.62	
Crude fibre	3.65		3.29	
Crude fat	7.13	6.12	5.58	4.85
Calcium	2.50		2.50	
Avail. Phosphorus	0.25		0.25	
Sodium	0.22		0.18	
Chloride	0.16		0.22	
Potassium	1.00		0.80	
Linoleic acid	3.81		3.20	

Table 3.2 Mixing of basal feed A and B to produce treatments T1-T4

Treatment	Basal Feed A	Basal Feed B
1	-	100%
2	33%	67%
3	67%	33%
4	100%	-

3.2.3 Eggs

A set of 504 eggs (84 eggs/treatment) were collected from breeder hens at 38, 48, and 60 weeks of age, after having been on dietary treatments for a period of 12, 22, and 34 weeks, respectively. Eggs were stored, in each case, for a period of 24 hours before they were set in incubators. They were set in two incubators with half the eggs from each treatment in each incubator and these eggs were marked with the treatment numbers from which they were collected.

3.2.4 Chicks

A total of 320, 401, and 390 chicks hatched from breeder hens at 38, 48, and 60 weeks of age, respectively. Immediately after hatch, 270 (84%), 384 (96%), and 384 (99%) unsexed chicks from breeder hens at 38, 48 and 60 weeks of age, respectively, were placed in an environmentally controlled room and randomly allocated (within a treatment) to single-tier pens measuring 80 × 50 cm. The room-floor was covered with saw-dust to collect the litter. 9 chicks from breeders at 38 weeks of age and 8 chicks from breeders at 48 and 60 weeks of age were placed in each pen; keeping chicks from the same treatment group together for 21 d. Chicks from each treatment group occupied 5 pens, for the first experiment, and 8 pens, for the second and third experiments. Each pen of chicks was weighed at 7, 14 and 21 d. Chicks were fed *ad libitum* on a commercial broiler starter feed fed as crumbles (Table 3.3) for 21 d and water was provided *ad libitum* throughout the duration of each trial. Chicks were exposed to continuous lighting of 23 hours for the 21 d period, with temperatures kept at 31ºC for the first day post-hatch and reduced by 0.5ºC everyday thereafter to reach 21ºC at 21 d of age. Lights were switched off for 30 minutes twice during the night. Mortality was recorded weekly.

Table 3.3 Analysed feed composition

Nutrient	**Composition** (%)
Protein	21.40
Calcium	0.98
Phosphorus	0.65
Moisture	10.53
Ash	6.15
TMEn (MJ/kg)	13.01

3.2.4 Measurements

Individual chick feed intake (FI) was measured by subtracting the amount of feed left in the troughs (feed-out) at the end of each week from the initial feed placed in the troughs (feed-in) at the beginning of each week, divided by the number of birds present in each pen. This figure was further divided by the number of days per week. Feed intake from 7 to 21 d was calculated by subtracting the individual FI at 7 d from the sum of FI obtained at 7, 14, and 21 d. Individual chick body weight gain (BWG) from 7 to 21 d was measured by subtracting 7 d body weight from body weight at 21 d, divided by the number of birds present in each pen. This figure was further divided by the number of days per week. Feed conversion ratio (FCR) was measured by dividing total FI from 7-21 d with BWG from 7-21 d. Since mortality was recorded weekly, feed intake was calculated disregarding the mortality which took place during the week.

3.2.5 Statistical analysis

Analysis of variance (ANOVA) was conducted to determine if there were differences in performance between offspring hatched from breeder hens fed on all six treatment groups (T1-T6), using a generalized linear model (GLM) of GenStat 12th edition (VSN, 2009). Mean treatment differences were detected using least significant difference (LSD) test (VSN, 2009). Simple linear regression analysis was conducted to determine if there was a response to maternal dietary lysine in FI, BWG and FCR of broiler chicks hatched from breeder hens fed on the first four treatments (T1-T4) at 38, 48, and 60 weeks of age, using GenStat 12th

edition (VSN, 2009). Differences among treatments were considered significant at $P < 0.05$. Maternal dietary lysine intake was the only independent variable fitted in the model.

3.3 RESULTS

3.3.1 Chicks hatched from 38-week-old breeder hens

3.3.1.1 Feed intake

Feed intake was significantly improved ($P < 0.05$) from 7-21 d, in chicks hatched from breeder hens fed 800 and 930 mg lysine/bird/d, than in chicks hatched from breeder hens fed 1200 mg of lysine/bird/d and those on 1050 mg lysine/bird/d (that were on treatment where maternal dietary lysine intakes decreased every two weeks) at 38 weeks of age (Table 3.4). Broiler chicks hatched from breeder hens fed 950 mg lysine/bird/d (treatment with maternal dietary lysine intakes increased every two weeks), also displayed significant improvements ($P < 0.05$) in feed intake from 7-21 d, than chicks hatched from breeder hens fed 1200 mg lysine/bird/d (Table 3.4).

Regression analysis of the offspring feed intake from 7-21 d on maternal dietary lysine intake from the first four treatments produced a significant linear response ($P < 0.05$), with offspring feed intake from 7-21 d showing a decrease with an increase in maternal dietary lysine intake (Figure 3.1), however, the R^2 was low (0.33).

3.3.1.2 Body weight gain

Broiler chicks hatched from breeder hens fed 800 mg lysine/bird/d, displayed a significantly improved ($P < 0.05$) body weight gain from 7-21 d, than chicks hatched from breeder hens fed 1050 (treatment with maternal dietary lysine intakes decreased every two weeks) and 1200 mg lysine/bird/d (Table 3.4).

Regression analysis for the offspring body weight gain from 7-21 d on maternal dietary lysine intake from the first four treatments produced a significant response ($P < 0.05$), and a decreasing trend was observed in chick body weight gain from 7-21 d, with an increase in maternal dietary lysine intake (Figure 3.2). However, the R^2 value was also low (0.41).

3.3.1.3 Feed conversion ratio

There were no differences observed in the feed conversion ratio (FCR) from 7-21 d, for chicks hatched from breeder hens fed on all treatment groups at 38 weeks of age (Table 3.4). Regression analysis of the offspring FCR from 7-21 d, for chicks hatched from breeder hens fed on the first four treatments, also showed no linear significant response (Figure 3.3).

Table 3.4 Means ± standard errors of feed intake (FI), body weight gain (BWG), feed conversion ratio (FCR) and overall mortality attained from 7-21 d of broiler chicks hatched from 38-week-old breeder hens

	Treatment means						**s.e.d.**	**Significance**
	T1	T2	T3	T4	T5	T6		
FI (g/bird/d)	142 ± 14.15[c]	128 ± 24.98[c]	102 ± 7.47[abc]	80 ± 9.56[a]	122 ± 9.83[bc]	81 ± 12.11[ab]	20.1	*
BWG (g/bird/d)	97 ± 8.96[b]	74 ± 15.05[ab]	62 ± 7.67[ab]	46 ± 8.06[a]	73 ± 8.04[ab]	47 ± 8.66[a]	13.8	*
FCR (g/g)	1.5 ± 0.02	1.8 ± 0.11	1.7 ± 0.15	1.8 ± 0.09	1.7 ± 0.09	1.8 ± 0.08	0.14	NS
Overall Mortality (%)	0.6 ± 0.32	0.8 ± 0.37	1.4 ± 0.78	1.8 ± 0.77	0.4 ± 0.18	1.4 ± 0.42	0.74	NS

[a, b, c]Means within a row with no common superscripts are significantly different from one another * ($P < 0.05$).

3.3.1.4 Mortality

Weekly mortality and overall mortality of chicks hatched from breeder hens fed on any of the treatments was not significantly different (Table 3.4).

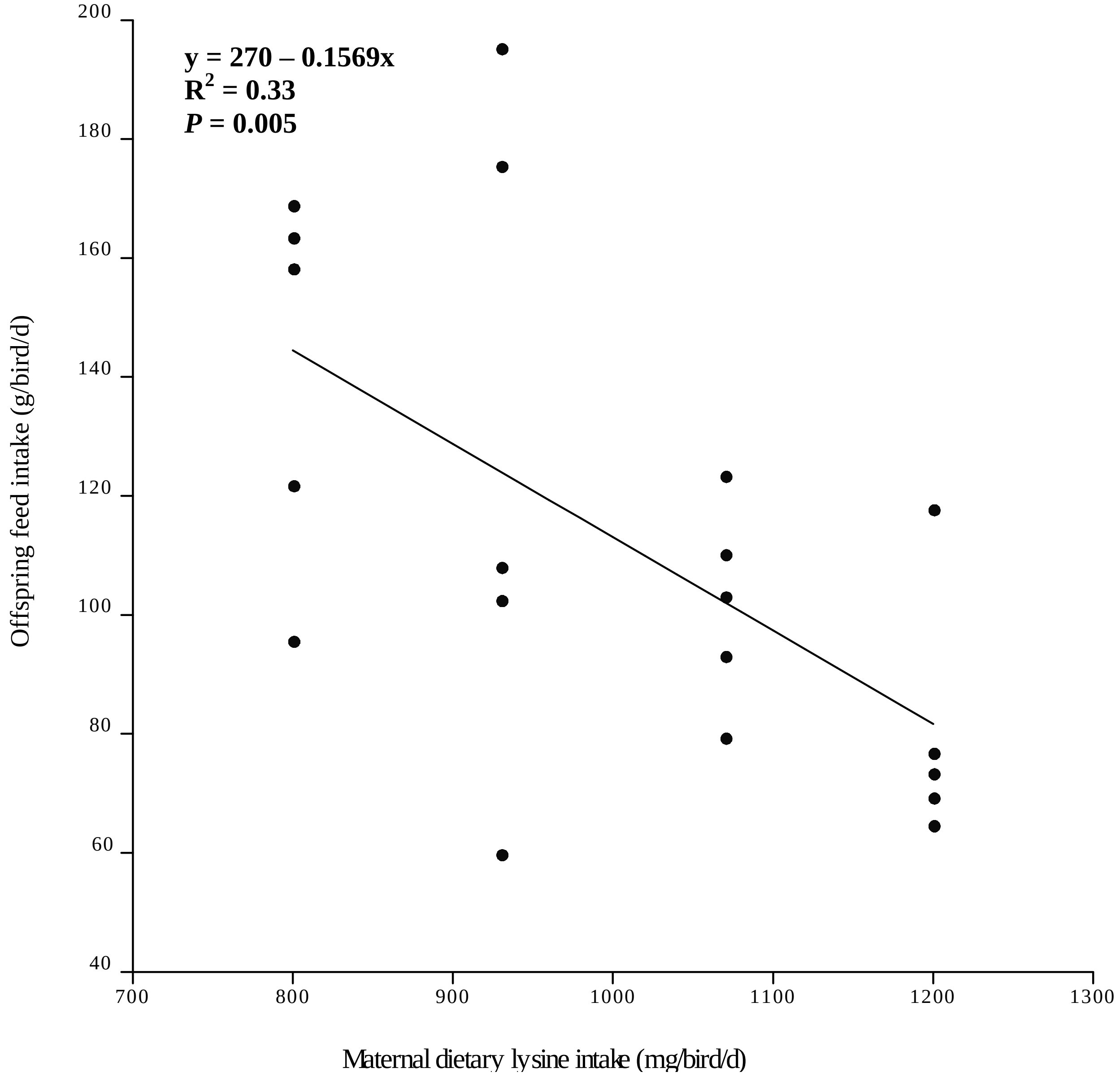

Figure 3.1 Relationship between 38-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring feed intake (FI) from 7-21 d of age.

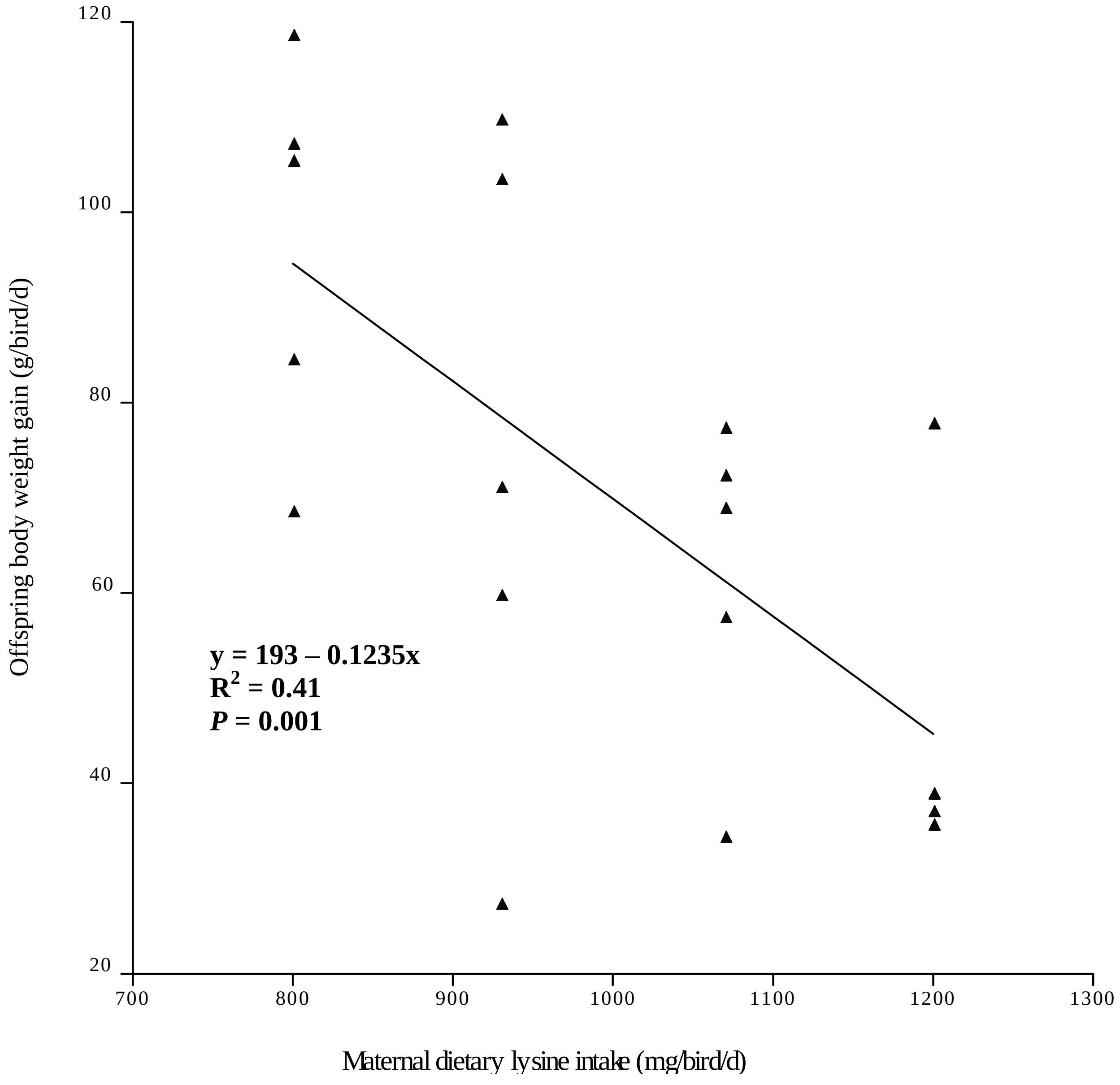

Figure 3.2 Relationship between 38-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring body weight gain (BWG) from 7-21 d of age.

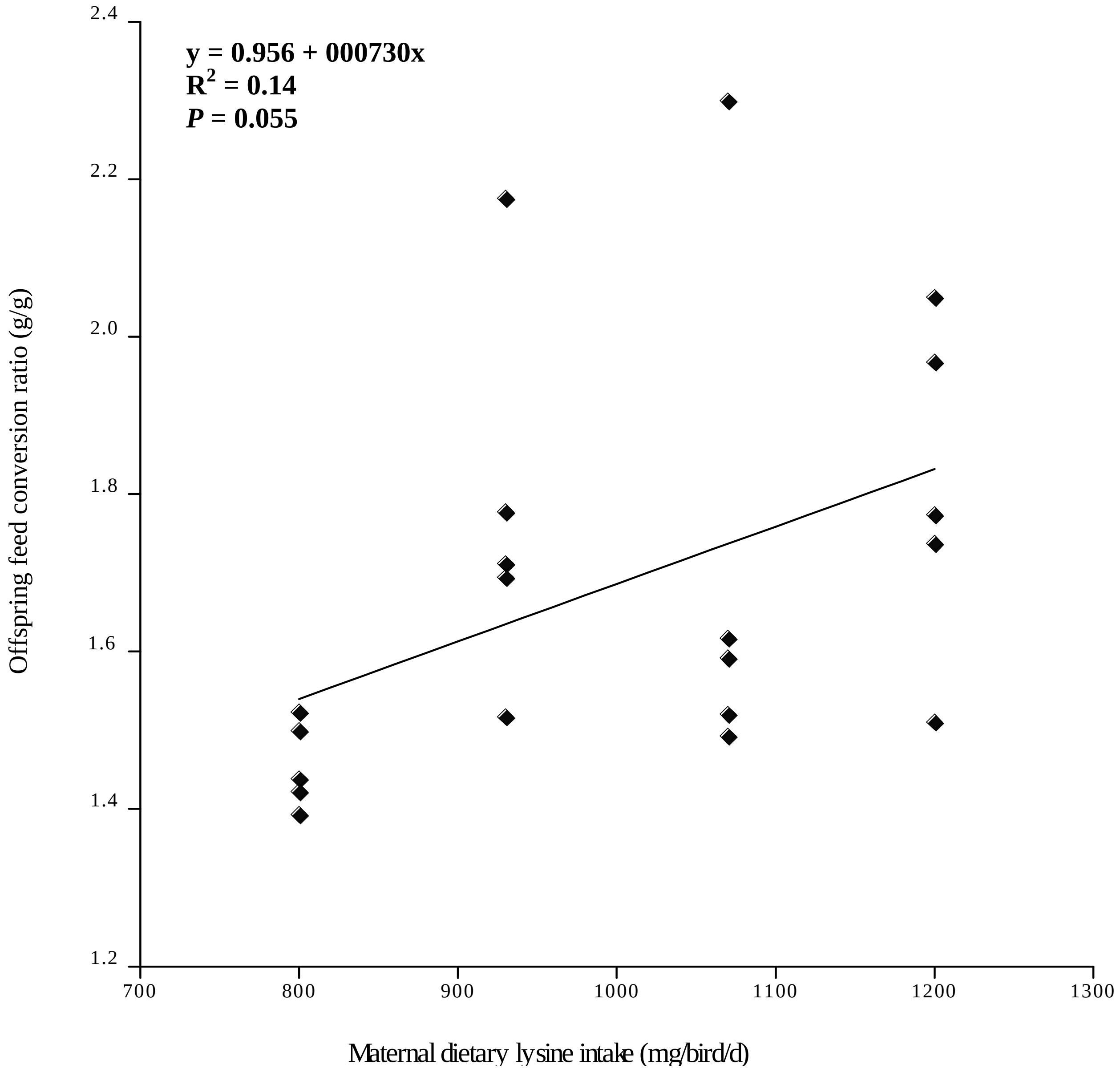

Figure 3.3 Relationship between 38-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring feed conversion ratio (FCR) from 7-21 d of age.

3.3.2 Chicks hatched from 48-week-old breeder hens

3.3.2.1 Feed intake

Broiler chicks hatched from breeder hens fed on the treatment where maternal dietary lysine intakes decreased by 25 mg/bird/d (diet offered an intake of 925 mg lysine/bird/d at 48 weeks) every two weeks, from 26 weeks, showed significant improvements ($P < 0.05$) in feed intake from 7-21 d than chicks hatched from breeder hens fed 800, 930, and 1200 mg lysine/bird/d (Table 3.5). Feed intake was also significantly improved ($P < 0.05$) from 7-21 d in chicks hatched from breeder hens fed treatment with maternal dietary lysine intakes increased by 25 mg/bird/d (diet provided an intake of 1075 mg lysine/bird/d at 48 weeks) every two weeks, from 26 weeks, than in chicks hatched from breeder hens fed 800 and 1200 mg lysine/bird/d (Table 3.5).

Regression analysis identified no response in feed intake from 7-21 d, for chicks hatched from breeder hens fed on the first four treatments (Figure 3.4).

3.3.2.2 Body weight gain

No significant differences were determined in offspring body weight gain from 7-21 d, for chicks hatched from breeder hens fed on all treatment groups (Figure 3.5). No significant response in body weight gain from 7-21 d was observed in chicks hatched from breeder hens fed on the first four treatments (Figure 3.5).

3.3.2.3 Feed conversion ratio

There were no significant differences in feed conversion ratio from 7-21 d of chicks hatched from breeder hens fed on all treatment groups at 48 weeks of age (Table 3.5). There was also no significant response of feed conversion ratio from 7-21 d, in chicks hatched from breeder hens fed on the first four treatments (Figure 3.6).

3.3.2.4 Mortality

There were no differences observed in weekly mortality and overall mortality of broiler chicks hatched from breeder hens fed on any of the treatments throughout the duration of the trial (Table 3.5).

Table 3.5 Means ± standard errors of feed intake (FI), body weight gain (BWG), feed conversion ratio (FCR) and overall mortality attained from 7-21 d of broiler chicks hatched from 48-week-old breeder hens

	Treatment means						s.e.d.	Significance
	T1	T2	T3	T4	T5	T6		
FI (g/bird/d)	151 ± 2.57[a]	154 ± 4.10[ab]	156 ± 2.66[abc]	149 ± 1.45[a]	159 ± 1.82[bc]	162 ± 2.72[c]	3.8	*
BWG (g/bird/d)	99 ± 2.27	97 ± 1.63	94 ± 1.80	94 ± 2.70	93 ± 3.10	99 ± 2.49	3.4	NS
FCR (g/g)	1.5 ± 0.04	1.6 ± 0.04	1.7 ± 0.04	1.6 ± 0.05	1.7 ± 0.07	1.6 ± 0.06	0.07	NS
Overall Mortality (%)	0.25 ± 0.16	0.25 ± 0.16	0.13 ± 0.13	0.13 ± 0.13	0.38 ± 0.18	0.50 ± 0.27	0.25	NS

[a, b, c]Means within a row with no common superscripts are significantly different from one another * ($P < 0.05$).

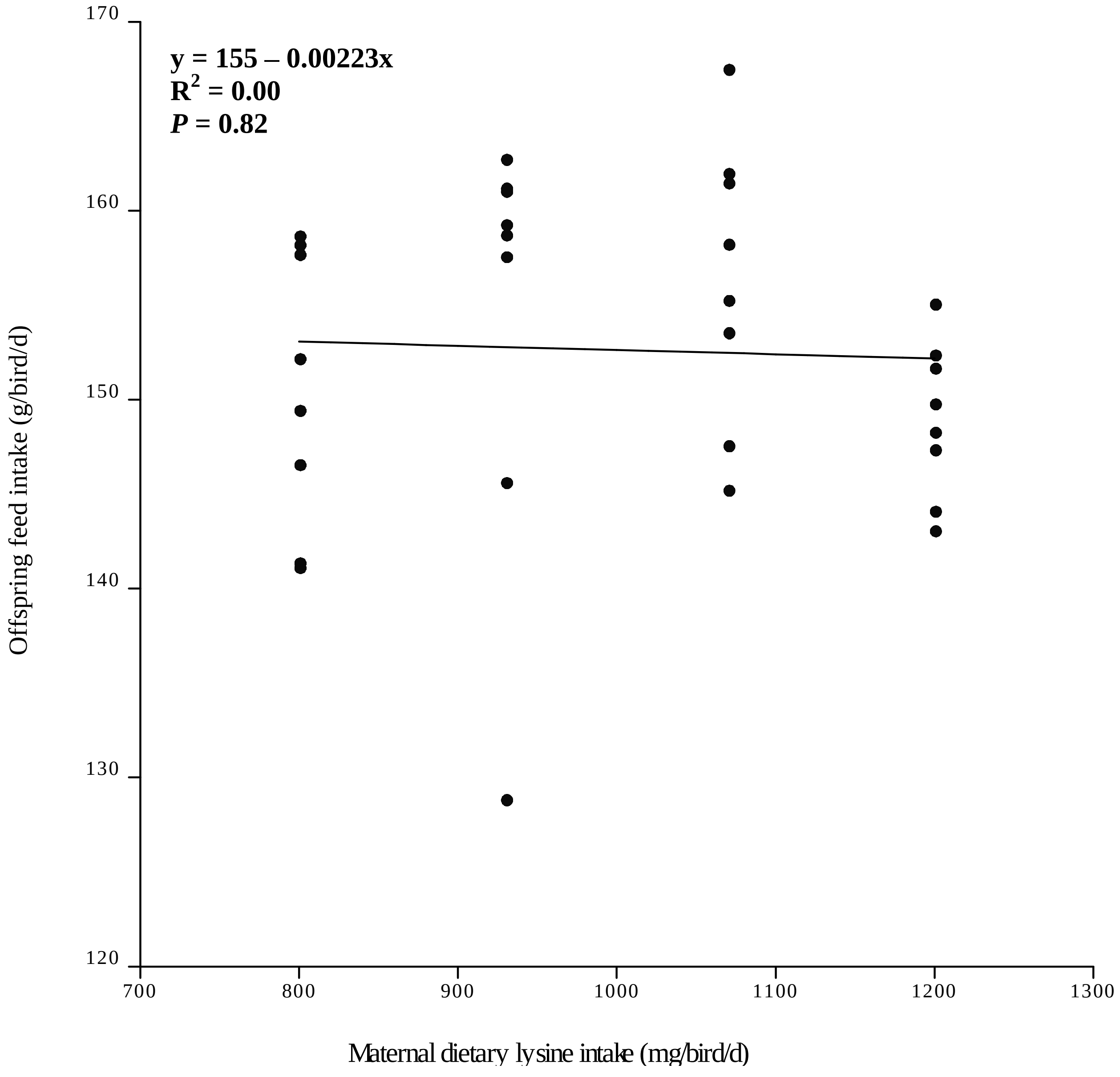

Figure 3.4 Relationship between 48-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring feed intake (FI) from 7-21 d of age.

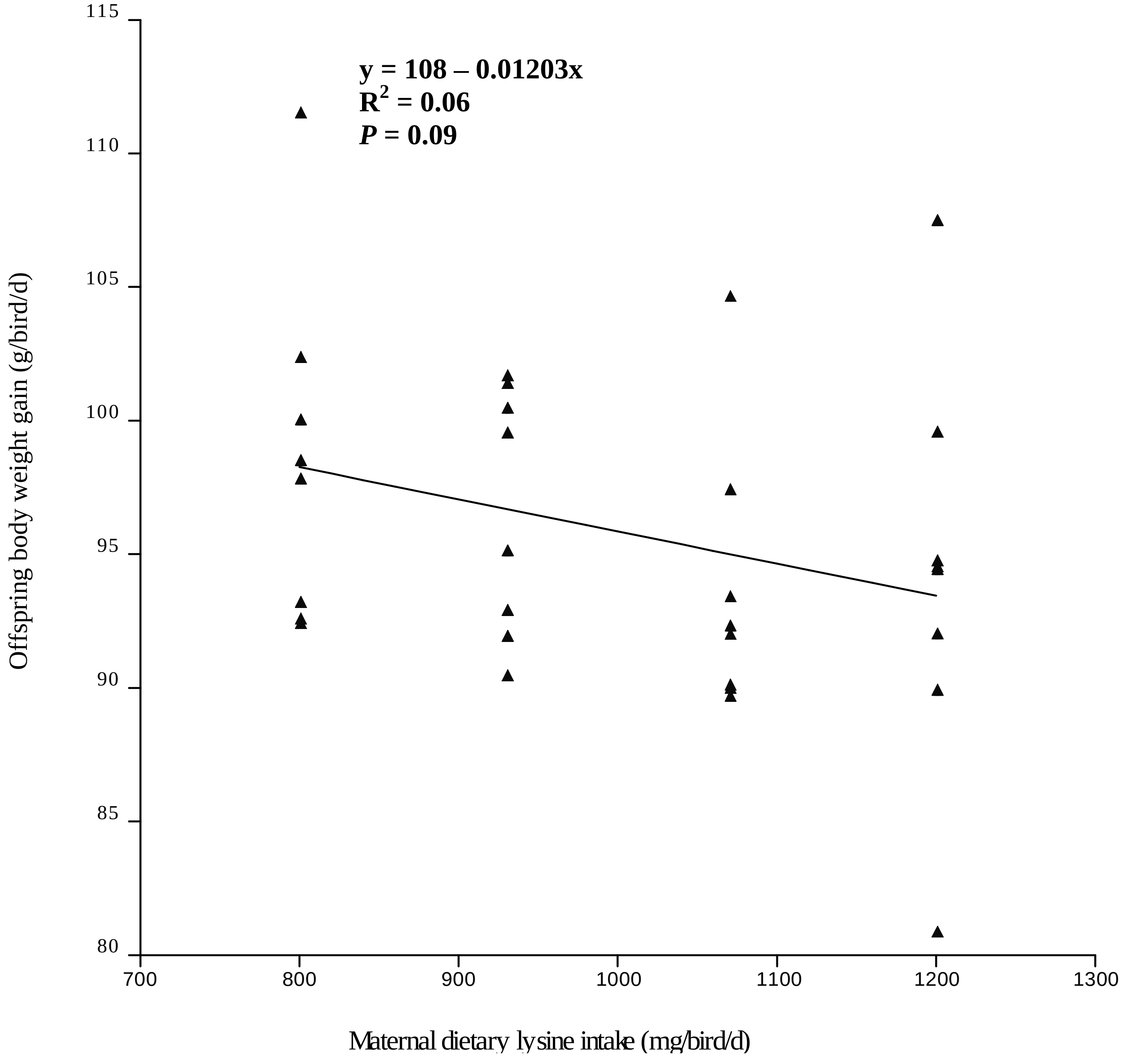

Figure 3.5 Relationship between 48-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring body weight gain (BWG) from 7-21 d of age.

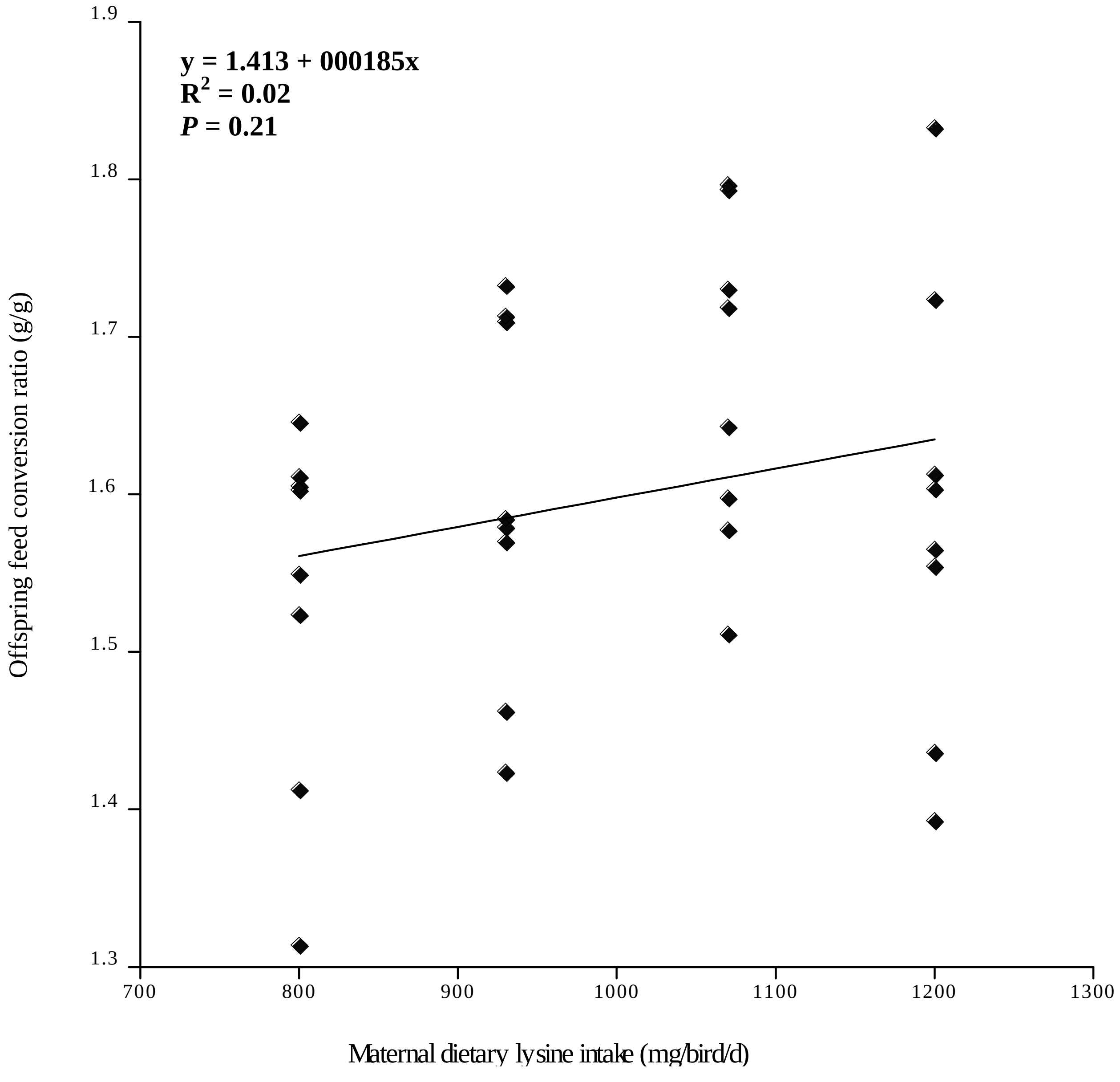

Figure 3.6 Relationship between 48-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring feed conversion ratio (FCR) from 7-21 d of age.

3.3.3 Chicks hatched from 60-week-old breeder hens

3.3.3.1 Feed intake

Offspring feed intake from 7-21 d showed no differences in chicks hatched from breeder hens fed on all treatment groups at 60 weeks of age (Table 3.6). No significant response in feed intake from 7-21 d, of chicks hatched from breeder hens fed on the first four treatments was observed (Figure 3.7).

3.3.3.2 Body weight gain

There were no significant differences in body weight gain from 7-21 d of broiler chicks hatched from breeder hens fed on all treatment groups at 60 weeks of age (Table 3.6). Significant responses were not observed in body weight gain from 7-21 d, of chicks hatched from breeder hens fed on the first four treatments (Figure 3.8).

3.3.3.3 Feed conversion ratio

Broiler chicks hatched from breeder hens fed on all treatment groups at 60 weeks of age, showed no differences in feed conversion ratio from 7-21 d (Table 3.6). There was also no significant response in feed conversion ratio from 7-21 d, of chicks hatched from breeder hens fed any of the treatments at 60 weeks of age (Figure 3.9).

3.3.3.4 Mortality

Weekly mortality and overall cumulative mortality of chicks hatched from breeder hens fed on all treatment groups at 60 weeks of age, showed no differences throughout the duration of the trial (Table 3.6).

Table 3.6 Means ± standard errors of feed intake (FI), body weight gain (BWG), feed conversion ratio (FCR) and overall mortality attained from 7-21 d of broiler chicks hatched from 60-week-old breeder hens

	Treatment means						**s.e.d.**	**Significance**
	T1	T2	T3	T4	T5	T6		
FI (g/bird/d)	140 ± 2.66	119 ± 17.3	135 ± 4.89	102 ± 22.4	138 ± 1.88	139 ± 4.00	16.8	NS
BWG (g/bird/d)	98 ± 1.75	84 ± 12.2	93 ± 3.31	72 ± 15.7	96 ± 0.96	100 ± 3.03	11.8	NS
FCR (g/g)	1.4 ± 0.03	1.2 ± 0.18	1.4 ± 0.02	1.1 ± 0.23	1.4 ± 0.01	1.4 ± 0.01	0.17	NS
Overall Mortality (%)	0.25 ± 0.16	0.38 ± 0.18	0.75 ± 0.49	0.12 ± 0.13	0.88 ± 0.30	0.50 ± 0.27	0.40	NS

No significant differences were observed and no superscripts used.

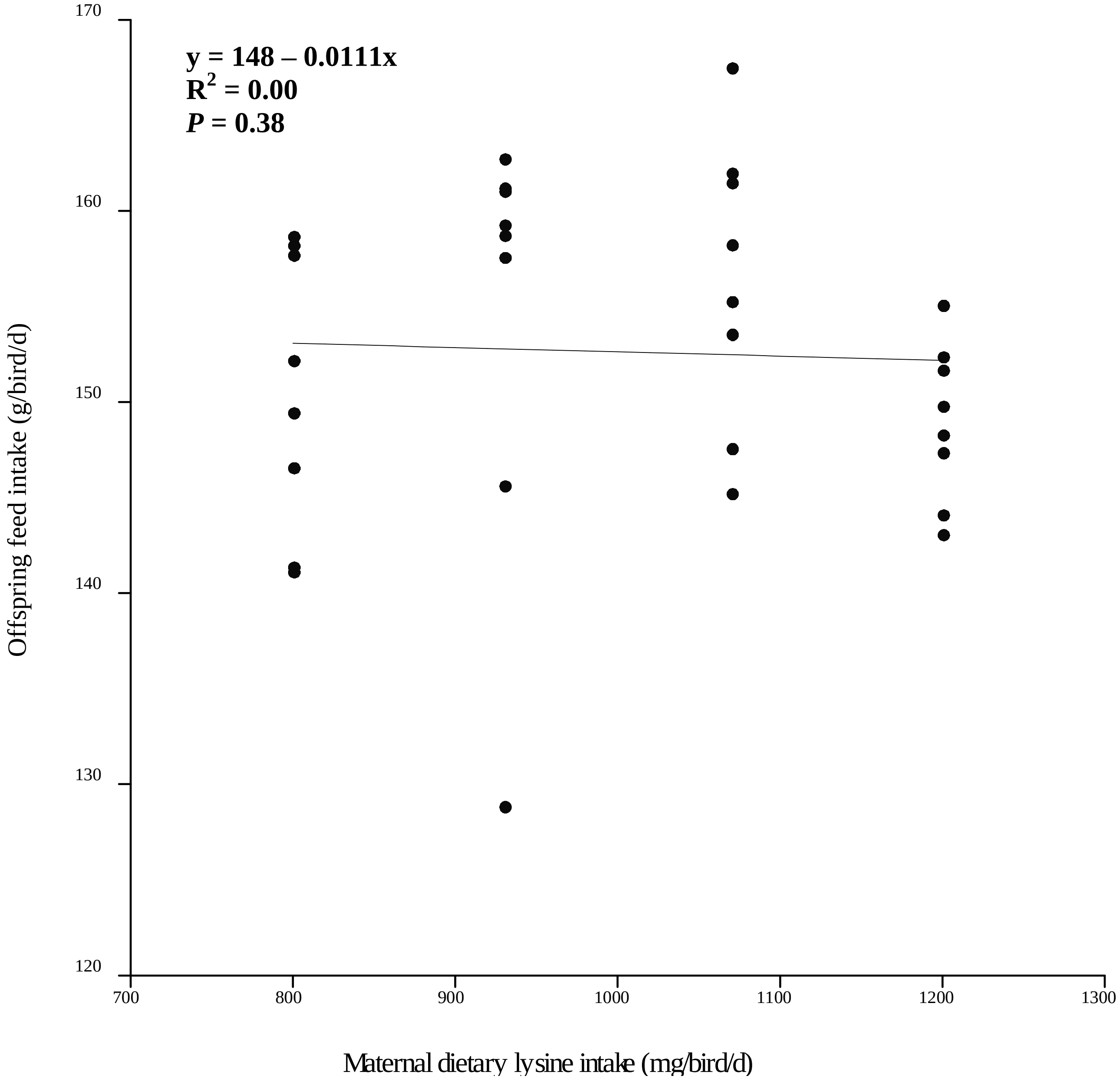

Figure 3.7 Relationship between 60-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring feed intake (FI) from 7-21 d of age.

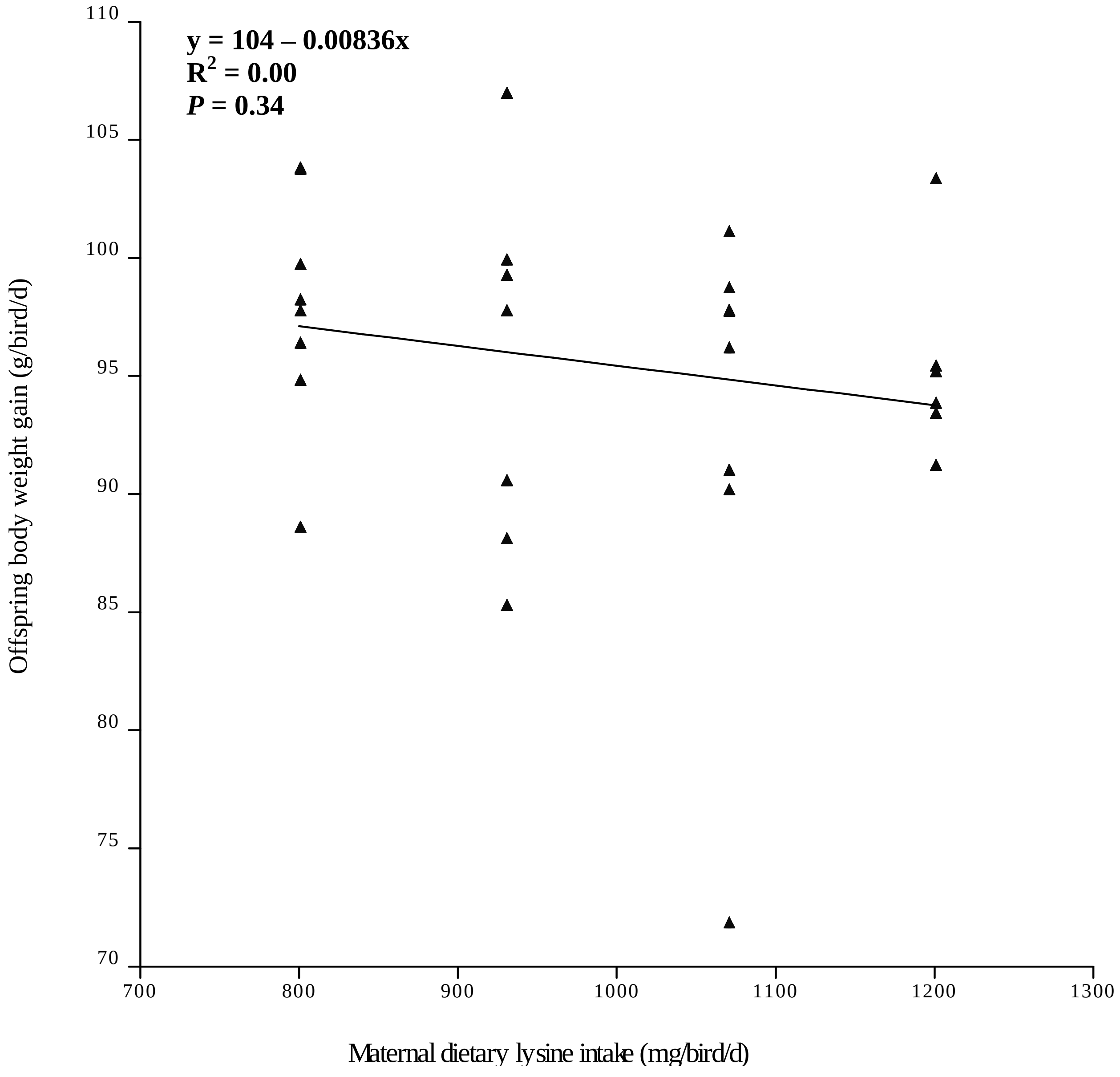

Figure 3.8 Relationship between 60-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring body weight gain (BWG) from 7-21 d of age.

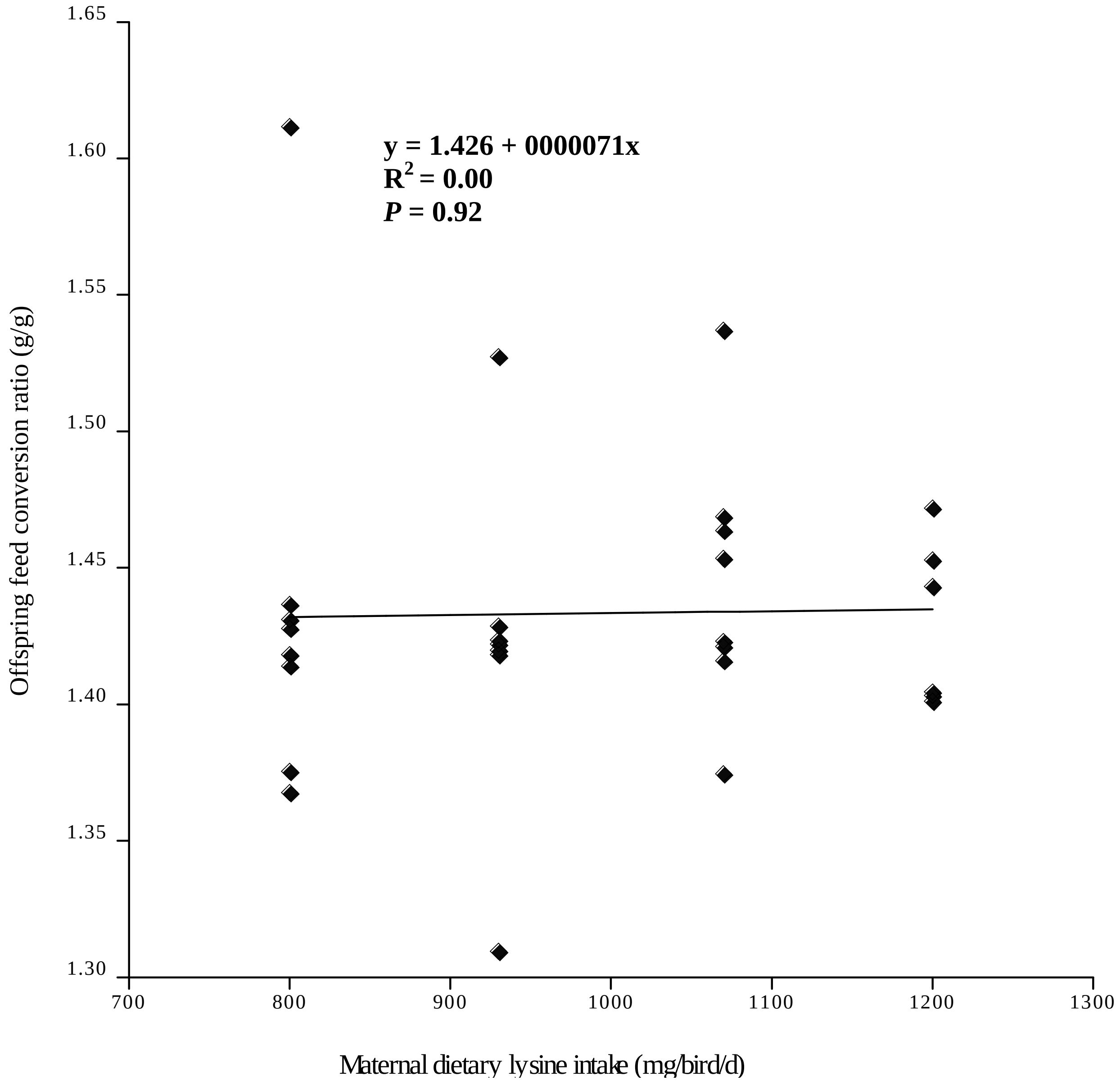

Figure 3.9 Relationship between 60-week-old broiler-breeder maternal dietary lysine intake of 800, 930, 1070 and 1200 mg/bird/d, and offspring feed conversion ratio (FCR) from 7-21 d of age.

3.4 DISCUSSION

The dramatic improvements observed in broiler performance, following intensive genetic selection for rapid growth and increased body weight, are posing a challenge in broiler-breeder reproductive performance. Broiler-breeder hens' ability to lay more fertile hatching eggs, has been negatively affected by these genetic selection developments. This is largely caused by the inverse correlation between the traits of increased body weight and egg production. Normally, heavy birds are unable to lay more eggs, due mainly to layers of fat covering their reproductive organs. The few eggs produced by broiler-breeder hens tend to exhibit shell defects and multiple ovulations, thus leading to lowered fertility and hatchability. This is a main concern that needs to be addressed in broiler-breeder operations. Extensive research has been conducted in using feed-restriction programs as possible solutions in tackling broiler-breeder reproductive-related problems. The potential of feed-restriction programs in reducing weight gain whilst increasing broiler-breeder egg production, has been reported in a number of studies. However, the effects of feed-restriction on broiler-breeder egg composition, fertility and hatchability have not been extensively studied.

Hocking (2007) proposed a research-need, for a cooperative investigation to evaluate the effects of optimum maternal dietary nutrient concentrations on chick quality. Investigation of possible ways to improve broiler-breeder reproductive efficiency, or quality of their few laid eggs, is also needed. This may help increase the production and quality of fertile hatching eggs, which produce high-quality chicks that can be used to produce the next generation of breeder birds, which have the capacity to put balance between growth and reproduction traits. There has been less attention dedicated to investigating the possible effects of broiler-breeder nutrition on egg composition and offspring performance, as an alternative towards tackling the reproductive challenges encountered in broiler-breeder production. This study was conducted to evaluate the effects of broiler-breeder maternal dietary lysine intake on offspring performance. Hocking (2007) suggested that research conducted to quantify the effects of maternal nutrition on chick quality, should not rely on assumed nutrient deficiencies in order to be able to guarantee responses. Dietary concentrations that are in excess of the current recommendations, need to be examined (Hocking, 2007). Therefore, maternal dietary lysine intakes ranging from 800 to 1200 mg/bird/d were used in the present study.

Tona *et al*. (2003, 2005), reported that a high-quality day-old-chick forms a significant starting material for the improved feed-conversion efficiency and body weight gain of a broiler flock at slaughter. In the present study, offspring performance with regards to feed intake, body weight gain and feed conversion ratio from 7-21 d, were compared in broiler chicks hatched from 38, 48 and 60-week-old breeder hens with differing dietary lysine intakes. The significant improvements observed in feed intake, from 7-21 d, of broiler chicks hatched from 38-week-old breeders with dietary lysine intakes of 800, 930 and 950 mg/bird/d, were indicating that broiler breeder hen nutrition may have positively affected the offspring performance at early breeder hen production stages. Broiler breeder hens at 38 weeks of age might have had lower dietary lysine maintenance requirements and, they were thus able to channel appreciable amounts of lysine toward supporting potential embryonic growth and development and the subsequent broiler performance, post-hatch.

These results were in agreement with the findings of Enting *et al*. (2007), who reported that offspring performance can be improved by feeding low-density maternal diets during the rearing and laying periods. Gous & Nonis (2010) assumed that the rules of broiler-breeder protein partitioning, give maintenance a higher priority, while yolk and albumen protein deposition are prioritised second and third, respectively. Joseph *et al*. (2000) also interpreted the increases in mean-egg weight and mean egg-production, obtained in their study after increasing broiler breeder dietary crude protein from 14 to 16 or 18% during the laying period, as suggesting that the additional protein was partitioned towards improving reproduction.

The significantly improved body weight gain from 7-21 d, of chicks hatched from 38 week-old breeder hens with dietary lysine intake of 800 mg/bird/d, was associated with the improved feed intake of these birds. This was however not reflected in an improved feed conversion ratio. These results were not expected, as it was thought that chick performance in feed intake and body weight gain, would increase with an increase in maternal dietary lysine intake. Enting *et al*. (2007) reported that an increase in offspring growth may be related to an increase in parental nutrient intake, however, this was contradicted by results of the present experiment. There is a possibility that progeny performance, might only be increasing with an increase in maternal dietary nutrient intake, up to a point where the animal reaches its maximum requirements for that particular nutrient. The current results were also in contrast with the findings of Spratt & Leeson (1987), who reported no effects of broiler-breeder protein intake at 29 weeks of age, on offspring body weight and feed conversion. Wilson & Harms (1984) also reported no effects of broiler-breeder nutrition at 39 and 56 weeks of age, on offspring 49-day body weight, however, chicks were only grown up to 21 days in the present study. There is no readily available explanation for the differences in the results of these studies.

Improvements in offspring feed intake and body weight gain from 7-21 d, in the present experiment, were mainly pronounced in chicks hatched from 38-week-old breeder hens with low dietary lysine intakes (800, 930 and 950 mg/bird/d). These findings were suggesting that the young 38-week-old breeder hens used in the present experiment and possessing low nutrient requirements, might have invested a reasonable amount of nutrients toward supporting potential embryonic growth and offspring performance, post-hatch. Harms & Ivey (1992) reported a reduction in the amount of lysine required to produce one gram of egg content-mass, which was pronounced with a decrease in broiler-breeder dietary protein and lysine intakes. They interpreted their findings as indicating better utilization of lysine at low broiler-breeder dietary protein levels. Contrarily, Cave (1984) reported a low feed required per egg in breeder hens fed high-protein diet, when compared to breeder hens fed a low-protein diet, during the pre-breeder period.

The decreasing trend observed in feed intake and body weight gain, from 7-21 d, in chicks hatched from 38-week-old breeder hens fed the first four treatments with an increase in maternal dietary lysine intake, indicated that providing low lysine diets (800, 930 and 950 mg lysine/bird/d) at 38 weeks of age, could reduce broiler-breeder production-costs in terms of feeding and improving offspring performance. This may, however, have a negative effect on egg production, as low broiler-breeder dietary protein and lysine intakes are known to reduce egg production (Harms & Ivey, 1992; Joseph *et al*., 2000).

The continuous increases or decreases in maternal dietary lysine intakes by 25 mg/bird/d every two weeks, from 26 weeks, showed no differing effects on offspring performance, to that exerted by diets with fixed maternal lysine intakes throughout the duration of the trial. This was noticed in chicks, hatched from 38-week-old breeder hens with dietary lysine intakes changed every two weeks, from 26 weeks, showing similar performances in feed intake and body weight gain from 7-21 d; to that of one or more groups of chicks hatched from breeder hens with fixed dietary lysine intakes. This indicates that continuously changing broiler breeder nutritional composition at 38 weeks of age, may have no affects in offspring post-hatch performance. There was a higher variability in feed intake and body weight gain observed among chicks hatched from 38-week-old breeder hens fed 930 mg lysine/bird/d. This was demonstrated by a higher standard error of mean (Table 3.4) and a wide distribution of points in Figure 3.1 & 3.2. There is no readily available explanation of what could have caused such variations in feed intake and body weight gain performance among chicks which hatched from breeder hens fed on this treatment.

At 48 weeks of age, the treatments in which maternal lysine intake was changing every two weeks, provided an intake of 925 and 1075 mg lysine/bird/d, for the increasing and decreasing intakes, respectively. These treatments were already regarded as treatments of low dietary lysine intake. Therefore, from the trend of results observed in chicks hatched from breeder hens at 38 weeks of age, it was not surprising to notice that chicks from these two treatments showed better performance in feed intake from 7-21 d, than chicks hatched from breeder hens fed higher dietary lysine intakes (1200 mg/bird/d) at 48 weeks of age. However, the differences observed between chicks hatched from breeder hens fed these treatments, and that of chicks hatched from breeder hens fed 800 mg lysine/bird/d, at 48 weeks, came as a surprise since all these treatments were regarded as low dietary lysine intake treatments. These results could be interpreted as indicating that 800 mg lysine/bird/d was not supplying adequate nutrients required to meet the maintenance requirements of the aging breeder hens. This, therefore, suggests that breeder hens fed 800 mg lysine/bird/d, at 48 weeks, were unable to channel sufficient nutrient amounts toward supporting the potential embryonic growth and performance of the broiler chick, post-hatch.

The explanation used previously about high maintenance requirements which increases with broiler breeder age, may also be applicable in results observed in chicks hatched from 60-week-old breeder hens. Broiler breeder hens at 60 weeks of age, may have invested inadequate amounts of nutrients needed to sufficiently support potential embryonic growth and offspring performance, post-hatch. This may possibly explain why there were no observed responses in chicks hatched from breeder hens fed on all treatment groups at 60 weeks of age. The present findings are in line with the results of Lopez & Leeson (1994a) and Kingori *et al*. (2010). These authors reported no effects of maternal dietary protein intake on egg components, egg composition, hatchability and post-hatch offspring performance, for chicks hatched from hens fed differing levels of dietary protein at 45 and 52 weeks of age, respectively. Lopez & Leeson (1994a) used Arbor Acre breeder hens while Kingori *et al*. (2010) used indigenous breeder hens to conduct their respective experiments. Using commercial broiler breeder and egg-type layer stock with the same dietary treatments as those used in this research, Ruck (2011) found an increasing response to maternal lysine intake in the offspring of the meat-type stock. Contrarily, the offspring of the egg type layer stock responded negatively to high levels of maternal lysine intake, with the best performance observed in chicks hatched from hens consuming less lysine. It is possible that the experimental diets used in those trials were not appropriate to elicit a response in the genotypes used.

Fisher (1998) and Gous & Nonis (2010) assumed that egg amino acid composition is expected to be constant throughout the life stages of differing bird strains. This assumption was supported by results of Lunven *et al*. (1973), which showed no breed or dietary effects on amino acid composition of egg protein for eggs collected from laying hens fed diets containing differing dietary protein levels from 4 to 48 weeks of age. Lopez & Leeson (1994a) also reported no maternal dietary protein effects on egg components, egg composition and offspring performance from breeder hens fed differing protein levels at 45 weeks of age. Increasing nutrient density in Leghorn strains during phase one, also had no effects on percentage yolk and whole-egg solids from 21 to 36 weeks of age (Wu *et al*., 2007). There were little to no changes observed in egg composition of 30 and 50-week-old breeder hens fed differing levels of crude protein diets supplemented with synthetic methionine and lysine (Lopez & Leeson, 1995). Increasing protein intake of 70-week-old molted Hy-Line W-36 hens, exhibited no effects on albumen, yolk, or whole-egg solids (Gunawardana *et al*., 2008a).

In contrast to these studies, Gunawardana *et al*. (2008b) reported an increase in albumen and whole-egg solids, with an increase in dietary lysine intake of 39-week-old different laying strains. Harms & Russell (1995) also reported an increase in egg content of broiler-breeders when supplemental lysine was added in a corn-soybean meal diet at 34 weeks of age. Egg composition was not measured in the present study. Therefore, it was not clear whether differences in offspring performance observed from 7-21 d, in chicks hatched from 38- and 48-week-old breeder hens with low dietary lysine intakes (800, 930 and 950 mg/bird/d), were due to possible changes in egg composition. This, following manipulation of the maternal nutrition or by means of an unknown mechanism, with which embryos efficiently utilized available nutrients.

The overall results of the present study were interpreted as indicating, that requirements for broiler-maternal dietary lysine, may increase with an increase in breeder-flock age from 26 to 48 weeks of age. This may explain the offspring performance improvements observed from 7-21 d, of chicks hatched from 38- and 48-week-old breeder hens with low dietary lysine intakes (800, 930 and 950 mg/bird/d). These improvements were no longer pronounced in chicks hatched from 60-week-old breeder-hens fed similar treatments. The correlation which was observed between offspring performance and maternal dietary lysine intake, from the first four treatments at 38 weeks of age, also disappeared with the aging of the flock (48 and 60 weeks). Therefore, improvements in offspring performance, particularly with the use of current treatments, were only pronounced when chicks hatched from young breeder flocks (38 weeks) with low dietary lysine intakes (800, 930 and 950 mg/bird/d).

The study reported herein was conducted at three broiler breeder ages; namely 38, 48 and 60 weeks of age. Broiler breeder age seemed to have an effect on offspring performance, since significant improvements in offspring feed intake and body weight gain from 7-21 d, were mainly pronounced in chicks hatched from 38-week-old breeder hens. These results were consistent with the findings of Peebles *et al*. (1999a), who observed a better performance, from 0 to 21 d, in chicks hatched from 35-week-old breeder hens, than that of chicks hatched from 51- and 65-week-old breeder hens. However, Ulmer-Franco *et al*. (2010) reported higher final body weigh in chicks hatched from 59-week-old breeder hens, than that of chicks hatched from 29-week-old breeder hens.

The current results were thought of as suggesting that, even though egg composition was not measured, changes in maternal dietary lysine intake may have modified egg composition of young broiler-breeder flocks from 26 to 48 weeks of age. These speculated changes in egg composition of young breeders were associated with the observed performance improvements of the offspring hatched from these eggs. The lack of response from broiler chicks hatched from breeder hens with high dietary lysine intakes is not clear, as they were expected to perform better than chicks hatched from breeder hens with low dietary lysine intakes. Breeder hens with high dietary lysine intakes, were expected to deposit more nutrients from their lysine-rich diet into the egg and support potential embryonic growth and post-hatch progeny performance, better than breeder hens with low dietary lysine intakes. However, excess consumption of an essential amino acid was reported as likely to limit the efficiency of nutrient utilisation relative to the optimum balance (D'Mello & Lewis, 1970). Hocking (1987) also reported that in cases where protein intake is excessive, apparent utilization becomes poor. It is possible, therefore, that high dietary lysine intakes (1200 mg/bird/d), of broiler breeder hens from 26 to 60 weeks of age, impaired the bird's ability to efficiently use nutrients and adequately support the growth of the offspring post-hatch.

It was concluded that, when the present specific treatments are used, lower maternal dietary lysine intakes (800, 930 and 950 mg/bird/d) are more likely to improve feed intake and body weight gain from 7-21 d, of broiler chicks hatched from younger breeder flocks (38 to 48 weeks). Since maternal dietary lysine intake showed no effects on offspring performance when chicks hatched from older flocks (48 and 60 weeks), it is likely that reducing lysine composition in maternal diets could reduce feed cost. However, the effects of this on egg weight and production as well as the subsequent chick weight are not known. The main focus of future studies can be directed on the effects of maternal nutrition, using differing ages of breeder flocks, on amino acid composition; fertility; and hatchability of broiler-breeder eggs. These are parameters which form the basis for the production of high-quality chicks and impact on the economics of poultry production systems.

4. GENERAL DISCUSSION

The objective of this research was to evaluate the effects of broiler breeder maternal dietary lysine intake. The results of this work were able to show that breeder hens given high dietary lysine levels (1070 and 1200 mg/bird/d), from 26 to 60 weeks of age, are unable to channel sufficient amount of nutrients toward supporting a better performance of their offspring. Therefore, feeding high dietary lysine concentrations from 26 to 60 weeks of age may increase the broiler breeder-cost of feeding and reduce bird's ability to utilize nutrients efficiently.

The current findings showed that, when the present specific treatments are used, feed intake and body weight gain, from 7-21 d of broiler chicks, can be improved by lower maternal dietary lysine intakes (800, 930 and 950 mg/bird/d) fed to younger breeder flocks (38 weeks). This further indicates that providing low lysine diets (800, 930 and 950 mg lysine/bird/d) at 38 weeks of age, is more likely to reduce broiler-breeder production-costs with regards to feeding and improving offspring performance. However, this may negatively affect egg production, since low dietary protein and lysine intakes have been reported to reduce egg production. The results of this study further suggested that broiler-breeder maternal dietary lysine requirements may increase, with an increase in flock age from 26 to 48 weeks of age.

Egg composition was not measured in the present study, therefore, it is still not clear whether improvements observed in offspring performance, for chicks hatched from younger breeder-flocks (38 weeks) with low dietary lysine intakes (800, 930 and 950 mg/bird/d), were due to any possible changes in egg composition caused by differing maternal dietary lysine intakes, from 26 to 48 weeks of age. It is, therefore, important to find the underlying mechanism affecting broiler offspring performance, and whether it is due to a change in egg composition, or to another mechanism affecting subsequent broiler growth. Using breeder-flocks of closely-related ages will facilitate noting when changes in offspring performance are caused by maternal dietary protein intake.

REFERENCES

Abdel-Maksoud, A., Yan, F., Cerrate, S., Coto, C., Wang, Z. and Waldroup, P.W., 2010. Effect of dietary crude protein, lysine level, and amino acid balance on performance of broilers 0 to 18 days of age. International Journal of Poultry Science, **9:**21-27.

Abudabos, A., 2010. The effect of broiler breeder strain and parent flock age on hatchability and fertile hatchability. International Journal of Poultry Science, **9(3):**231-235.

Adedokun, S.A., Utterback, P., Parsons, C.M., Adeola, O., Lilburn, M.S. and Applegate, T.J., 2009. Comparison of amino acid digestibility of feed ingredients in broilers, laying hens and caecectomised roosters. British Poultry Science, **50:**350-358.

Ahn, D.U., Kim, S.M., and Shu, H., 1997. Effect of egg size and strain and age of hens on the solids content of chicken eggs. Poultry Science, **76:**914-919.

Almeida, J.G., Vieira, S.L., Reis, R.N., Berres, J., Barros, R., Ferreira, A.K. and Furtado, F.V.F., 2008. Hatching distribution and embryo mortality of eggs laid by broiler breeders of different ages. Brazilian Journal of Poultry Science, **10:**89-96.

Al-Murrani, W.K., 1978. Maternal effects on embryonic and post-embryonic growth in poultry. British Poultry Science, **19:**277-281.

Al-Murrani, W.K., 1982. Effect of injecting amino acids into the egg on embryonic and subsequent growth in the domestic fowl. British Poultry Science, **23:**171-174.

Anderson, K.E., Tharrinton, J.B., Curtis, P.A. and Jones, F.T., 2004. Shell characteristics of eggs from historic strains of single comb white leghorn chickens and the relationship of egg shape to shell strength. International Journal of Poultry Science, **3:**17-19.

Angel, A., 2007. Metabolic disorders: Limitations to growth of and mineral deposition into the broiler skeleton after hatch and potential implications for leg problems. Journal of Applied Poultry Research, **16:**138-149.

Atencio, A., Edwards, H.M., Jr. and Pesti, G., 2005. Effects of vitamin D_3 dietary supplementation of broiler breeder hens on the performance and bone abnormalities of the progeny. Poultry Science, **84:**1058-1068.

Barbato, G.F., 1994. Genetic control of food intake in chickens (Conference: Food intake regulation: Neuropeptides, Circulating factors and Genetics). Journal of Nutrition, **124:**1341-1348.

Batal, A.B. and Parsons, C.M., 2002. Effects of age on nutrient digestibility in chicks fed different diets. Poultry Science, **81:**400-407.

Berri, C., Le Bihan-Duval, E., Debut, M., Santé-Lhouteller, V., Baéza, E., Gigaud, V., Jégo, Y. and Duclos, M.J., 2007. Consequence of muscle hypertrophy on characteristics of Pectoralis major muscle and breast meat quality of broiler chickens. Journal of Animal Science, **85:**2005-2011.

Berri, C., Wacrenier, N., Millet, N. and Le Bihan-Duval, E., 2001. Effect of selection for improved body composition on muscle and meat characteristics of broilers from experimental and commercial lines. Poultry Science, **80:**833-838.

Beumont, C., Guillaumin, S., Geraet, P.A., Mignon-Grasteau, S. and Lecrercq, B., 1998. Genetic parameters of body weight of broiler chickens measured at 22˚C or 32˚C. British Poultry Science, **39:**488-491.

Bennett, C.D., 1992. The influence of shell thickness on hatchability in commercial broiler breeder flocks. Journal of Applied Poultry Research, **1:**61-65.

Board, R.G. and Scott, V.D., 1980. Porosity of the avian eggshell. American Society of Zoologists, **20:**339-349.

Bornstein, S., 1970. The lysine requirement of broilers during their finishing period. British Poultry Science, **11:**197-207.

Bottje, W., Tang, Z.X., Iqbal, M., Cawthon, D., Okimoto, R., Wing, T. and Cooper, M., 2002. Association of mitochondrial function with feed efficiency within a single genetic line of male broilers. Poultry Science, **81:**546-555.

Bowmaker, J.E. and Gous, R.M., 1991. The Response of broiler breeder hens to dietary lysine and methionine. British Poultry Science, **32:**1069-1088.

Brake, J., Garlich, J.D. and Peebles, E.D., 1985. Effect of protein and energy intake by broiler breeders during the prebreeder transition period on subsequent reproductive performance. Poultry Science, **64:**2335-2340.

Brand, Z., Brand, T.S. and Brown, C.R., 2003. The effect of different combinations of dietary energy and protein on the composition of ostrich eggs. South African Journal of Animal Science, **33:**193-200.

Bruggeman, V., Onagbesan, O., D'Hondt, E., Buys, N., Safi, M., Vanmontfort, D., Berghman, L., Vandesande, F. and Decuypere, E., 1999. Effects of timing and duration of feed restriction during rearing on reproductive characteristics in broiler breeder females. Poultry Science, **78:**1424-1434.

Bruggeman, V., Onagbesan, O., Ragot, O., Metayer, S., Cassy, S., Favreau, F., Jego, Y., Trevidy, J.J., Tona, K., Williams, J., Decuypere, E. and Picard, E., 2005. Feed allowance – Genotype interactions in broiler breeder hens. Poultry Science, **84:**298-306.

Bruggeman, V., Vanmontfort, D., Renaville, R., Portetelle, D. and Decuypere, E., 1997. The effect of food intake from two weeks of age to sexual maturity on plasma growth hormone, insulin-like growth factor-I, insulin-like growth factor binding proteins, and thyroid hormones in female breeder chickens. General and Corporative Endocrinology, **107:**212-220.

Bullock, D.W., Morris, T.R. and Fox, S., 1963. Protein and energy restriction for replacement pullets. British Poultry Science, **4:**227-237.

Byng, A.J. and Nash, D., 1962. The effects of egg storage on hatchability. British Poultry Science, **3:**81-87.

Cave, N.A.G., 1984. Effect of high-protein diet fed prior to the onset of lay on performance of broiler breeder pullets. Poultry Science, **63:**1823-1827.

Cegielska-Radziejewska, R., Lesnierowski, G. and Kijowski, J., 2009. Antibacterial activity of hen egg white lysozyme modified by thermochemical technique. European Food Research and Technology, **228:**841-845.

Cheema, M.A., Qureshi, M.A. and Havenstein, G.B., 2003. A comparison of the immune response of a 2001 commercial broiler with a 1957 random bred broiler strain when fed representative 1957 and 2001 broiler diets. Poultry Science, **82:**1519-1529.

Chen, S.E., McMurtry, J.P. and Walzem, R.L., 2006. Overfeeding-induced ovarian dysfunction in broiler breeder hens is associated with lipotoxicity. Poultry Science, **85:**70-81.

Cherian, G., Bautista-Ortega, J. and Goeger, G.E., 2009. Maternal dietary n-3 fatty acids alter cardiac ventricle fatty acid composition, prostaglandin and thromboxane production in growing chicks. Prostaglandins, Leukotrienes and Essential Fatty Acids, **80:**297-303.

Chien, Y.-C., Hincke, M.T. and McKee, M.D., 2009. Ultrastructure of avian eggshell during resorption following egg fertilization. Journal of Structural Biology, **168:**527-538.

Chien, Y.-C., Hincke, M.T., Vali, H. and McKee, M.D., 2008. Ultrastructural matrix-mineral relationships in avian eggshell, and effects of osteopontin on calcite growth *in vitro*. Journal of Structural Biology, **163:**84-99.

Chwalibog, A., Tauson, A.,-H., Ali, A., Matthiesen, C., Thorhauge, K. and Thorbek, G., 2007. Gas exchange, heat production and oxidation of fat in chicken embryos from a fast or slow growing line. Comparative Biochemistry and Physiology, Part A, **146:**305-309.

Crouch, A.N., Grimes, J.L., Christensen, V.L. and Krueger, K.K., 2002. Effect of physical feed restriction during rearing on large white turkey breeder hens: 2. Reproductive performance. Poultry Science, **81:**16-22.

Danbaro, G., Oyama, K., Mukai, F., Tsuji, S., Tateishi, T. and Mae, M., 1995. Genetic trends from a selection experiment in broiler breeder lines using Best Linear Unbiased Prediction Methodology. Journal of Poultry Science, **32:**379-386.

de Beer, M., 2009. Current approaches to feeding broiler breeders. The Proceedings of the 17th European Symposium on Poultry Nutrition, Edinburgh, Scotland, UK.

Deeb, N. and Lamont, S.J., 2002. Genetic architecture of growth and body composition in unique chicken populations. The American Genetic Association, **93**:107-118.

Decuypere, E. and Bruggeman, V., 2007. The endocrine interface of environmental and egg factors affecting chick quality. Poultry Science, **86:**1037-1042.

Decuypere, E., Hocking, P.M., Tona, K., Onagbesan, O., Bruggeman, V., Jones, E.K.M., Cassy, S., Rideau, N., Metayer, S., Jego, Y., Putterflam, J., Tesseraud, S., Collin, A., Duclos, M., Treviddy, J.J. and Williams, J., 2006. Broiler breeder paradox: a project report. World's Poultry Science Journal, **62:**443-453.

Decuypere, E., Tona, K., Bruggeman, V. and Bamelis, E., 2001. The day-old-chick: a crucial hinge between breeders and broilers. World's Poultry Science Journal, **57:**127-138.

De Koning, D.J., Haley, C.S., Windsor, D., Hocking, P.M., Griffin, H., Morris, A., Vincent, J. and Burt, D.W., 2004. Segregation of QTL for production traits in commercial meat-type chickens. Genetic Research, Cambridge, **83:**211-220.

De Oliveira, J.E., Uni, Z. and Ferket, P.R., 2008. Important metabolic pathways in poultry embryos prior to hatch. World's Poultry Science Journal, **64:**488-499.

Dibner, J.J., 2005. Early nutrition of zinc and copper in chicks and poults: Impact on growth and immune function. The Proceedings of the 3rd Mid-Atlantic Nutrition Conference, Timonium, Maryland, USA, pp. 23-32.

D'Mello, J.P.F. and Lewis, D., 1970. Amino acid interactions. British Poultry Science, **11:**299-311.

Douglas, J.H. and Buddiger, C., 2002. How today's social, political, and consumer-driven environment influences business objectives of the primary breeders: genotype, environment and nutritional interactions. In: Hafez (H.M., Ed.) Proceedings of the 4th International Symposium on Turkey Diseases, Berlin, Verlad DVG, Gissen, 1-11.

Dozier, W.A., III, Corzo, A., Kidd, M.T. and Schilling, M.W., 2008a. Dietary digestible lysine requirements of male and female broilers from forty-nine to sixty-three days of age. Poultry Science, **87:**1385-1391.

Dozier, W.A., III, Kidd, M.T. and Corzo, A., 2008b. Dietary amino acid responses of broiler chickens. Journal of Applied Poultry Research, **17:**157-167.

Druyan, S., 2010. The effects of genetic line (broilers vs. layers) on embryo development. Poultry Science, **89:**1457-1467.

Emmerson, D.A., 1997. Commercial approaches to genetic selection for growth and feed conversion in domestic poultry. Poultry Science, **76:**1121-1125.

Enting, H., Boersma, W.J.A., Cornelissen, J.B.W.J., van Winden, S.C.L., Verstegen, M.W.A. and van der Aar, P.J., 2007. The effect of low-density broiler breeder diets on performance and immune status of their offspring. Poultry Science, **86:**282-290.

Etches, R.J., 1996. Reproduction in poultry. CAB International, Wallingford, Oxon, UK, pp. 10-39.

Everaert, N., Willemsen, H., De Smit, L., Witters, A., De Baerdemaeker, J., Decuypere, E. and Bruggeman, V., 2008. Comparison of a modern broiler and layer strain during embryonic development and the hatching process. British Poultry Science, **49:**574-582.

Ewing, W.R., 1963. Poultry Nutrition. 5th Edition (Revised). The Ray Ewing Company, Pasadena, California, pp. 16-27.

Fakhraei, J., Loutfollahian, H., Shivazad, M., Chamani, M. and Hoseini, S.A., 2010. Reevaluation of lysine requirement based on performance responses in broiler breeder hens. African Journal of Agricultural Research, **5:**2137-2142.

Fasenko, G.M. and O'Dea, E.E., 2008. Evaluating broiler growth and mortality in chicks with minor navel conditions at hatching. Poultry Science, **87:**594-597.

Farrell, D.J., Mannion, P.F. and Perez-Maldonado, R.A., 1999. A comparison of total and digestible amino acids in diets for broilers and layers. Animal Feed Science and Technology, **82:**131-142.

Finkler, M.S., Van Orman, J.B. and Sotherland, P.R., 1998. Experimental manipulation of egg quality in chickens: influence of albumen and yolk on the size and body composition of near-term embryos in a precocial bird. Journal of Comparative Physiology, Part B, **168:**17-24.

Fisher, C., 1998. Amino acid requirements of broiler breeders. Poultry Science, **77:**124-133.

Fisher, C., 2008. Recent evidence about the protein and amino acid nutrition of broiler breeders. The Proceedings of the 27th World's Poultry Science Association Scientific Day, CSIR Convention Centre, Pretoria, South Africa, pp. 104-114.

Fisher, C. and Morris, T.R., 1967. Some effects of changing protein levels during the pullet laying year. British Poultry Science, **8:**153-161.

Freeman, B.M., and Vince, M.A., 1974. Development of the avian embryo. Chapman and Hall, London, pp. 3-36.

French, N.A., 1997. Modeling incubation temperature: the effects of incubator design, embryonic development, and egg size. Poultry Science, **76:**124-133.

Fuller, M.F., 1994. Amino acid requirements for maintenance, body protein accretion and reproduction in pigs. In: D'Mello, J.P.F. Amino acids in farm animal nutrition. CAB International, pp. 155-184.

Fulton, J.E., 2006. Avian genetic stock preservation: an industry perspective. Poultry Science, **85:**227-231.

Geraert, P.A., Guillaumin, S. and Leclercq, B., 1993. Are genetically lean broilers more resistant to hot climate? British Poultry Science, **34:**643-653.

Garcia, E.A., Mendes, A.A., Pizzolante, C.C., Saldanha, E.S.P.B., Moreira, J., Mori, C. and Pavan, A.C., 2005. Protein, Methionine + Cystine and Lysine levels for Japanese Quails during the production phase. Brazilian Journal of Poultry Science, **7:**11-18.

Gous, R.M., 1978. A comparison of three methods of food restriction of laying-type pullets on growth and laying performance. British Poultry Science, **19:**441-448.

Gous, R.M., 2010. Nutritional limitations on growth and development in poultry. Livestock Science, **130:**25-32.

Gous, R.M., Moran, E.T., Jr., Stilborn, H.R., Bradford, G.D. and Emmans, G.C., 1999. Evaluation of the parameters needed to describe the overall growth, the chemical growth, and the growth of feathers and breast muscles of broilers. Poultry Science, **78:**812-821.

Gous, R.M. and Nonis, M.K., 2010. Modelling egg production and nutrient responses in broiler breeder hens. Journal of Agricultural Science, **148:**287-301.

Gowe, R.S., Johnson, A.S., Crawford, R.D., Downs, J.H., Hill, A.T., Mountain, W.F., Pelletier, J.R. and Strain, J.H., 1960. Restricted versus full-feeding during the growing period for egg production stock. British Poultry Science, **1:**37-56.

Gunawardana, P., Roland, D.A., Sr. and Bryant, M.M., 2008a. Effect of energy and protein on performance, egg components, egg solids, egg quality, and profits in molted Hy-Line W-36 Hens. Journal of Applied Poultry Research, **17:**432-439.

Gunawardana, P., Roland, D.A. and Bryant, M.M., 2008b. Performance comparison and lysine requirements of seven commercial brown egg layer strains during phase two. International Journal of Poultry Science, **7:**1156-1162.

Hall, J.A., Jha, S., Skinner, M.M. and Cherian, G., 2007. Maternal n-3 fatty acid alter immune cell fatty acid composition and leukotriene production in growing chicks. Prostaglandins, Leukotrienes and Essential Fatty Acids, **76:**19-28.

Hank, C.R., Kunkel, M.E., Dawson, P.L., Acton, J.C. and Wardlaw, F.B., Jr., 2001. The effect of shell egg pasteurization on the protein quality of the albumen. Poultry Science, **80:**821-824.

Harms, R.H. and Ivey, F.J., 1992. An evaluation of the protein and lysine requirement for broiler breeder hens. Journal of Applied Poultry Research, **1:**308-314.

Harms, R.H. and Russell, G.B., 1995. A re-evaluation of the protein and lysine requirement for broiler breeder hens. Poultry Science, **74:**581-585.

Hartmann, C., Johansson, K., Strandberg, E. and Rydhmer, L., 2003. Genetic correlations between the maternal genetic effect on chick weight and the direct genetic effects on egg composition traits in a while leghorn line. Poultry Science, **82:**1-8.

Havestein, G.B., 2006. Performance changes in poultry and livestock following 50 years of genetic selection. Lohmann Information, **41:**30-37.

Havestein, G.B., Ferket, P.R. and Quereshi, M.A., 2003a. Carcass composition and yield of 1957 versus 2001 broilers when fed representative 1957 and 2001 broiler diets. Poultry Science, **82:**1509-1518.

Havestein, G.B., Ferket, P.R. and Quereshi, M.A., 2003b. Growth, livability, and feed conversion of 1957 versus 2001 broilers when fed representative 1957 and 2001 broiler diets. Poultry Science, **82:**1500-1508.

Heck, A., Onagbesan, O., Tona, K., Metayer, S., Putterflam, J., Jego, Y., Trevidy, J.J., Decuypere, E., Williams, J., Picard, M. and Bruggeman, V., 2004. Effects of *ad libitum* feeding on performance of different strains of broiler breeders. British Poultry Science, **45:**695-703.

Hocking, P.M., 1987. Nutritional interactions with reproduction in birds. Proceedings of the Nutritional Society, **46:**217-225.

Hocking, P.M., 2007. Optimum feed composition of broiler breeder diets to maximise progeny performance. The Proceedings of the 16th European Symposium on Poultry Nutrition, Strasbourg, France, pp. 101-108.

Hocking, P.M., Bernard, R. and Robertson, G.W., 2002. Effects of low dietary protein and different allocations of food during rearing and restricted feeding after peak rate of lay on egg production, fertility and hatchability in female broiler breeders. British Poultry Science, **43:**94-103.

Hocking, P.M., Gilbert, A.B., Walker, M. and Waddington, D., 1987. Ovarian follicular structure of while leghorns fed *ad libitum* and dwarf and normal broiler breeders fed *ad libitum* or restricted until point of lay. British Poultry Science, **28:**493-506.

Hocking, P.M., Waddington, D., Walker, M. and Gilbert, A.B., 1989. Control of the development of the ovarian follicular hierarchy in broiler breeder pullets by food restriction during rearing. British Poultry Science, **30:**161-174.

Hoffmann, I., 2005. Research and investment in poultry genetic resources – challenges and options for sustainable use. World's Poultry Science Journal, **61:**57-70.

Howie, J.A., Tolkamp, B.J., Avendano, S. and Kyriazakis, I., 2009. The structure of feeding behavior in commercial broiler lines selected for different growth rates. Poultry Science, **88:**1143-1150.

Hudson, B.P., Fairchild, B.D., Wilson, J.L., Dozier, W.A. III and Buhr, R.J., 2004. Breeder age and zinc source in broiler breeder hen diets on progeny characteristics at hatching. Journal of Applied Poultry Research, **13:**55-64.

Hulet, R.M., 2007. Symposium: Managing the embryo for performance. Managing incubation: Where are we and why? Poultry Science, 86:1017-1019.

Joseph, N.S. and Moran, E.T., Jr., 2005. Characteristics of eggs, embryos, and chicks from broiler breeder hens selected for growth or meat yield. Journal of Applied Poultry Research, **14:**275-280.

Joseph, N.S., Robinson, F.E., Korver, D.R. and Renema, R.A., 2000. Effect of dietary protein intake during the pullet-to-breeder period on early egg weight and production in broiler breeders. Poultry Science, **79:**1790-1796.

Julian, R.J., 1998. Rapid growth problems: Ascites and skeletal deformities in broilers. Poultry Science, **77:**1773-1780.

Karlsson, O. and Lilja, C., 2008. Eggshell structure, mode of development and growth rate in birds. Zoology, **111:**494-502.

Kerr, B.J., Kidd, M.T., Halpin, K.M., McWard, G.W. and Quarles, C.L., 1999. Lysine level increases live performance and breast yield in male broilers. Journal of Applied Poultry Research, **8:**381-390.

Khaksar, V. and Golian, A., 2009. Comparison of ileal digestible versus total amino acid feed formulation on broiler performance. Journal of Animal and Veterinary Advances, **8:**1308-1311.

Kidd, M.T., 2006. Maternal nutrition effects on progeny development and performance. The Proceedings of the 33rd Annual Carolina Poultry Nutrition Conference, Sheraton Imperial Hotel, RTP, NC.

Kidd, M.T., Kerr, B.J., Halpin, K.M., McWard, G.W. and Quarles, C.L., 1998. Lysine levels in starter and grower-finisher diets affecting broiler performance and carcass traits. Journal of Applied Poultry Research, **7:**351-358.

Kingori, A.M., Tuitoek, J.K., Muiruri, H.K. and Wachira, A.M., 2010. Effect of dietary crude protein levels on egg production, hatchability and post-hatch offspring performance of indigenous chickens. International Journal of Poultry Science, **9:**324-329.

Kirk, S., Emmans, G.C., McDonald, R. and Arnot, D., 1980. Factors affecting the hatchability of eggs from broiler breeders. British Poultry Science, **21:**37-53.

Koutsos, E.A., Clifford, A.J., Calvert, C.C. and Klasing, K.C., 2003. Nutrient metabolism: maternal carotenoid status modifies the incorporation of dietary carotenoids into immune tissues of growing chickens (*Gallus gallus domesticus*). Journal of Nutrition, **133:**1132-1138.

Lapão, C., Gama, L.T. and Soares, M.C., 1999. Effects of broiler breeder age and length of egg storage on albumen characteristics and hatchability. Poultry Science, **78:**640-645.

Leclercq, B., 1998. Specific effects of lysine on broiler production: comparison with threonine and valine. Poultry Science, **77:**118-123.

Leeson, S., 2005. Breeder nutrition – Maintaining breeder performance while feeding to meet the needs of the developing embryo. The Proceedings of the 3rd Mid-Atlantic Nutrition Conference, Timonium, Maryland, USA, pp. 33-37.

Leeson, S., 2008. Prediction for commercial poultry nutrition. Journal of Applied Poultry Research, **17:**315-322.

Leksrisompong, N., Romero-Sanchez, H., Plumstead, P.W., Brannan, K.E. and Brake, J., 2007. Broiler incubation. 1. Effect of elevated temperature during late incubation on body weight and organs of chicks. Poultry Science, **86:**2685-2691.

Lemme, A., Ravindran, V. and Bryden, W.L., 2004. Ileal digestibility of amino acids in feed ingredients for broilers. World's Poultry Science Journal, **60:**423-444.

Liu, Z., Wu, G., Bryant, M.M. and Roland, D.A., Sr., 2005. Influence of added synthetic lysine in low-protein diets with the methionine plus cystine to lysine ratio maintained at 0.75. Journal of Applied Poultry Research, **14:**174-182.

Lopez, G. and Leeson, S., 1994a. Response of older broiler breeders to medium-high intakes of protein. Journal of Applied Poultry Research, **3:**157-163.

Lopez, G. and Leeson, S., 1994b. Egg weight and offspring performance of older broiler breeders fed low-protein diets. Journal of Applied Poultry Research, **3:**164-170.

Lopez, G., and Leeson, S., 1995. Response of broiler breeders to low-protein diets. 1. Adult breeder performance. Poultry Science, **74:**685-695.

Lunven, P., Le Clement, C., St Marcq, D., Carnovale, E. and Fratoni, A., 1973. Amino acid composition of hen's egg. British Journal of Nutrition, **30:**189-194.

Maiorka, A., Dahlke, F. and Morgulis, M.S.F.A., 2006. Broiler adaptation to post-hatching period. Ciência Rural, **36:**701-708.

MacRae, V.E., Mahon, M., Gilpin, S., Sandercock, D.A., Hunter, R.R. and Mitchell, M.A., 2007. A comparison of breast muscle characteristics in three broiler great-parent lines. Poultry Science, **86:**382-385.

Manson, J.M., Picken, K.J., Draper, M.H. and Thompson, R., 1993. Variation among individual white-leghorn hens in the concentration of minerals in the albumen and yolk content of their eggs. British Poultry Science, **34:**899-909.

Marcato, S.M., Sakomura, N.K., Munari, D.P., Fernandes, J.B.K., Kawauchi, Í.M. and Bonato, M.A., 2008. Growth and body nutrient deposition of two broiler commercial genetic lines. Brazilian Journal of Poultry Science, **10:**117-123.

Melnychuk, V.L., Kirby, J.D., Kirby, Y.K., Emmerson, D.A. and Anthony, N.B., 2004. Effect of strain, feed allocation program, and age at photostimulation on reproductive development and carcass characteristics of broiler breeder hens. Poultry Science, **83:**1861-1867.

Milisits, G., Kovács, E., Pőcze, O., Ujvári, J., Taraszenkó, Zs., Jekkel, G., Locsmándi, L., Bázár, Gy., Szabó, A., Romvari, R. and Sütő, Z., 2010. Effect of egg composition on hatchability and on growth and slaughter characteristics of meat-type chicks. British Poultry Science, **51:**289-295.

Moran, E.T., Jr., 2007. Nutrition of the developing embryo and hatchling. Poultry Science, **86:**1043-1049.

Morris, A.J. and Pillot, G.E., 1997. Comparison of selection based on phenotype, selection index and best linear unbiased prediction using data from a closed broiler line. British Poultry Science, **38:**249-254.

Morris, T.R. and Gous, R.M., 1988. Partitioning of the response to protein between egg number and egg weight. British Poultry Science, **29:**93-99.

Morris, T.R. and Njuru, D.M., 1990. Protein requirement of fast- and slow-growing chicks. British Poultry Science, **31:**803-809.

Muir, W.M., Wong, G.K., Zhang, Y., Wang, J., Groenen, M.A.M., Crooijmans, R.P.M.A., Megens, H., Zhang, H., Okimoto, R., Vereijken, A., Jungerius, A., Albers, G.A.A., Lawley, C.T., Delany, M.E., MacEachern, S. and Cheng, H.H., 2008. Genome-wide assessment of worldwide chicken SNP genetic diversity indicates significant absence of rare alleles in commercial breeders. Proceedings of National Academy of Sciences of the United States of America, **105:**17312-17317.

Muramatsu, T., Hiramoto, K., Koshi, N., Okumura, J., Miyoshi, S. and Mitsumoto, T., 1990. Importance of albumen content in whole-body protein synthesis of the chicken embryo during incubation. British Poultry Science, **31:**101-106.

Narushin, V.G. and Romanov, M.N., 2002. Egg physical characteristics and hatchability. World's Poultry Science Journal, **58**:297-303.

Nelson, T.C., Groth, K.D. and Sotherland, P.R., 2010. Maternal investment and nutrient use affect phenotype of American alligator and chicken hatchlings. Comparative Biochemistry and Physiology, Part A, **157:**19-27.

Nielsen, B.L., Litherland, M. and Nøddegaard, F., 2003. Effects of qualitative and quantitative feed restriction on the activity of broiler chickens. Applied Animal Behaviour Science, **83:**309-323.

Noble, R.C. and Cocchi, M., 1990. Lipid metabolism and the neonatal chicken. Progress in Lipid Research, **29:**107-140.

Noble, R.C. and Connor, K., 1983. Lipid metabolism in the chick embryo of the domestic fowl (*Gallus domesticus*). World's Poultry Science Journal, **39:**114-120.

Notter, D.R., 1999. The importance of genetic diversity in livestock populations in future. Journal of Animal Science, **77:**61-69.

Novak, C., Yakout, H.M. and Scheideler, S.E., 2006. The effect of dietary protein level and total sulfur amino acid: lysine ratio on egg production parameters and egg yield in Hy-Line W-98 Hens. Poultry Science, **85:**2195-2206.

Novo, R.P., Gama, L.T. and Soares, M., 1997. Effects of oviposition time, hen age, and extra dietary calcium on egg characteristics and hatchability. Journal of Applied Poultry Research, **6:**335-343.

Noy, Y. and Sklan, D., 1999. Energy utilization in newly hatched chick. Poultry Science, **78:**1750-1756.

O'Dea, E.E., Fasenko, G.M., Feddes, J.J.R., Robinson, F.E., Segura, J.C., Ouellette, C.A. and van Middelkoop, J.H., 2004. Investigating the eggshell conductance and embryonic metabolism of modern and unselected domestic avian genetic strains at two flock ages. Poultry Science, **83:**2059-2070.

Pappas, A.C., Zoidis, E., Surai, P.F. and Zervas, G., 2008. Selenoproteins and maternal nutrition. Comparative Biochemistry and Physiology, Part B, **151:**361-372.

Pedroso, A.A., Andrade, M.A., Café, M.B., Leandro, N.S.M., Menten, J.F.M. and Stringhini, J.H., 2005. Fertility and hatchability of eggs laid in the pullet-to-breeder transition period and in the initial production period. Animal Reproduction Science, **90:**355-364.

Peebles, E.D., Doyle, S.M., Pansky, T., Gerard, P.D., Latour, M.A., Boyle, C.R. and Smith, T.W., 1999a. Effects of breeder age and dietary fat on subsequent broiler performance. 1. Growth, mortality, and feed conversion. Poultry Science, **78:**505-511.

Peebles, E.D., Doyle, S.M., Pansky, T., Gerard, P.D., Latour, M.A., Boyle, C.R. and Smith, T.W., 1999b. Effects of breeder age and dietary fat on subsequent broiler performance. 2. Slaughter yield. Poultry Science, **78:**512-515.

Peebles, E.D., Doyle, S.M., Zumwalt, C.D., Gerard, P.D., Latour, M.A., Boyle, C.R. and Smith, T.W., 2001. Breeder age influences embryogenesis in broiler hatching eggs. Poultry Science, **80:**272-277.

Peebles, E.D., Pansky, T., Doyle, S.M. and Smith, T.W., 1998. Effects of breeder dietary fat and eggshell cuticle removal on subsequent broiler growout performance. Journal of Applied Poultry Science, **7:**377-383.

Perić, L., Milošević, N., Milić, D. and Vukić-Vranješ, M., 2007. Effect of Sel-Plex in broiler breeder diets on the subsequent day-old chick quality. The Proceedings of the 16th European Symposium on Poultry Nutrition, Strasbourg, France, pp. 605-608.

Powell, J.G. and Bowman, J.C., 1964. An estimate of maternal effects in early growth characteristics and their effects upon comparative tests of chicken varieties. British Poultry Science, **5:**121-132.

Puterflam, J., Merlet, F., Faure, J.M., Hocking, P.M. and Picard, M., 2006. Effects of genotype and feed restriction on the time-budgets of broiler breeders at different ages. Applied Animal Behaviour Science, **98:**100-113.

Rajman, M., Jurani, M., Lamosova, D., Macajova, M., Sedlackova, M., Kostal, L., Jesova, D. and Vyboh, P., 2006. The effects of feed restriction on plasma biochemistry in growing meat type chickens (Gallus gallus). Comparative Biochemistry and Physiology, Part A, **145**:366-371.

Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N. and Grommers, F.J., 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. Livestock Production Science, **56:**15-33.

Reijrink, I.A.M., Berghmans, D., Meijerhof, R., Kemp, B. and van den Brand, H., 2010. Influence of egg storage time and preincubation warming profile on embryonic development, hatchability, and chick quality. Poultry Science, **89:**1225-1238.

Renema, R.A. and Robinson, F.E., 2004. Defining normal: comparison of feed restriction of female broiler breeders. World's Poultry Science Journal, **60:**508-522.

Renema, R.A., Robinson, F.E. and Zuidhof, M.J., 2007. Reproductive efficiency and metabolism of female broiler breeders as affected by genotype, feed allocation, and age at photostimulation. 2. Sexual maturation. Poultry Science, **86:**2267-2277.

Richards, M.P., 2003. Genetic regulation of feed intake and energy balance in poultry. Poultry Science, **82:**907-916.

Richards, M.P., Poch, S.M., Coon, C.N., Rosebrough, R.W., Ashwell, C.M. and McMurtry, J.P., 2003. Feed restriction significantly alters lipogenic gene expression in broiler breeder chickens. Journal of Nutrition, **133**:707-715.

Robinson, F.E., Classen, H.L., Hanson, J.A. and Onderka, D.K., 1992. Growth performance, feed efficiency and the incidence of skeletal and metabolic disease in full-fed and feed restricted broiler and roaster chickens. Journal of Applied Poultry Research, **1:**33-41.

Robinson, F.E. and Wilson, J.L., 1996. Reproductive failure in overweight male and female broiler breeders. Animal Feed Science Technology, **58**:143-150.

Robinson, F.E., Zuidhof, M.J. and Renema, R.A., 2007. Reproductive efficiency and metabolism of female broiler breeders as affected by genotype, feed allocation, and age at photostimulation. 1. Pullet growth and development. Poultry Science, **86:**2256-2266.

Rol'nik, V.V., 1970. Bird embryology. Israel Program for Scientific Translations. Jerusalem, pp. 23-56.

Romanoff, A.L., 1960. The avian embryo: structural and functional development. The Macmillan Company, New York, Brett-Macmillan Ltd., Galt, Ontario, pp. 75-101.

Romanoff, A.L., and Romanoff, A.J., 1949. The avian egg. John Wiley & Sons, Inc., New York, Chapman & Hall, Limited, London, pp. 17-570.

Romero, L.F., Zuidhof, M.J., Renema, R.A., Naeima, A.N. and Robinson, F., 2009. Effects of maternal energetic efficiency on egg traits, chick traits, broiler growth, yield, and meat quality. Poultry Science, **88:**236-245.

Rostagno, H.S., Pupa, J.M.R. and Pack, M., 1995. Diet formulation for broilers based on total versus digestible amino acids. Journal of Applied Poultry Research, **4:**293-299.

Ruck, S.B., 2011. The response of broiler breeder hens to dietary lysine: hatchability, embryo growth and subsequent offspring performance. Master of Science in Agriculture dissertation. University of KwaZulu-Natal.

Sainz, F., Gonzalez, M., Roca, P. and Alemany, M., 1983. Physical and chemical nature of eggs from six breeds of domestic fowl. British Poultry Science, **24:**301-309.

Sandilands, V., Tolkamp, B.J. and Kyriazakis, I., 2005. Behaviour of food restricted broilers during rearing and lay – effects of an alternative method. Physiology and Behaviour, **85:**115-123.

Sandilands, V., Tolkamp, B.J., Savory, C.J. and Kyriazakis, I., 2006. Behaviour and welfare of broiler breeders fed qualitatively restricted diets during rearing: Are there viable alternatives to quantitative restriction? Applied Animal Behaviour Science, **96:**53-67.

Sato, M., Noda, K., Kino, K., Nakamura, A. and Furuse, M., 2007. Comparison of heat production and plasma lipid metabolism between meat- and egg-types of Nagoya breed chicken during embryonic development. Animal Science Journal, **78:**613-618.

Sato, M., Techibana, T. and Furuse, M., 2006. Heat production and lipid metabolism in broiler and layer chickens during embryonic development. Comparative Biochemistry and Physiology, Part A, **143:**382-388.

Savory, C.J. and Lariviere, J.-M., 2000. Effects of qualitative and quantitative food restriction treatments on feeding motivational state and general activity level of growing broiler breeders. Applied Animal Behaviour Science, **69:**135-147.

Schaible, P.J., 1970. Poultry: Feeds and nutrition. The AVI Publishing company, Inc. Westport, Connecticut, pp. 56-541.

Scheuermann, G.N., Bilgili, S.F., Hess, J.B. and Mulvaney, D.R., 2003. Breast muscle development in commercial broiler chickens. Poultry Science, **82:**1648-1658.

Schmidt, C.J., Persia, M.E., Feierstein, E., Kingham, B., and Saylor, W.W., 2009. Comparison of a modern broiler line and a heritage line unselected since the 1950s. Poultry Science, **88:**2610-2619.

Sell, J.L., 1996. Physiological limitations and potential for improvement in gastro intestinal tract function of poultry. Journal of Applied Poultry Research, **5:**96-101.

Shafey, T.M., Shalaby, M.I. and Bayoumi, M.S., 2007. Effects of electric field during incubation of eggs on the hatchability and post-hatch performance of meat chickens. International Journal of Poultry Science, **6:**1-7.

Skinner-Noble, D.O. and Teeter, R.G., 2003. Components of feed efficiency in broiler breeding stock: Energetics, performance, carcass composition, metabolism, and body temperature. Poultry Science, **82:**1080-1090.

Speake, B.K., Murray, A.M.B. and Noble, R.C., 1998a. Transport and transformations of yolk lipids during development of the avian embryo. Progress in Lipid Research, **37:**1-32.

Speake, B.K., Noble, R.C. and Murray, A.M.B., 1998b. The utilization of yolk lipids by the chick embryo. World's Poultry Science Journal, **54:**319-333.

Spradley, J.M., Freeman, M.E., Wilson, J.L. and Davis, A.J., 2008. The influence of a twice-a-day feeding regimen after photostimulation on the reproductive performance of broiler breeder hens. Poultry Science, **87:**561-568.

Spratt, R.S. and Leeson, S., 1987. Effect of protein and energy intake of broiler breeder hens on performance of broiler chicken offspring. Poultry Science, **66:**1489-1494.

Sterling, K.G., Pesti, G.M. and Bakalli, R.I., 2003. Performance of broiler chicks fed various levels of dietary lysine and crude protein. Poultry Science, **82:**1939-1947.

Sterling, K.G., Pesti, G.M. and BakaLli, R.I., 2006. Performance of different broiler genotypes fed diets with varying levels of dietary crude protein and lysine. Poultry Science, **85:**1045-1054.

Sterling, K.G., Vedenov, D.V., Pesti, G.M. and Bakalli, R.I., 2005. Economically optimal dietary crude protein and lysine levels for starting broiler chicks. Poultry Science, **84:**29-36.

Surai, P.F., Noble, R.C. and Speake, B.K., 1996. Tissue-specific differences in antioxidant distribution and susceptibility to lipid peroxidation during development of the chick embryo. Biochimica et Biophysica Acta, **1304:**1-10.

Taherkhani, R., Zaghari, M., Shivazad, M. and Shahneh, A.Z., 2010. A twice-a-day feed regimen optimizes performance in broiler breeder hens. Poultry Science, **89:**1692-1702.

Tharrington, J.B., Curtis, P.A., Jones, F.T. and Anderson, K.E., 1999. Comparison of physical quality and composition of eggs from historic strains of single comb white leghorn chickens. Poultry Science, **78:**591-594.

Tixier-Boichard, M., Bordas, A. and Rognon, X., 2009. Characterisation and monitoring of poultry genetic resources. World's Poultry Science Journal, **65:**272-285.

Tolkamp, B.J., Sandilands, V. and Kyriazakis, I., 2005. Effects of qualitative feed restriction during rearing on the performance of broiler breeders during rearing and lay. Poultry Science, **84:**1286-1293.

Tona, K., Agbo, K., Kamers, B., Everaert, N., Willemsen, H., Decuypere, E. and Gbeassor, M., 2010a. Comparison of lohmann white and lohmann brown strains in embryo physiology. International Journal of Poultry Science, **9:**907-910.

Tona, K., Bamelis, F., Coucke, W., Bruggeman, V. and Decuypere, E., 2001. Relationship between broiler breeder's age and egg weight loss and embryonic mortality during incubation in large-scale conditions. Journal of Applied Poultry Research, **10:**221-227.

Tona, K., Bamelis, F., De Ketelaere, B., Bruggeman, V. and Decuypere, E., 2002. Effect of induced molting and albumen quality, hatchability, and chick body weight from broiler breeders. Poultry Science, **81:**327-332.

Tona, K., Bamelis, F., De Ketelaere, B., Bruggeman, V., Moares, V.M.B., Buyse, J., Onagbesan, O. and Decuypere, E., 2003. Effects of egg storage time on spread of hatch, chick quality, and chick juvenile growth. Poultry Science, **82:**736-741.

Tona, K., Bruggeman, V., Onagbesan, O., Bamelis, F., Gbeassor, M., Mertens, K. and Decuypere, E., 2005. Day-old-chick quality: Relationship to hatching egg quality, adequate incubation practice and prediction of broiler performance. Avian and Poultry Biology Reviews, **16:**109-119.

Tona, K., Onagbesan, O.M., Jego, Y., Kamers, B., Decuypere, E. and Bruggeman, V., 2004. Comparison of embryo physiological parameters during incubation, chick quality, and growth performance of three lines of broiler breeders differing in genetic composition and growth rate. Poultry Science, **83:**507-513.

Tona, K., Onagbesan, O.M., Kamers, B., Everaert, N., Bruggeman, V. and Decuypere, E., 2010b. Comparison of Cobb and Ross strains in embryo physiology and chick juvenile growth. Poultry Science, **89:**1677-1683.

Tuan, R.S., 1983. Supplemented eggshell restores calcium transport in chorioallontoic membrane of cultured shell-less chick embryos. Journal of Embryology and Experimental Morphology, **74:**119-131.

Ulmer-Franco, A.M., Fasenko, G.M. and O'Dea, E.E., 2010. Hatching egg characteristics, chick quality, and broiler performance at 2 breeder flock ages and from 3 egg weights. Poultry Science, **89:**2735-2742.

Urdaneta-Rincon, M. and Leeson, S., 2002. Quantitative and qualitative feed restriction on growth characteristics of male broiler chickens. Poultry Science, **81:**679-688.

Vakili, R., and Akbarogli, F., 2006. Effect of feed restriction method during rearing on growth and blood indices of stress in broiler breeder. XII European Poultry Conference, Verona, Italy. Electronic proceedings available online:

www.cabi.org/animalscience/Uploads/File/AnimalScience/additionalFiles/wpsaverona.htm (last accessed March 2011).

Vieira, S.L. and Moran, E.T., Jr., 1999. Effects of egg origin and chick post-hatch nutrition on broiler live performance and meat yields. World's Poultry Science Journal, **55:**125-142.

Virden, W.S., Yeatman, J.B., Barber, S.J., Willeford, K.O., Ward, T.L., Fakler, T.M., Wideman, R.F., Jr. and Kidd, M.T., 2004. Immune system and cardiac functions of progeny chicks from dams fed diets differing in zinc and manganese level and source. Poultry Science, **83:**344-351.

Virden, W.S., Yeatman, J.B., Barber, S.J., Zumwalt, C.D., Ward, T.L., Johnson, A.B. and Kidd, M.T., 2003. Hen mineral nutrition impacts progeny livability. Journal of Applied Poultry Research, **12:**411-416.

VSN International, 2009. GenStat, 12th Edition, Version 12.1. Rothamsted Experimental Station. Ltd., Hemel Hempstead, UK.

Walsh, T.J. and Brake, J., 1997. The effect of nutrient intake during rearing of broiler breeder female of subsequent fertility. Poultry Science, **76:**297-305.

Walsh, T.J., and Brake, J., 1999. Effects of feeding program and crude protein intake during rearing on fertility of broiler breeder females. Poultry Science, **78:**827-832.

Wellman-Labadie, O., Picman, J. and Hincke, M.T., 2008. Comparative antibacterial activity of avian egg white protein extracts. British Poultry Science, **49:**125-132.

Willemsen, H., Kamers, B., Dahlke, F., Han, H., Song, Z., Pirsaraei, Z.A., Tona, K., Decuypere, E. and Everaert, N., 2010. High- and low-temperature manipulation during late incubation: Effects on embryonic development, the hatching process, and metabolism in broilers. Poultry Science, **89:**2678-2690.

Willemsen, H., Everaert, N., Witters, A., De Smit, L., Debbone, M., Verschuere, F., Garain, P., Berchmans, D., Decuypere, E. and Bruggeman, V., 2008. Critical assessment of chick quality measurements as an indicator of post-hatch performance. Poultry Science, **87:**2358-2366.

Wilson, H.R., 1997. Effects of maternal nutrition on hatchability. Poultry Science, **76:**134-143.

Wilson, H.R. and Harms, R.H., 1984. Evaluation of nutrient specifications for broiler breeders. Poultry Science, **63:**1400-1406.

Wolanski, N.J., Renema, R.A., Robinson, F.E., Carney, V.L. and Fancher, B.I., 2007. Relationship among egg characteristics, chick measurements, and early growth traits in ten broiler breeder strains. Poultry Science, **86:**1784-1792.

Wolanski, N.J., Renema, R.A., Robinson, F.E., Carney, V.L. and Fancher, B.I., 2006. Relationship between chick conformation and quality measures with early growth traits in males of eight selected pure or commercial broiler breeder strains. Poultry Science, **85:**1490-1497.

Wolc, A., White, I.M.S., Olori, V.E. and Hill, W.G., 2009. Inheritance of fertility in broiler chickens. Genetic Selection Evolution, **41:**47-55.

Wu, G., Bryant, M.M., Gunawardana, P. and Roland, D.A., Sr., 2007. Effect of nutrient density on performance, egg components, egg solids, egg quality, and profits in eight commercial Leghorn strains during phase one. Poultry Science, **86:**691-697.

Wu, G., Bryant, M.M. and Roland, D.A., Sr., 2005. Performance comparison and nutritional requirements of five commercial layer strains in phase IV. International Journal of Poultry Science, **4:**182-186.

Wylie, L.M., Robertson, G.W. and Hocking, P.M., 2003. Effects of dietary protein concentration and specific amino acids on body weight, body composition and feather growth in young turkeys. British Poultry Science, **44:**75-87.

Yadgary, L., Cahaner, A., Kedar, O. and Uni, Z., 2010. Yolk sac nutrient composition and fat uptake in late-term embryos in eggs from young and older breeder hens. Poultry Science, **89:**2441-2452.

Yassin, H., Velthuis, A.G.J., Boerjan, M., van Riel, J. and Huirne, R.B.M., 2008. Field study on broiler egg hatchability. Poultry Science, **87:**2408-2417.

Yassin, H., Velthuis, A.G.J., Boerjan, M. and van Riel, J., 2009. Field study on broiler's first-week mortality. Poultry Science, **88:**798-804.

Yildirim, I. and Yetisir, R., 2004. Effects of different hatcher temperatures on hatching traits of broiler embryos during the last five days of incubation. South African Journal of Animal Science, **34:**211-216.

Yilmaz-Dikmen, B. and Sahan, U., 2009. The relationship among age, yolk fatty acids content, and incubation results of broiler breeders. Poultry Science, **88:**185-190.

Zuidhof, M.J., Renema, R.A. and Robinson, F.E., 2007. Reproductive efficiency and metabolism of female broiler breeders as affected by genotype, feed allocation, and age at photostimulation. 3. Reproductive efficiency. Poultry Science, **86:**2278-2286.