University of Alberta

Effect of Broiler Breeder Nutrition on Reproductive and Offspring Performance

by

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DEDICATION

To my loving husband Josué Romão for being my love, my best friend and my greatest example of a hard working person. I love and admire you!

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ABSTRACT

The effects of broiler breeder dietary energy and protein during rearing and dietary energy level of lay diets on egg composition, offspring performance and carcass yield were evaluated. Pullets were fed a diet containing high ME (2,736 kcal/kg; HE_{REAR}), or low ME (2,528 kcal/kg; LE_{REAR}) combined with either high protein (15.3% CP; HP_{REAR}) or low protein (13.7% CP; LP_{REAR}). During lay birds were fed either a high ME (2,900 kcal/kg; HE_{LAY}), or low ME (2,800 kcal/kg; LE_{LAY}) diet. For 28 wk old hens, a higher protein intake per unit of hen metabolic BW resulted in higher progeny BW only in the female progeny. Carcass yield of broiler progeny was lower when energy to protein ratio in maternal diet decreased upon transition from rearing to laying diet. For 35 wk old hens, effect on offspring BW was transient, higher maternal nutrient intake (feed, protein, energy) during rearing reduced progeny carcass yield.

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LIST OF NOMENCLATURE AND ABBREVIATIONS

ADG	Average daily gain
BW	Body weight
CP	Crude protein
CP_{REAR}	Crude protein during rearing
d	Day
df_{pool}	Degrees of freedom from pooled data curve
df_{sep}	Degrees of freedom from separated curves
df_{tmt1}	Degrees of freedom from treatment 1
df_{tmt2}	Degrees of freedom from treatment 2
E:P	Energy to protein ratio
$E:P_{REAR}$	Energy to protein ratio for rearing diets
$E:P_{LAY}$	Energy to protein ratio for lay diets
FCR	Feed conversion ratio
h	Hour
HE_{LAY}	High dietary energy during lay
HE_{REAR}	High dietary energy during rearing
HP_{REAR}	High dietary protein during rearing
IGF-I	Insulin-like growth factor 1
IGF-IR	Type 1 insulin-like growth hormone receptor
IU	International units
$kg^{0.75}$	Metabolic body weight
L:D	Hours light:hours darkness in the photoperiod

LE_{LAY}	Low dietary energy during lay
LE_{REAR}	Low dietary energy during rearing
LP_{REAR}	Low dietary protein during rearing
ME	Metabolizable energy
ME_{LAY}	Metabolizable energy during lay
MEn	Metabolizable energy N-corrected
ME_{REAR}	Metabolizable energy during rearing
R	Correlation coefficient
RH	Relative humidity
SEM	Standard error of the mean
SS_{pool}	Sum of squares from pooled data curve
SS_{sep}	Sum of squares from separated curves
SS_{tmt1}	Sum of squares from treatment 1
SS_{tmt2}	Sum of squares from treatment 2
Wk	Week

CHAPTER 1: Literature Review

1.1. Introduction

Protein and energy-yielding nutrients are the most important and expensive nutrients required by broiler breeders (Summers, 2008). Energy is usually selected as the starting point for poultry diet formulations (National Research Council, 1994). It is important to give an adequate level of energy to bird's maintenance, growth and reproduction as energy intake significantly influences reproductive performance of broiler breeders (Summers, 2008).

Reproductive performance in female broiler breeders is expressed as egg production and in males it is expressed as semen production. The energy requirement for egg synthesis is 120 kcal ME/d on average (Leeson and Summers, 2005), with the total female ME intake of 386 kcal ME/d, while semen production requires less than 3.8 kcal ME/d for a 3.75 kg rooster (less than 1% of basal metabolic rate; Kunz and Orrell, 2004) and the total male energy intake is 364 kcal ME/d at 26 wk (Aviagen, 2007).

The first priority for energy use in broiler breeders is for maintenance and development of vital organs (Figure 1-1; Schneider et al., 2008). Secondly, energy is used for growth of muscles and bones and egg production, with deposition of some fat that is necessary for onset of lay (Schneider et al., 2008). However if birds get an excess of nutrients they will become obese with an excessive deposition of fat (Schneider et al., 2008). Excessive production of large follicles in the ovary can be observed in overfed birds and that will result in erratic

oviposition and defective egg syndrome (EODES) with the production of unsettable eggs such as double yolk eggs, soft shelled, and shelless eggs (Renema and Robinson, 2004). However, not only excessive fat deposit decreases egg production. If birds grow excessive breast muscles more dietary energy will be used for muscle maintenance (De Beer, 2009) and, as consequence, egg production may be reduced.

Broiler breeders do not require a specific level of crude protein per se, therefore nutritionists pay more attention to the amino acid content of the diet and less attention is paid to the amount of protein consumed by the bird (National Research Council, 1994). As a consequence, dietary protein is often in excess of the amounts needed for maintenance, growth and reproduction (Summers, 2008). Nitrogen is excreted in the form of uric acid and nitrogen excretion can be increased by excessive protein intake (Lopez and Leeson, 1995). Nitrogen excretion causes environmental concerns in terms of soil, water and air quality (Nahm, 2000). Also synthesis and excretion of excess of protein as uric acid requires a considerable amount of energy (330 kcal/mol; Buttery and Boorman, 1976).

Another challenge in broiler breeder nutrition is the practice of feed restriction. Feed restriction is used as a means to control the body weight (BW) of individual birds in a group-housed flock, and to maintain a reproductive performance acceptable for industry standards (Renema and Robinson, 2004). The potential negative consequences of feed restriction are that broiler breeders can suffer hunger and develop behavioral vices such as overdrinking due to frustration

caused by unfulfilled feeding motivation (Savory et al., 1996). Alternative diets are being studied as a way of improving bird welfare without causing an increase in BW. Qualitatively restricted diets give birds more access to feed. However, voluntary nutrient intake is decreased due to reduction of protein levels (Hocking et al., 2002), use of appetite suppressants such as calcium propionate (Tolkamp et al., 2005; Sandilands et al., 2006) or decreased diet density with addition of bulky dietary diluents such as oat hulls (Tolkamp et al., 2005).

1.2. Broiler breeder nutrition

1.2.1. Females

Broiler breeder management can be divided into 2 main phases, the rearing phase and the laying phase. Each phase has unique goals. During the rearing phase, bird nutrition is focused on growth and skeletal development. During the laying phase, the focus of nutrition is to support long-term reproduction of sexually mature broiler breeders.

Feeding of immature pullets during rearing must be managed so that the birds achieve a recommended BW and skeletal conformation target as uniformly as possible by the time of photostimulation, which occurs between 22 and 24 wk of age (Zuidhof et al., 2007). If at time of photostimulation birds are smaller than the adequate BW, they are more likely to produce smaller eggs because egg and yolk size are influenced by BW. Smaller birds can also produce fewer eggs, because at time of photostimulation they can still be growing and developing their ovary, which could contribute to delayed onset of egg production (Renema et al., 2003).

Excessive BW caused by an excessive intake of nutrients reduces reproductive efficiency in broiler breeders (Renema and Robinson, 2004). In order to avoid that, feed restriction is universally used to control the growth of broiler breeders. Overweight broiler breeders have poor fertility and hatchability. Obese birds usually lay eggs erratically which can result in poor shell quality and higher embryonic mortality (McDaniel et al., 1981a). Excessive BW also results in a reduction in the production of settable eggs because of the fast recruitment of small yellow follicles. As a consequence, the formation of multiple follicle hierarchies will result in various large yellow follicles in the ovary at the same time which can increase the formation of double yolk eggs or in the formation of a poor or abnormal shell (Renema and Robinson, 2004).

The traditional system of feed restriction has been a skip-a-day regimen, where pullets are only fed on alternate days. That system allows a higher feed allowance on feed days, reducing competition between birds and improving flock uniformity. When feed allowance is higher, there is a greater chance that even after dominant birds eat there will be feed left on the feeder for the other birds to consume (Holm, 2010). Pullets can also have a limited feed allocation daily; which is considered more efficient because it reduces the cost of storing and mobilizing nutrients and can help birds to achieve better uniformity (Leeson and Summers, 2005), however, this feeding system requires careful management and an adequate feeder space to reduce competition and obtain good uniformity. In both feeding systems, nutrient density of the diet and environmental conditions will influence feed requirements (Leeson, 2010).

After photostimulation, broiler breeders are usually fed every day because egg production starts and the bird needs adequate nutrient intake to deposit in the egg that is produced daily (Leeson and Summers, 2005). During this period, the amount of protein in the diet, especially methionine concentration, is very important because it can affect egg size (Bowmaker and Gous, 1991). A rapid increase in feed allocation can also increase early egg size, but determining the optimal feed allocation will depend on the weight of the bird and the energy density of the diet (Leeson and Summers, 2005). Broiler breeder feed allocation is normally adjusted according to the energy density of the diet because energy intake is the major factor controlling egg production (Leeson, 2010). Most breeder flocks will be overfed protein, because nutritionists are more concerned about meeting the amino acid requirements of birds and less attention is paid to the protein content of the diet. As a consequence, excess protein can be converted to muscle growth resulting in over-fleshed birds (Leeson, 2010).

1.2.2. Males

Broiler breeder males are typically fed the same diet as females up to sexual maturity (24 wk; Moyle et al., 2011). Because there are a lot more females than males (1 male to 10 females) in the breeder house, some producers feed males and females the same diet during the entire production period. However, males have different nutrient requirements than females. Broiler breeder males require less protein and less calcium than females (National Research Council, 1994). Excess calcium intake can cause problems in the kidney of the roosters such as kidney

asymmetry and urolithiasis (Moyle et al., 2011). Excess protein intake will increase rooster BW and that can affect fertility negatively because more energy will be needed to support a greater BW and maintain sperm production and mating activity (Romero-Sanchez et al., 2007).

Like females, males are also feed restricted to control body weight and body condition and skip-a-day program is the most commonly used. Controlling the feed intake of male breeders is difficult because aggressive males eat more of the available feed and therefore gain more weight than non aggressive males. The result is that fertility will be reduced in both over-fed (Hocking and Duff, 1989) and under-fed males (Crespo and Shivaprasad, 2010). With male and female birds raised in the same barn, grills are placed on the female feeders to prevent the male birds from accessing feed from these feeders. However, some young males with narrow heads can still eat from female feeders making it very difficult to control their feed intake (Brake et al., 1993). In order to exclude males from the female feeders so males would only eat from their own feed line, 'nose-bars' ("Noz Bonz") which are plastic rods that are inserted through the nostrils of roosters can be used (Millman et al., 2000). Other techniques to control male feed intake can be done in the base of head height (accomplished by not dubbing male combs) or delaying the placement of the males in the breeder house until 23 wk of age when males will have wider heads which will not fit into female feeders (Leeson and Summers, 2005).

1.3. Effects of broiler breeder nutrition on reproductive performance

1.3.1. Males

1.3.1.1. Fertility

Optimizing male fertility is a key step to improve hatchability in poultry production, which is fundamental to the supply of chicks. Several factors may impact male fertility such as male BW. Overweight males cannot mate efficiently, because it is difficult anatomically to achieve cloacal contact with the hens (Hocking and Duff, 1989). Depressed fertility can also be caused by reduction of mating activity as a consequence of musculoskeletal diseases that can appear in males when they are heavier and older (Hocking and Duff, 1989). If excess BW decreases fertility the same can also happens when there is a nutritional deficiency caused by excessive feed restriction. Cerolini et al. (1995) found evidence that fertility can also be decreased in males due to ME deficiency and that problems would happen more often at the end of the production period. Romero-Sanchez et al. (2008) suggested that ME deficiency would affect the largest males more considerably than smaller males and the largest males in the flock would show reduced semen production and mating activity sooner in the flock.

Cerolini et al. (1995) fed Ross broiler breeder males with a standard diet (12% CP and approx. 2,746 kcal ME/kg) from 23 to 54 wk of age with 110, 120, 130 g/bird/d or ad libitum (corresponding to 120, 128, 136, and 184 kcal/kg$^{0.75}$, respectively) and observed the effect of feed allocation on body weight and fertility when hens were artificially inseminated. They found that male 54 wk BW (3,421, 3,523, 3,621 and 3,621 g, respectively) increased with increasing feed

allocation and fertility was increased for males fed increasing amounts of feed (59%, 72%, 79.2% and 79.2% for males fed 110, 120, 130 g/bird/day or ad libitum, respectively; 302, 329.5, 375, 483.3 kcal ME/day, respectively; Cerolini et al.; 1995). These results are supported by Mench (2002) who said that for males used for artificial insemination the level of feed restriction could probably be reduced.

1.3.1.2. Semen quality

Semen quality is essential for successful program of artificial insemination in the poultry industry. Sperm motility, ratio of live-to-dead sperm cells and morphological evaluation are ways to predict semen quality and its fertilizing ability (Alkan et al., 2002). There are several factors that influence semen quality including BW (Bowling et al., 2003), collection techniques such as collection frequency (Riaz et al., 2004) and also dietary manipulations (Buckner et al., 1986). Body weight was shown to influence semen quality as broiler breeder males separated according to sperm motility phenotype (high or low) had a significant BW difference, with the low phenotype males averaging 227 g more than high phenotype males (Bowling et al., 2003).

Nutrition also can influence BW, therefore it plays a role in semen quality as Buckner et al. (1986) fed broiler breeder males (from 20 to 60 wk) 136, 125, 113, 102 or 91 g/bird/day (141, 133, 126, 121 and 112 kcal/kg$^{0.75}$, respectively) of a diet containing 13.1% CP and 3,167 kcal ME/kg and showed that severe feed restriction decreased BW, semen volume, number of spermatozoa in the ejaculate,

testicle weight, hematocrit and the percentage of males producing semen. They concluded that 113 g/bird/d (358 kcal/bird/d) was the minimum feed allocation that did not affect the reproductive traits negatively.

On the other hand Cerolini et al. (1995) fed Ross broiler breeder males different intakes (110, 120, 130 g/bird/d or ad libitum) and observed that increasing the daily quantity of feed fed to roosters decreased their overall sperm concentration but improved sperm motility, and increased the number of live spermatozoa in the semen.

These findings show that semen quality is the result of several management practices and the balance among all these parameters has to be pursued in order to maximize semen quality and optimize the reproduction performance of broiler breeder males.

1.3.2. Females

1.3.2.1. Egg production

Management of the broiler breeder female to improve egg production is very important for the poultry industry as egg production directly influences chick production. Because of that, there are attempts to improve egg production by changing amount of nutrients in broiler breeder diet because it was previously observed that broiler breeder nutrition can affect egg production (Lopez and Leeson, 1994a; De Beer and Coon, 2006). When broiler breeder hens were fed 14, 16 or 18% CP (18, 20, 22 g protein/bird/d, respectively) during pre-lay and early-lay phases, it was observed that hens fed 14% CP had reduced production at 29

wk of age, however protein level did not affect overall egg production (Joseph et al., 2000). Similarly, egg production was not affected when old broiler breeders (58 to 61 wk) were fed diets with protein level varying from 9 to 15% CP (13 to 22 g protein/bird/d; Lopez and Leeson, 1994b). Proudfoot and Hulan (1986) fed broiler breeder hens with different levels of protein and energy in their grower and adult diet, however no diet effect was observed in egg production.

In contrast, Kingori et al. (2010) observed a decrease in egg production in 46 wk old Kenya indigenous chickens fed high levels of protein (17% CP dry matter basis; 22.1%) when compared to hens fed diets containing 10, 12 or 14 CP on a dry matter basis. They also found that hens fed moderate protein (12 and 14% CP) had better overall egg production (43.6% for both). Kenyan indigenous chickens are very different from modern breeders. They only lay 15 eggs per clutch with a maximum of 3 clutches per year (Ondwasy et al., 2006). However, Kingori et al. (2010) had results similar to Lopez and Leeson (1994a) who observed that hens (46-55 wk) fed 20% CP had reduced egg production when compared to hens fed 14, 16 or 18% CP.

Overall, if dietary protein and energy are low, the hen will not have enough nutrients to produce the egg and production will drop (Joseph et al., 2000). A high level of nutrients in the diet will increase the amount of nutrients that will be available to be used in the egg production. However, if there is an excess of energy or protein that can result in increased BW and decreased egg production (Joseph et al., 2000). Therefore a balance is needed to supply broiler breeder with nutrients for their egg production requirements without excessively increasing

their BW and that ideal broiler breeder requirements can vary according to hen age and strain.

1.3.2.2. Egg weight and composition

The egg has the function to supply the embryo chick with protection and nutrients during its development. Egg weight has been associated with chick weight and posterior broiler performance (Willemsen et al., 2008). There are reports that egg weight can increase with the increased intake of dietary fat, in particular, linoleic acid (Grobas et al., 1999), protein (Lopez and Leeson, 1994b), and certain essential amino acids such as lysine and methionine (Bowmaker and Gous, 1991). Joseph et al. (2000) fed broiler breeders during pre-lay and early-lay phase diets containing 14, 16 or 18% CP and found that hens fed low (14%) CP produced eggs with lower average weight (50.1 g, 51.3 g, 51.5 g, respectively) and albumen weight (32.0 g, 33.7 g, 33.3 g, respectively) from 25 to 29 wk. Average yolk weight during the same period was unaffected by protein level.

No significant effects of dietary protein on the proportion of egg components such as yolk and albumen were observed when old broiler breeders (58 to 61 wk) were fed 9, 11, 13 or 15% CP (13, 16, 19 and 22 g protein/bird/d, respectively; Lopez and Leeson, 1994b). However, hens fed 9 and 11% CP produced smaller eggs (71.1 g and 71.2 g, respectively) when compared to hens that were fed 13 and 15% CP (73.2 g and 72.7 g, respectively; Lopez and Leeson, 1994b). Kingori et al. (2010) fed 46 wk old Kenya indigenous chickens with diets containing 10, 12, 14 or 17% CP on a dry matter basis and observed that egg weight decreased in hens

fed low protein levels (10% CP; 42.9 g). Hens fed moderate protein (12 and 14% CP) had better overall egg weights (46 and 47.2 g, respectively). Proudfoot and Hulan (1986) fed different levels of protein and energy during rearing and laying phases of broiler breeders, however no diet effect was observed in egg weight.

Lopez and Leeson (1994b) fed broiler breeders diets varying from 9 to15% CP and observed that protein level did not change protein or fat content of the egg That indicates that the amount of macronutrients in the egg is very stable, not being affected by hen nutrition. However, hen diet can influence micronutrients such as fatty acids (Poureslami et al., 2011) and the amount of some vitamins (Barreto et al., 1999a) and minerals (Neto et al., 2011) in the egg; which could potentially influence embryo development and broiler performance.

1.3.2.3. Fertility

Female fertility can affect the number of chicks hatched as unfertile eggs do not produce chicks. Nutritional factors can impact female broiler breeder BW and that is the main factor affecting female fertility. An excessive intake of nutrients, resulting in obese hens will decrease fertility due to a decrease in hen ability to store and transport sperm cells as a consequence of fat blockage of storage tubules (McDaniel et al., 1981b). Broiler breeder hen fertility can also be affected by cumulative protein intake during rearing. Walsh and Brake (1997) fed broiler breeders rearing diets (0 to 18 wk) containing 11, 14, 17 or 20% CP and observed that hens fed a low protein diet (11% CP) had lowest overall fertility up to 37 wk

of age, that can be because the hen needs a minimum protein intake in order to develop its oviduct and storage tubules completely (Walsh and Brake; 1997).

On the other hand, other studies did not find effect of varying protein content of diets during laying phase on female fertility. Barreto et al. (1999b) fed Ross breeders 14% or 16% CP (21.6 and 24.7 g bird/d and 19.64 and 17.18 kcal/g protein, respectively) and did not find a significant effect of breeder diet on fertility (95.16% and 93.83%, respectively). Similarly, Wilson and Harms (1984) fed broiler breeders with different daily intakes of protein ranging from 19.9 to 23 g/bird/d with energy to protein (E:P) ratio varying from 24.67 to 18.45 kcal/g protein and found that protein intake had no effect on fertility. Proudfoot and Hulan (1986) fed 3 strains of broiler breeders with different levels of protein and energy during 15 to 20 wk and 21 to 60 wk and they observed that there was no effect of the different diets on fertility. According to the previous studies it seems that nutritional protein variations during the lay do not impact female fertility.

1.3.2.4. Hatchability

Hatchability is one of the most important economic performance indicators for broiler hatching egg industry. Hatchability means the amount of chicks hatched from the total of eggs incubated and it can be affect by several management factors, including hen nutrition. Pearson and Herron (1982) studied broiler breeders from 21 to 64 wk of age fed 3 energy intakes (approximately 449, 413 or 363 kcal ME/bird/d) associated with 1 of 2 protein intakes (21.3 or 27 g/bird/d). Low hatchability was reported between 26 and 36 wk in birds fed high protein (27 g/bird/d) and low energy (363 kcal ME/bird/d). According to these

authors, decreased hatchability was likely caused by a nutritional deficiency in the egg that resulted in increased embryonic mortality in mid-incubation and unhatched pips (Pearson and Herron, 1982). Dietary maternal protein level did not influence hatchability when Kingori et al. (2010) fed Kenyan indigenous chickens with diets containing varying levels of CP (10, 12, 14 or 17% CP on a dry matter basis). The results found in indigenous chicken are in agreement with Barreto et al. (1999b) who fed Ross breeders 14% or 16% CP (21.6 and 24.7 g bird/d and 19.64 and 17.18 kcal/g protein, respectively) and did not find a significant effect on hatchability (89.34% and 87.50%, respectively) and with Lopez and Leeson (1994a) who fed 45 wk old broiler breeders with 14, 16, 18 or 20% CP (21, 24, 27, 30 g/bird/d and 20, 17.5, 15.5, 14 kcal/g protein, respectively) and found no effect in hatchability of fertile eggs. Similarly, Wilson and Harms (1984) fed broiler breeders with different daily intakes of protein ranging from 19.9 to 23 g/bird (24.67 to 18.45 kcal/g protein) and found that protein intake had no effect on hatchability.

Proudfoot and Hulan (1986) fed 3 strains of broiler breeders with different levels of protein and energy from 15 to 20 wk (22.5 and 17.0 kcal/g, respectively) and 21 to 60 wk (17.9, 15.6, 14.8, kcal/g, respectively) and they observed that there was no effect of the different diets on hatchability.

Diet dilution (15% or 30%) with ground oat hulls was tested in hens' diet from starter diet up to the breeding diet (Zuidhof et al., 1995). Diets with 15% dilution had E:P ratios of 13.8, 17.2, 18.0 and 15.9 kcal/g while diets with 30% dilution had 13.0, 16.0, 16.7, and 14.9 kcal/g and, control diets 14.3, 18.1, 19.0, and 16.8

kcal/g for starter, grower, prebreeder and laying diet, respectively. Zuidhof et al. (1995) observed that a 15% dilution of a standard broiler breeder diet caused no significant effect on overall fertility or hatchability but did significantly increase the number of chicks produced per hen by 8.7% when compared to control diet, which means that a decrease in diet density, if not too extreme, do not decrease hatchability and can have benefits in terms of chick production per hen due to a higher egg production.

Fattori et al. (1991) studied broiler breeders with standard BW, 8% increase, 8% decrease, 16% decrease or 24% decrease in BW. They fed the birds from 22 to 140 d different feed allocations to reach the treatment BW desired and they found that their treatments had no effect on hatchability or fertility. It was concluded that relatively severe reductions of protein and energy intake during the growing period of broiler breeders did not affect subsequent hatchability of the hens` egg (Fattori et al., 1991).

Effects of dietary protein and energy in hen diet on hatchability are hard to evaluate because the nutritional requirement can change according to the hen age and strain and also because there is a lack of information of all the nutrients in the diet that can act as confounding factors (such as amino acid content) as well as a lack of understanding of the interaction of different nutrients (Wilson, 1997).

1.4. Effect of broiler breeder hen nutrition on offspring performance

Hen nutrition can affect offspring development and performance through nutrient content of the egg and gene expression (Wilson, 1997). All required nutrients

should be provided within the egg for normal embryonic growth and development (Wilson, 1997). Nutrient deposition in the egg depends heavily on maternal diet and metabolism (Wilson, 1997). In non-integrated production systems, a lot of attention is given to broiler breeder performance, mainly egg production and the number of saleable chicks produced per hen and less attention is paid to the quality of the saleable chick and to improving its growth potential. Parental nutrition can affect the performance of offspring therefore it should be better studied because proper hen nutrition may bring advantages for both broiler breeder and broiler producers.

To make sense of the complexity of this subject area, the results of a number of different research projects that have evaluated the effect of broiler breeder nutrition on the resulting offspring are summarized in Table 1-1 and Table 1-2. The results were likely affected by bird strain and age as well as the level and intake of nutrients used in the experiment. Additionally, a number of these studies were conducted years ago. Broiler breeders have been selected during the years for desirable qualities such as a better egg production, faster growth rate, increased yield and improved feed conversion ratio (FCR; Pollock, 1999). Due to this selection their genetic makeup has changed considerably during the past 6 decades. It is likely that with the changes in broiler breeder bird genetics over the last number of years that the nutritional effects of maternal diet on broiler progeny may have changed as well.

1.4.1. Embryo development

The amount of time it takes a broiler to grow to market weight is decreasing. A broiler strain from 1957 would take 84 d to reach 1.4 kg (Havenstein et al., 2003). It currently takes 40 d for a broiler to reach 3 kg market weight (Leeson, 2012). As a consequence, the duration of embryonic development is becoming a greater proportion of the total broiler`s productive life. Any improvement that can result in heavier or healthier chicks at hatch may have a positive impact on overall broiler growth (Fasenko and O`Dea, 2008; Molenaar et al., 2008; Willemsen et al., 2008).

Once the egg is laid, all the nutrients required for embryo development must be in place. Therefore, it is important that broiler breeders receive adequate nutrients in their diet so they can provide the optimum nutrients for normal embryo development (Moran, 2007). Embryos can obtain nutrients from the 3 major egg components: yolk, albumen and shell. These components contain specific nutrients that are mobilized and used by the embryo during its development. A normal egg contains approximately 74% water, 13% protein, 11% fat and 2% ash (Campos, 2003).

Because the egg is formed using nutrients the hen obtained in the diet, hen nutrition can influence the composition of the egg components (Vieira, 2007). Eggshells are mostly composed of calcium carbonate (Vieira, 2007), but other minerals such as copper are also important for eggshell formation. Single Comb White Leghorn laying hens fed a copper-deficient diet produced shell-less eggs or eggs with abnormal shell and membranes which was detrimental for hatchability

(Baumgartner et al., 1978). Albumen composition is mostly water and proteins but if hens are fed a diet deficient in riboflavin, the concentration of this vitamin in the albumen will be reduced, increasing embryonic mortality (Vieira, 2007). Yolk is the component of the egg that is richest in lipids and because of that an increase in the amount of dietary fat-soluble vitamin can increase the concentration of these vitamins in the yolk (Vieira, 2007).

Hens deliver nutrients in the egg yolk through the ovary, and via oviduct albumen, egg shells and membranes are deposited (Vieira, 2007). Through the process of embryonic development, the embryo receives protein and energy first from the yolk and later from the albumen after 14 d of incubation (Vieira, 2007). Nutritional deficiencies to the breeder hen during egg formation may affect embryo development at any time (Moran, 2007).

An adequate deposition of protein in the egg by the breeder hen is particularly important at the end of incubation because during this period protein is highly used for gluconeogenesis by the embryo (Moran, 2007). The protein deposited in the egg can be obtained by the embryo in the amniotic fluid or in the embryonic tissue protein reserves (Moran, 2007). Overall, maternal nutrition has the potential to have a major influence on embryo growth and development. There does not appear to be a lot of research to verify the effect of maternal protein and energy intake on the offspring before hatch.

In ovo nutrition consists of providing external nutrients to poultry embryos into the egg at late stages of incubation. Amino acids (Ohta and Kidd, 2001), carbohydrates (Tako et al., 2004), proteins (Foye et al., 2006), and vitamins (Gore

and Qureshi, 1997) were injected in ovo during experiments. They found that birds fed in ovo had higher BW at hatch (Foye et al., 2006), as well as an enhanced intestinal development (Tako et al., 2004) and immunity (Gore and Qureshi, 1997). However, this technique is still in experimental phase in order to determine nutrients that can be injected as well as their volume, concentration and injection site without decreasing hatchability. In ovo feeding allows the embryo to have access to more nutrients than those initially deposited in the egg by the hen. As consequence, embryo development and post-hatch performance can be improved. However, because in ovo injections are usually performed at transfer (18 d), it has less influence in the embryo development than maternal nutrition, and nutrient deficiencies that affect early embryonic development would not be corrected by in ovo injections (Vieira, 2007).

1.4.2. Hatch time

Lopez and Leeson (1994b) fed broiler breeders different levels of CP (9, 11, 13 or 15% CP) and they observed that chicks from hens fed a 15% CP diet hatched on average 4 h later than offspring from hens fed a 9% CP diet. Commercial hatcheries usually pull chicks from hatchers only once during the hatching period. Five hundred and four (504) h after the start of incubation is considered the optimal time because most eggs should have hatched (Almeida et al., 2006). Hatch time is an important parameter for chick performance. There is usually a hatch window of 24 to 36 h (Decuypere et al., 2001). Chicks that hatch too early have delayed access to feed and water which decreases their post-hatch

performance, while chicks that hatch after all other chicks are pulled from the hatchers will be culled, following standard industry practice.

1.4.3. Chick quality

Chick quality is important to broiler producers as it can be related to the health state of the chick. Chicks that are not healthy and active will not search for food properly and will die or grow less (Fasenko and O`Dea, 2008). Chick activity and signs of beak, navel and hock abnormalities are some of the parameters used by commercial hatcheries to evaluate quality of day old chicks (Tona et al., 2005).

Chicks with even minor navel conditions grow less efficiently because unhealed navels can cause infections and affect chick performance (Fasenko and O`Dea, 2008). Birds that had button navel (unhealed navel with a scab) at hatch weighed 1,921 g at 41 d while birds that had healed navels at hatch weighed 2,029 g at 41 d (Fasenko and O`Dea, 2008). Higher mortality was also observed in chicks with button navels (12.7%) than in chicks with healed navels (5.7%; Fasenko and O`Dea, 2008). Therefore, chick quality evaluation is an important tool to predict chick performance and mortality, as well as to detect problems in the breeder house or the hatchery.

1.4.4. Chick weight

Hatch weight is also an important aspect of chick quality because it is considered a predictor of broiler BW at processing age (Willemsen et al., 2008). Willemsen et al. (2008) found that 10.9 % of variation in 42 d old broiler BW from 39 wk old

Ross hens could be explained by hatch weight. However, relation between hatch weight and processing weight is not consistent in all experiments since several pre-incubation factors, such as egg storage and maternal nutrition, may determine hatching egg characteristics that may affect chick weight and market BW.

De Brum et al. (1996) fed broiler breeders from 2 different strains (Embrapa and Arbor Acres) at 36 wk diets containing 12, 13.5, 15, 16.5 or 18% CP. No differences in egg weights were observed, but birds that were fed 12, 13.5 or 15% CP had lighter offspring at hatch than birds fed 16.5% or 18% CP, in 1 of 2 strains tested. In contrast, Kingori et al. (2010) fed Kenya indigenous chickens with diets containing 10, 12, 14 or 17% CP on a dry matter basis and observed that dietary maternal protein level did not significantly influence chick weights for this breed of chickens. This result was consistent with a study conducted by Lopez and Leeson (1994a). They fed 45 wk old broiler breeders different levels of CP (14, 16, 18 or 20% CP) and found no effect on chick weights or chick yield. Lopez and Leeson (1994b) fed older broiler breeders (58 to 61 wk) diets with 9, 11, 13 or 15% CP. They did not observe any difference in absolute chick weights at hatch (Lopez and Leeson, 1994b).

1.4.5. Progeny growth

Broiler growth is an important performance parameter. A rapid growth rate is achieved by healthy birds with adequate management and that combined with genetic improvements results in broilers reaching market weight earlier every year. A number of studied have been conducted to verify the effects of maternal

nutrition on progeny growth. Wilson and Harms (1984) found no effect of maternal protein intake (varying from 19.9 to 23 g/d) on broiler BW at 49 d. Similarly, broiler BW at 7, 21, 35 and 49 d were not affected when older broiler breeders (45 to 55 wk old) were fed 21, 24, 27 or 30 g protein/bird/d (14, 16, 18, or 20% CP; Lopez and Leeson, 1994a). No effect of maternal dietary CP level on BW of the offspring at 42 d was observed when De Brum et al. (1996) fed 36 wk old broiler breeders from 2 different strains with 12, 13.5, 15, 16.5 or 18% CP. However, when Rao et al. (2009) compared 2 diets containing 10% or 15% CP for Langshan breeder hens, they observed that offspring from hens fed a low protein diet had significantly heavier BW at 4 wk post-hatch compared to offspring from hens fed a high protein diet.

Other studies examined varying levels of both energy and protein in maternal diets. Proudfoot and Hulan (1986) observed no effect on the BW of the offspring at 42 d of 3 broiler strains when different levels of protein and energy were used in the maternal rearing (15 to 20 wk; 12.9% CP and 2,902 kcal/kg or 15.8% CP and 2,699 kcal/kg) and laying diets (21 to 60 wk; 15.3% CP and 2,746 kcal/kg or 17.6% and 2,746 kcal/kg or 17.8% CP and 2,651 kcal/kg).

Spratt and Leeson (1987) fed Hubbard broiler breeders 150 g/bird/day and divided the birds into 6 treatments according to their energy and protein intake. Birds were fed 19 or 25 g protein and 325, 385 or 450 kcal MEn. These authors found that the BW of male offspring at 20 d was influenced by the energy intake of the broiler breeder hen. While the higher energy fed hens produced heavier male offspring at 20 d (575, 586 and 601 g from hens fed low energy, standard energy

and high energy intake, respectively) the broiler weight differences did not carry through to 41 d (Spratt and Leeson, 1987).

Aitken et al. (1969) fed 3 strains of meat type hens with low density (14.6% CP and 2,490 kcal/kg) or high density diet (17.5% CP and 2,880 kcal/kg) with micro-nutrient levels (0.5%) being the same for both diets. Birds fed the low density diet had higher feed intakes (160 g/bird/d vs. 140 g/bird/d) and as consequence protein and energy intake were similar in both diets (low density: 23.4 g/bird/d, 397 kcal/bird/d and high density: 24.5 g/bird/d, 403 kcal/bird/d). Aitken et al. (1969) reported that broilers from parents fed a high nutrient density diet were significantly heavier at 42 and 63 d in comparison with chicks from breeders fed low energy diets. However, the treatment difference in the broiler BW disappeared when broilers were weighed at 147 d (Aitken et al., 1969).

When hens are fed to reach a target BW, dietary energy levels can influence feed allocation and with the increase in feed allocation there is also an increase in the intake of micronutrients. Studies have shown that a higher intake of vitamins and minerals by the hen can improve chick livability (Virden et al., 2003), immunity (Haq et al., 1996) and BW gain (Attencio et al., 2005). However, these studies observed effects based on higher differences in micronutrient intakes than the ones that would occur due to differences in dietary energy level.

Increasing progeny growth with maternal diet manipulation would bring huge benefits to the poultry industry, as costs with maternal feed would be small when compared to the economic benefits of a fast growing broiler (Calini and Sirri, 2007). It is complex to compared effects of maternal diet on progeny growth as

there are a lot of confounding factors that have the potential to influence the outcome, such as hen age, strain and sex of progeny. To the best of my knowledge there is no research evaluating the effects of dietary protein and energy in modern Ross broiler breeder hens on broiler progeny, therefore studies in this topic are needed.

1.4.6. Feed conversion ratio

Feed conversion ratio is the relation between feed intake and product (weight gain or eggs). Lower FCR can be interpreted as a bird being more efficient in converting feed into weight gain. Reduced FCR yields can have huge financial benefits for the poultry industry (Pollock, 1999).

No effect of maternal dietary CP level on FCR of the offspring was observed when De Brum et al. (1996) fed 36 wk old broiler breeders from 2 different strains with varying levels of protein (12 to 18% CP).

Different levels of protein and energy were used in the rearing and laying diets of 3 strains of broiler breeders and no diet effect was observed in the FCR of broiler offspring (Proudfoot and Hulan, 1986). Similarly, Spratt and Leeson (1987) did not find any influence of maternal dietary intake of protein and energy on the FCR of the offspring. In that study, Hubbard broiler breeders were fed 150 g/bird/d and divided into 6 treatments according to their energy and protein intake (Spratt and Leeson, 1987).

Based on the above literature, there is little evidence for a maternal nutrition effect on broiler FCR.

1.4.7. Carcass yield

Carcass yield is an indication of the amount of edible, saleable meat generated by meat animals and it is usually expressed as a percentage of the live BW (Pollock, 1997). Therefore a higher yield means a higher profit for the poultry industry. Due to its economic importance, there are some studies that tried to increase broiler carcass yield by manipulation of broiler breeder diet. However, more work needs to be done to evaluate the effect of maternal diet (mainly dietary protein and energy) on progeny carcass yield because there is little consistency in the findings to date and results can vary a lot depending on the age and strain of birds. Lopez and Leeson (1994b) fed 58 to 61 wk old broiler breeders with 9, 11, 13 or 15% CP and observed that protein level in the diet had no effect on carcass weight and breast meat yield of the offspring at 49 d.

On the other hand, Rao et al. (2009) observed heavier Pectoralis major muscle of broiler (28 d old) offspring of Langshan breeder hens fed low protein (10%) when compared to Pectoralis major of broiler offspring of hens fed high protein (15%). Rao et al. (2009) hypothesized that protein restriction in the maternal diet programmed myogenesis during chick embryo development for the low protein treatment offspring.

1.5. Nutrigenomics, nutritional imprinting and epigenetics

Nutrigenomics is a term developed in the 21st century to explain a research field that aims to verify how diet impacts gene expression (Ashwell, 2010). Nutrition-induced changes in gene expression can affect not only the individual but also

their offspring performance and health. Nutritional imprinting is also studied in nutrigenomics. This represents an animal response to nutrient restriction that results in increased absorption rates and improved nutrient utilization efficiency, which decreases excretion of the restricted nutrient (Ashwell, 2010). It is an adaptation to low nutrient intakes that is applicable in mammals and birds. It is suspected that the adaptation to low nutrient intakes is caused by an interaction of the nutrient with genes and that would affect growth and gene expression in the animal through changes in regulatory elements at the cellular level (Ashwell and Angel, 2010).

Yan et al. (2005) suggested that broilers that have phosphorous and calcium restriction early in life can adapt to the nutritional change and excrete less phosphorous. However, more study is needed to determine the amount, timing, and duration of the restriction that will not negatively affect animal performance (Ashwell and Angel, 2010). Another example is dietary calcium for laying pullets. There is an increase of calcium requirements when they are closer to lay onset in order to promote deposition of calcium in the medullary bones. However, if calcium is included in the prelay diet in excess of requirements then the hens will absorb calcium less efficiently when they start to produce eggs (Nunes et al., 2006).

Maternal diets have affected gene expression of the offspring (Rao et al., 2009). The effect of a 10% and a 15% CP diet for Langshan breeder hens was evaluated and the authors observed that offspring from hens fed low protein had significantly heavier Pectoralis major muscle at 4 wk post-hatch when compared

to offspring of hens fed a high protein diet (Rao et al., 2009). According to gene expression analysis done by the authors, maternal protein restriction was associated to an up-regulated expression of insulin-like growth factor 1 (IGF-I) and type 1 insulin-like growth factor receptor (IGF-IR) mRNA in the Pectoralis major muscle of the low protein treatment offspring (Rao et al., 2009). This up-regulated expression of IGF-I will result in increased breast muscles because it is a regulator of bird metabolism and muscle development (Duclos, 2005). It is still not clear if the changes in gene expression as a result of nutritional imprinting will be epigenetic in nature. If they are the changes in gene expression will be heritable and its effect on the offspring will be permanent (Ashwell and Angel, 2010).

Some nutrients such as methionine and folic acid can increase the occurrence of the epigenetic phenomena in nutritional studies. It happens because these nutrients can become methyl donors for DNA methylation reaction (Choi and Friso, 2010). Epigenetics results in a change in gene expression and chromatin structure without changing DNA sequence (Choi and Friso, 2010). Some of the processes that can be involved in alterations of gene expression are DNA methylation and histone modifications (Choi and Friso, 2010). The addition of a methyl group to the 5 position of the cytosine pyrimidine ring characterizes the DNA methylation process (Li et al., 2011). It happens naturally during embryo development and cellular differentiation and it can also cause epigenetic changes in gene expression (Isagawa et al., 2011). DNA methylation can silence gene expression when the binding of the transcription factor to its recognition element in the gene does not

happen due to an interference of a methyl residue (McGowan and Szyf, 2010). It can also happen indirectly when methylated-DNA-binding proteins that attracted to bind in an area of the gene with a concentration of DNA methylation results in an altered chromatin configuration (McGowan and Szyf, 2010). Most of the studies to evaluate epigenetic mechanisms were done in mammals, but Li et al. (2011) found that the DNA methylation in chickens had similar patterns to those of mammals and plants. Histone modification usually happens at the N-terminal tails of the histones (15 to 38 amino acids) that can be modified by different processes such as methylation, phosphorylation and acetylation (McGowan and Szyf, 2010). These modifications on the N-terminal tails can change the accessibility of the DNA enclosed around the nucleosome core and, consequently, modify the gene expression (McGowan and Szyf, 2010).

1.6. Objectives and Hypotheses

Few studies have associated the effect of the broiler breeder nutrition with broiler offspring performance. An objective of the current thesis was to evaluate the effect of dietary energy and protein levels during rearing and energy level of laying diets on egg composition and progeny chick quality (CHAPTER 2), as well as progeny growth, feed conversion ratio and carcass yield (CHAPTER 3 and CHAPTER 4). The current study also investigated the effect of male BW on semen quality, fertility and duration of fertility of artificially inseminated hens (CHAPTER 5).

1.6.1. Hypotheses for CHAPTER 2

Hens fed high protein during rearing were expected to use more nutrients for maintenance. As a consequence, these birds were expected to have smaller eggs with less albumen weight. Because yolk size has been associated with energy intake (Peebles et al., 2000), we hypothesized that yolk size would be increased with the increase of energy level during lay. Fertility can be reduced when birds have excess fat pad due to inability to store and transport sperm cells properly (McDaniel et al., 1981b). Based on that our hypothesis was that hens with higher fat pad weight would have reduced fertility and deposition of fat would increase with the increase of dietary energy and protein. Chicks of hens fed low energy diets were expected to be heavier due to higher maternal intake of vitamins and minerals. We also hypothesized that hens fed low protein during rearing would have less breast muscle and were expected to deposit more nutrients in the eggs resulting in heavier chicks at hatch.

1.6.2. Hypotheses for CHAPTER 3

Hens fed low protein during rearing phase were expected to deposit less breast muscles, therefore fewer nutrients during laying would be partitioned toward maintenance and more would be deposited in the egg resulting in heavier offspring.

1.6.3. Hypotheses for CHAPTER 4

In CHAPTER 4 hens were older so it was expected that broiler progeny performance would not be influenced as much by maternal diet during rearing phase. It was hypothesized that the 10 wk difference that happened between the time the hens stopped receiving the rearing diet at 25 wk and the egg collection at 35 wk would be enough time for the hens to readjust its metabolism to the laying diet independently of the diet received during rearing. It was also hypothesized that the maternal diet during lay would influence broiler offspring similarly as in CHAPTER 3.

1.6.4. Hypotheses for CHAPTER 5

Roosters from extreme body weight treatments were expected to have lower fertility, lower duration of fertility and poorer semen quality than males from control BW profile.

1.7. Approach

A broiler breeder experiment was performed using 774 Ross 708 pullets. Hens were fed different dietary levels of energy and protein during rearing and different levels of energy during the laying phase. Eggs were collected from hens at 29 and 37 wk of age and egg weight and composition were evaluated (CHAPTER 2).

From the same broiler breeder hens, eggs were collected at 30 and 35 wk of age and were incubated. Eggs were open in different incubation ages, embryos were

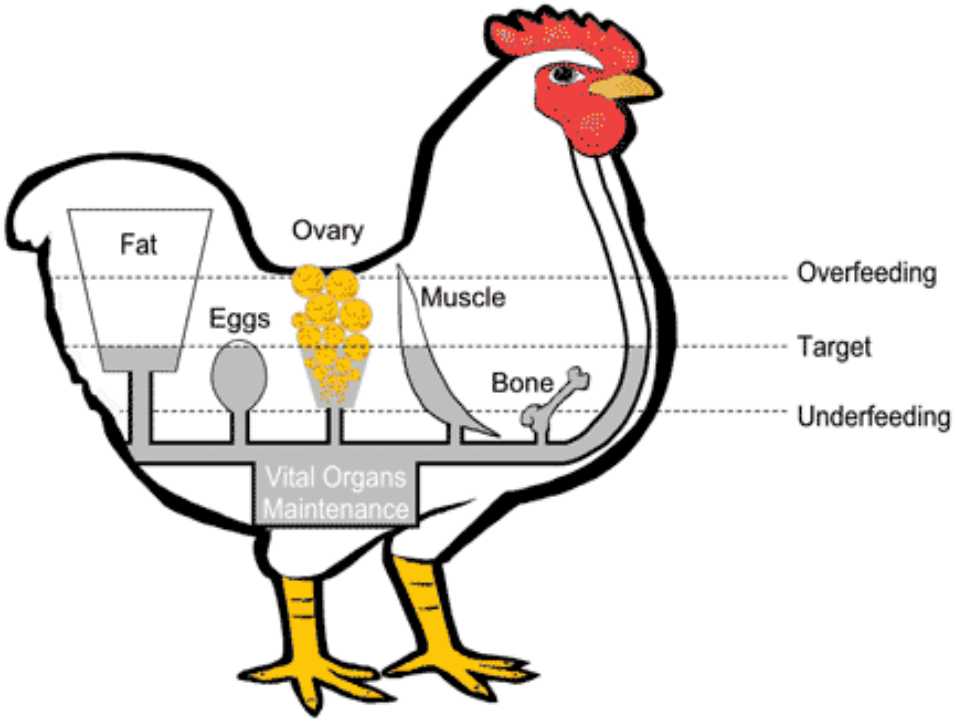
humanely sacrificed and embryo weight and length were measured (CHAPTER 2).

Eggs collected from 28 (CHAPTER 3) and 35 (CHAPTER 4) wk old broiler breeder hens were incubated. At hatch, hatch time, chick weight and chick quality were measured. Broilers were fed ad libitum and individual broiler BW were measured weekly. At 40 d, broilers were processed and carcass yield was measured.

An experiment was performed using 36 Ross 344 males (CHAPTER 5). Rooster were divided into 3 treatment groups and were fed to reach the target BW, 5% lower than target BW or 10% heavier than target BW. Semen was collected during 4 different male ages and used to inseminate hens. Fertility and duration of fertility were evaluated. Semen was also collected and evaluated for sperm concentration and mobility.

1.8. FIGURES AND TABLES

Figure 1-1. Hydrostatic nutrient partitioning model of a broiler breeder hen



Source: Schneider et al., 2008.
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Table 1-1. Summary of studies that evaluated the effect of different protein levels on broiler breeder diets on offspring performance

Strain	Age	CP level	Effect on offspring					Authors
			Chick weight	BW	Breast yield	FCR	ADG	
Indigenous[1]	46-54 wk	10, 12, 14, 17[2]	No	-	-	-	No	Kingori et al., 2010
Langshan	44-48 wk	10, 15	Yes (*)	Yes (**)	Yes (**)	-	-	Rao et al., 2009
Embrapa	36-46 wk	12, 13.5, 15, 16.5, 18	Yes (*)	No	-	No	No	De Brum et al., 1996
Arbor Acres	36-46 wk	12, 13.5, 15, 16.5, 18	No	No	-	No	No	De Brum et al., 1996
Arbor Acres	58-62 wk	9, 11, 13, 15	No	No	-	-	-	Lopez and Lesson, 1994b
Cobb	24-29 wk	15.8, 14.7, 13.9, 13.0, 12.2	-	No	-	-	-	Wilson and Harms, 1984

[1]Indigenous chickens of Kenya
[2]CP values on a dry matter basis
(*): increase in CP level increased parameter on offspring
(**): decrease in CP level increased parameter on offspring
(-): parameter was not evaluated

Table 1-2. Summary of studies that evaluated the effect of different energy and protein levels on broiler breeder diets on offspring performance

Strain	Age	Protein and energy level	Effect on offspring					Authors
			Chick weight	BW	Breast yield	FCR	ADG	
1 normal and 2 dwarfs	15-20 wk	12.9% CP and 2,902 kcal/kg or 15.8% CP and 2,699 kcal/kg	No	No	-	No	-	Proudfoot and Hulan, 1986
1 normal and 2 dwarfs	21-60 wk	15.3% CP and 2,746 kcal/kg or 17.6% and 2,746 kcal/kg or 17.8% CP and 2,651 kcal/kg	No	No	-	No	-	Proudfoot and Hulan, 1986
Hubbard	19-40 wk	12.6% or 16.6% CP and 2,166 or 2,566 or 3,000 kcal/kg	Yes (*)	Yes (*)	-	No	-	Spratt and Leeson, 1987

(*): increase in energy level increased parameter on offspring
(-): parameter was not evaluated

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CHAPTER 2: Effect of maternal dietary energy and protein on egg composition, embryo development and chick quality

2.1. INTRODUCTION

Maternal nutrition plays an important role in egg production, egg weight, embryo development and hatchability of eggs not just in terms of the nutrient content of the egg, but in gene expression and metabolism in the progeny (Wilson, 1997).

Chick weight at hatch affects subsequent broiler growth and chick weight is related to egg weight (Zuidhof, 2009). Egg weight can also be influenced by dietary fat, in particular, linoleic acid (Grobas et al., 1999), protein (Lopez and Leeson, 1994a), and certain amino acids such as lysine and methionine (Bowmaker and Gous, 1991). However, the influence of dietary energy and protein on egg weight and composition and chick weight are inconsistent and may change with hen age and strain of the birds studied. Eggs from broiler breeders fed a low dietary energy (430 kcal/hen/d) at 35 wk had significantly reduced yolk percentage and increased albumen percentage, while eggs from hens fed high dietary energy (467 kcal/hen/d) had decreased albumen percentage (Peebles et al., 2000).

It has been reported that high maternal dietary energy (450 kcal MEn) increased hatch weight of male offspring when broiler breeders were fed diets with different energy intakes (325 or 385 or 450 kcal MEn; Spratt and Leeson, 1987). Pearson and Herron (1982) observed lower hatchability in broiler breeders from 26 and 36

wk fed high protein (27 g/bird/d) and low energy (363 kcal ME/bird/d) due to an increase in embryo mortality during the second week of incubation.

The objective of this research was to evaluate the effect of different dietary levels of energy and protein in broiler breeder diets during the rearing and different dietary energy levels in laying diets on egg composition, embryo development, hatchability, hatch time, hatch weight and chick quality.

2.2. MATERIAL AND METHODS

2.2.1. Experimental Design

The animal protocol for the study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles established by the Canadian Council on Animal Care (CCAC, 1993).

A total of 774 Ross 708 (Aviagen Inc., Huntsville, Alabama) day-old pullets were randomly allocated to 20 floor pens (39 pullets/pen). Pullets received water and feed ad libitum for 14 d. Feed restriction started at 15 d of age, and birds received a standard diet until 21 d (Table 2-1). After 21 d, pullets were fed a diet containing high ME (2,736 kcal/kg; HE_{REAR}), or low ME (2,528 kcal/kg; LE_{REAR}) combined with either high protein (15.3% CP; HP_{REAR}) or low protein (13.7% CP; LP_{REAR}; Table 2-2).

At 23 wk of age, 256 broiler breeders were randomly selected and individually caged for the laying phase. At 25 wk, experimental diets were changed and birds were fed either a high ME (2,900 kcal/kg; HE_{LAY}), or low ME diet (2,800 kcal/kg;

LE_{LAY}) containing 15% CP (Table 2-3), making a 2 x 2 x 2 factorial arrangement of treatments.

2.2.2. Stocks and Management

Group BW of pullets were recorded twice per wk while individual BW were recorded once every two wk. After broiler breeder hens were caged they were weighed individually twice per wk and feed allocations were calculated bi-weekly based on the recommendations for target BW (Aviagen, 2007a).

Prior to photostimulation, day length was 24L:0D for the first 3 d. After that, day length was 8L:16D until 23 wk when the photostimulation started. At 23 wk, day length was increased to 12L:12D in one step and then increased by 1 h/wk until a photoperiod of 15L:9D was achieved. Hens were artificially inseminated at 27, 29, 34 and 35 wk of age with 0.5 mL of pooled fresh undiluted semen.

2.2.3. Data Collection

2.2.3.1. ***Experiment 1: Egg Composition.*** Eggs were collected from hens at 29 (n=411) and 37 wk of age (n=519). They were weighed, identified by hen and stored for 1 d at 20ºC. Albumen height was measured with a QCH albumen height gauge (Technical Services and Supplies Ltd, Dunnington, York, United Kingdom) and yolks were weighed with a Mettler PJ6 scale (Mettler Toledo, Mississauga, Ontario, Canada). All eggshells were washed in warm water to remove remaining albumen and shell membranes and then dried at room temperature, after which they were weighed and the shell thickness measured using a digital micrometer

(H-2782 Mahr, ULINE®, Brampton, Ontario, Canada) at 3 different equidistant locations in the eggshell equator. Albumen weight was calculated by subtracting the yolk plus eggshell weight from total egg weight.

2.2.3.2. ***Experiment 2: Embryo Development.*** Eggs were collected at 30 (n=319) and 35 wk of age (n=328) from hens that received the following diet combinations during rearing and laying phases: HE_{REAR} x LP_{REAR} x LE_{LAY}; HE_{REAR} x LP_{REAR} x HE_{LAY}; LE_{REAR} x HP_{REAR} x HE_{LAY}; or LE_{REAR} x HP_{REAR} x LE_{LAY} (Figure 2-1). The rearing treatments were selected because they had the greatest difference in energy to protein ratio (E:P), and were used in attempt to observe differences in embryo development related to maternal E:P differences. Weight, dam and date laid were recorded for each egg. Eggs were incubated at 99.4 ± 0.4ºF, 84.2 ± 2% RH in a Jamesway large J incubator (PT100 Incubator, Jamesway Incubator Company Inc., Cambridge, Ontario, Canada), which automatically turned the eggs every h in the incubator. Based on the number of available eggs per treatment, a minimum of 10 eggs per treatment were broken open at 5, 7, 10, 13, 15, 18 and 20 d of incubation. Embryos were euthanized by cervical dislocation, weighed with a Scaltec® Analytical balance (SBC31, Scaltec Instruments GmbH, Goettingen, Lower Saxony, Germany). Embryo length was measured of all 196 embryos older than 15 d of incubation.

2.2.3.3. ***Experiment 3: Chick Quality.*** Eggs were collected from hens at 28 (n=1,976) and 35 wk of age (n=1,250). Weight, dam, and date laid were recorded

for each egg. Eggs were incubated at the same conditions mentioned in experiment 2. At 18 d of incubation, eggs were transferred to individual pedigree hatcher baskets and placed in a Jamesway PT100 Hatcher (Jamesway Incubator Company Inc., Cambridge, Ontario, Canada). A pedigree hatcher basket allowed each egg to be isolated from the others, so that each chick could be linked back to its mother. During the hatching process starting at 493 h of incubation (20.5 d), trays in the hatcher were examined every 4 h and hatch time was recorded to the nearest 4 h. Chicks were returned to the hatcher until all chicks were pulled at 521 h of incubation (21.7 d). At this time, chicks were weighed, sexed, and individually identified with bar-coded neck tags. Chick quality was assessed using a simplified Pasgar score (Boerjan, 2002). The hock, beak and navels of each chick along with their activity were evaluated and scores assigned from 0 to 1 for each trait, where 0 was good and 1 represented a poor chick quality score assessment (Table 2-4). Hatchability was calculated as a percentage of the total eggs incubated.

From the total of chicks hatched, 526 chicks hatched from 28 wk old hens and 314 hatched from the same hens when they were 35 wk old were euthanized by cervical dislocation. Yolk sacs were removed and weighed. Effect of maternal diet on yolk sac weight and yolk sac free BW were evaluated.

2.2.4. Statistical Analysis

Egg weight and egg composition data were analyzed as a 4-way ANOVA with dietary energy during rearing, dietary protein during rearing, and dietary energy

during lay, and hen age as main effects. Hen was considered a random term. Hatch weight, yolk sac and yolk free BW data were analyzed as a 5-way ANOVA with dietary energy during rearing, dietary protein during rearing, and dietary energy during lay, hen age and chick sex as main effects using the MIXED procedure of SAS (Version 9.2. SAS Institute Inc., Cary, NC, 2009). The tray in which the eggs were allocated during hatching and the hen were considered as random terms in the model for the analysis of hatch weight, yolk sac, and yolk free BW.

Embryo weight and length data were analyzed as a 3-way ANOVA with maternal diet during rearing (HE_{REAR} x LP_{REAR} and LE_{REAR} x HP_{REAR}), maternal dietary energy during lay and hen age as main effects using the MIXED procedure of SAS. The hen was considered a random term.

Hatchability, hatch time and day-old chick quality scores were analyzed with a chi-square test of frequencies using the CATMOD procedure of SAS. Pairwise comparisons were used to determine significant differences between means. Differences of means were reported within hen age, in order to account for maternal age effects focusing on maternal nutritional effects. Unless reported otherwise, differences between means were considered significant at $P < 0.05$.

2.3. RESULTS AND DISCUSSION

2.3.1. Experiment 1

Effects of hen diet on egg weight and composition are shown on table 2-5. Relative yolk weight (%) was influenced by a 3-way interaction between hen age

and maternal dietary energy during rearing and during lay (Table 2-6). Eggs from 29 wk old hens fed LE_{REAR} x LE_{LAY} had higher relative yolk weight (28.7%) than eggs from 29 wk old hens fed LE_{REAR} x HE_{LAY} (28.0%). Eggs of 29 wk old hens fed HE_{REAR} x HE_{LAY} and HE_{REAR} x LE_{LAY} had relative yolk weight similar to all the other dietary treatments. Eggs from 37 wk old hens had higher relative yolk weight when hens received HE_{REAR} x LE_{LAY} (30.5%) when compared to eggs of hens that were fed HE_{REAR} x HE_{LAY} (29.8%) and LE_{REAR} x HE_{LAY} (29.9%). Absolute yolk weight of 37 wk old hens was similarly affected by diet. Relative albumen weight from 29 wk old hens was higher for eggs of hens fed LE_{REAR} x HE_{LAY} (63.3%) when compared to eggs from hens fed LE_{REAR} x LE_{LAY} (62.5%). Albumen weight was not influenced by diet in eggs of 37 wk old hens. It has been previously observed that albumen weight increases with an increase in protein intake (Joseph et al., 2000), however the differences in albumen weight in the current research could not be associated to protein intake.

It was observed that hens fed LE_{REAR} x HE_{LAY} had a decrease in feed intake per unit of metabolic BW when diets changed from rearing to lay. The decrease in feed intake may have caused the decrease in their relative yolk weight at 29 wk. However, feed intake did not affect relative yolk weight when hens from two different lines were fed 128 or 170 g at 29 wk (Li et al., 2011). Hens fed HE_{REAR} x LE_{LAY} had a decrease in energy to protein ratio when diets changed from rearing to lay, that resulted in a great increase in daily feed (5.2 g/kg $BW^{0.75}$), protein intake (1.1 g) and energy intake (17.8 kcal) per unit of metabolic BW. Increase in energy intake has previously been related to increase in relative yolk weight

(Peebles et al., 2000), therefore the increase in energy intake (kcal/$BW^{0.75}$) when diets changes from HE_{REAR} to LE_{LAY} may explain the increased relative yolk weight in the eggs of 37 wk old hens fed this dietary treatment. Changes in egg composition may indicate changes in the amount of nutrients that are available to the embryo. However, in the current experiment, we observed less than a 1% difference in egg components which may not be important for chick performance because we did not observe any relation between egg composition and offspring performance from same hens in different experiments (Chapter 3 and Chapter 4).

Young hens (29 wk old) fed LE_{REAR} laid eggs with thinner eggshells and lower relative shell weight than eggs of young hens fed HE_{REAR} (Table 2-5). That resulted in an increased number of eggs with defective shells and a decrease in the number of settable eggs from hens fed LE_{REAR} (Mba et al., unpublished). However that effect was not observed in eggs from 37 wk old hens, probably because the effect of rearing diets decreased as hens grew older. Hens fed LE_{REAR} had higher feed intake (67.93 g/bird/d; 0.61 g calcium/bird/d) and, as consequence, higher calcium intake than hens fed HE_{REAR} (62.92 g/bird/d; 0.57 g calcium/bird/d). It has been previously reported that broiler breeder pullets fed high levels of calcium before sexual maturity have problems with shell quality (Petruk and Korver, 2004) because excess calcium would be excreted instead of stored in the medullary bone for later use in eggshell formation. In the current study that may be a possibility of why the broiler breeder pullets fed LE_{REAR} had thinner eggshells in early lay, however the difference in calcium intake between our treatments is much lower than the difference mentioned by Petruk and Korver

(2004). Therefore, it is still to be confirmed if our small change in calcium intake was related to the decrease in shell quality.

2.3.2. Experiment 2

2.3.2.1. Embryo Weight. Embryos from 35 wk old hens were heavier throughout incubation than embryos from 30 wk old hens (Table 2-7). It has been previously observed that chicks from older hens are heavier than chicks from younger hens (Gualhanone et al., 2012), our results show that difference in progeny weight is influenced by maternal age since the embryonic stages and that is probably due to differences in egg size (Vieira and Moran., 1998). Maternal diet treatments did not influence embryo weight at any stage of development.

2.3.2.2. Embryo Length. Embryos from older hens were shorter by 0.5 cm and 1.6 cm at 18 and 20 d, respectively than embryos from younger hens (Table 2-7). This result was surprising because Nangsuay et al. (2011) did not find any effect of breeder age on embryo length at 18 d. Also, it was previously observed that chick length is correlated with chick weight (Wolanski et al., 2004), therefore as embryos from older hens are heavier it was expected that they would be longer as well. Similar findings of shorter embryos in older hens were not found in the literature, therefore the result observed still needs to be clarified.

Embryos from 30 wk old hens fed HE_{REAR} x LP_{REAR} were longer at 18 d than embryos from hens fed LE_{REAR} x HP_{REAR} (Table 2-8). Independent of maternal age, embryos from hens fed HE_{REAR} x LP_{REAR} were longer at 20 d than embryos

from hens fed LE_{REAR} x HP_{REAR} (Table 2-7). The maternal diet HE_{REAR} x LP_{REAR} had a higher E:P ratio (20 kcal/g) than diet LE_{REAR} x HP_{REAR} (16.5 kcal/g) which may have positively affected embryo development. Older hens (30 wk old) fed HE_{LAY} had longer embryos (at 20 d of incubation) than 30 wk old hens fed LE_{LAY} (Table 2-8). That may be because HE_{LAY} had higher E:P ratio (19.4 kcal/g) than LE_{LAY} diet (18.5 kcal/g). It is not clear why embryo length was not affected in the offspring of 35 wk old hens. Longer 20 d old embryos were observed when hens were fed HE_{REAR} x LP_{REAR} x HE_{LAY} which was the diet interaction with the lowest protein intake per unit of metabolic BW (Table 2-8).

Embryo length can be considered a measurement of embryo development (Nangsuay et al., 2011). It is also associated with hatchling length, which is positively correlated with broiler weight at processing (Molenaar et al., 2008). Based on the results of the current study it appears that maternal diet has more influence in embryo length of younger hens, plus the E:P ratio of hen intake had more influence on embryo length than individual energy or protein levels.

2.3.3. Experiment 3

2.3.3.1. Hatchability. Maternal rearing diets did not influence hatchability (Table 2-9), however laying diets did as eggs from hens fed the HE_{LAY} had higher hatchability (81.9%) then eggs from hens fed the LE_{LAY} diet (78.1%; Table 2-9). It was observed that hens fed HE_{LAY} diets had higher E:P ratio than hens fed LE_{LAY} diet (19.4 vs. 18.5 kcal/g, respectively), lower protein intake (8.1 vs. 8.6 g/kg $BW^{0.75}$, respectively) and feed intake (53.8 vs. 56.8 g/kg $BW^{0.75}$, respectively;

Appendix 1). Patel and McGinnis (1977) fed diets with 16 or 32% CP to 46 wk old Single Comb White Leghorns and observed that the high protein treatment decreased hatchability. According to the authors, high protein diets increase hen requirement for vitamin B_{12}, as consequence hen diet should have an increase in the vitamin content to maintain a good hatchability. However, the difference in protein intake was much higher in Patel and McGinnis study than the one observed in the diets of the current study, plus our diets had 0.02 mg of vitamin B_{12} which is the amount recommended by the breeder management guide (Aviagen, 2007b). More recent studies (Lopez and Leeson, 1994b; Barreto et al., 1999; Mohiti-Asli et al., 2012) have not shown any influence of protein level on hatchability. Therefore the effect of protein intake on hatchability is not totally clarified and it needs further investigation due to confounding effects such as amino acid content and amount of vitamins and minerals in the diet (Wilson, 1997).

2.3.3.2. Hatch Time. Hatch time varied from 493 to 521 h (496.7 ± 0.13) for chicks from 28 wk old hens and from 496 to 521 h (499.4 ± 0.18) for chicks from 35 wk old hens. However, eggs from hens of different ages were not incubated at the same time and for practical reasons, hatch time for eggs of 35 wk old hens only began to be measured at 496 hours of incubation. Hatch time was not affected by maternal diets (data not shown). It was previously observed that hens fed 15% CP had a 4h delay in chick hatch when compared to hatch time of chicks from hens fed 9% CP (Lopez and Leeson, 1994c). An increase in amino acid

intake by hens can increase albumen height (Balnave et al., 2000). Therefore an increase in protein intake may increase albumen thickness, which decreases gas exchange between the embryo and the environment (Vick et al., 1993), consequently delaying embryo development and hatch time. However, in the current study hen diet did not influence albumen height (Table 2-5).

2.3.3.3. Chick yield. Maternal diet did not influence chick weight at hatch, residual yolk sac weight or yolk free BW (Table 2-10). Chicks from 28 wk old hens fed LE_{REAR} had a higher chick yield (70.2%) than chicks from hens fed HE_{REAR} (69.8%; Table 2-11). This could be due to the higher feed intake and protein intake by hens fed the LE_{REAR} diets than HE_{REAR} diets. In agreement with our findings, high protein intake (16% CP) increased chick yield of offspring of 30 and 52 wk old Hubbard broiler breeder when hens were fed 10, 12, 14 or 16% CP (Lopez and Leeson, 1995). However, hens from Lopez and Leeson were fed different protein levels during lay, while we observed an effect of rearing diets on chick yield. In the current research, maternal energy level during rearing phase did not influence chick yield of 35 wk old hens, probably because of the 10 wk difference between the time the hens were last fed the rearing diet and the time the eggs were collected.

Offspring of hens fed $HE_{REAR\ X}\ LP_{REAR\ X}\ LE_{LAY}$ had higher chick yield (69.6%) when compared to offspring of hens fed $HE_{REAR\ X}\ LP_{REAR\ X}\ HE_{LAY}$ and $HE_{REAR\ X}\ HP_{REAR\ X}\ LE_{LAY}$ (68.9% and 68.7%, respectively), but was not different than the chick yield of progeny of hens fed all the other dietary treatments (Table 2-11). It

is still not clear why this occurred, possibly hens fed $HE_{REAR\ x}\ LP_{REAR\ x}\ LE_{LAY}$ had the highest increase in protein intake when diets changed from rearing to lay (7.2 to 8.6 g/$BW^{0.75}$). Chick yield is chick weight expressed as percentage of egg weight. A higher chick yield means that the chick obtained more from the egg. However, despite the differences in chick yield, maternal diet did not affect egg weight or chick weight and there was less than 1% difference between higher and lower chick yield, therefore further research is needed to confirm these results.

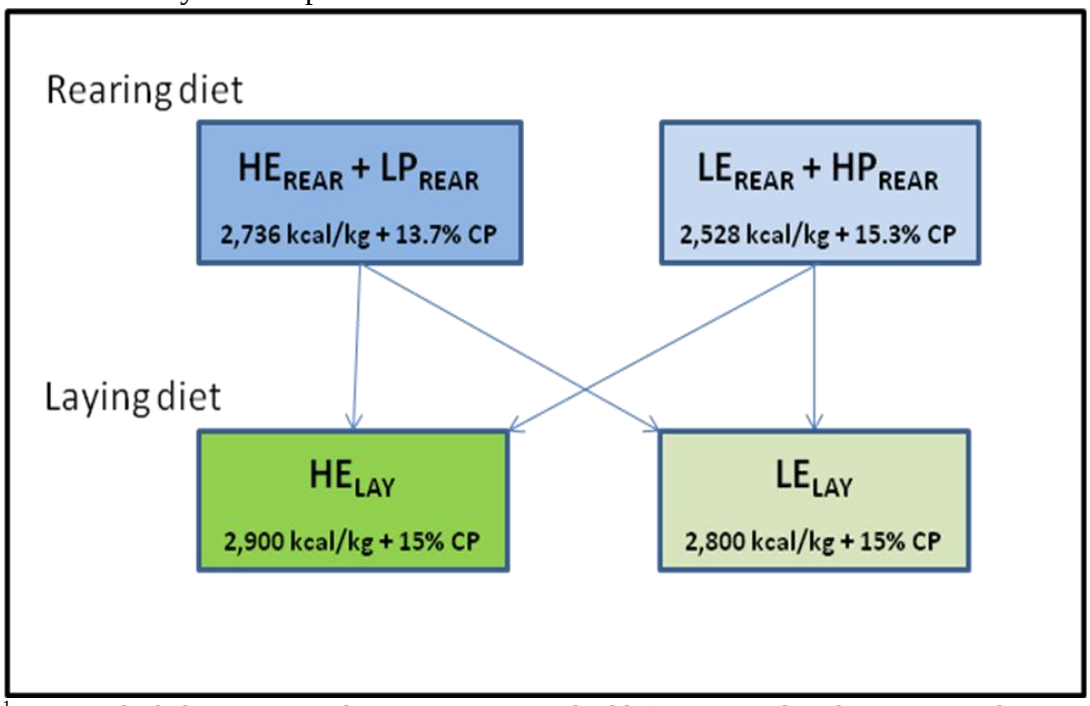
2.3.3.4. Chick Quality. Chick quality scores for activity, hock and beak were not influenced by maternal diet during rearing or maternal dietary energy during lay (Table 2-12). Navel score was influenced by the interaction of dietary protein during rearing and energy during lay (P=0.02; Table 2-13). Hens that were fed LP_{REAR} x HE_{LAY} had lower percentage of chicks with good navel score (41.42%) when compared to navel score of chick from hens fed HP_{REAR} x HE_{LAY} (47.67%) and LP_{REAR} x LE_{LAY} (47.76%). Hens fed LP_{REAR} x HE_{LAY} had a decrease in feed intake per unit of metabolic BW when diets changed from rearing to lay, that may be the cause of the higher number of bad quality navel chicks hatched from these hens. There is evidence that chicks with even minor navel conditions grow less efficiently because unhealed navels can cause subclinical infections and the bird is going to use energy to fight the infection, reducing the amount of energy used for growth (Fasenko and O`Dea, 2008).

2.3.4. Conclusions

The effects of maternal diet on egg composition were age-dependent with eggs from younger hens being more influenced by maternal diet than eggs from older hens, consistent with the hypothesis that the effect of rearing diets would decrease as hens grew older. Egg weight, chick weight, hatch time and yolk sac weight were not affected by maternal diet. Decrease in maternal feed intake per unit of metabolic BW from rearing to lay diets increased the number of chicks with poor navel quality. Maternal nutrition is very important because it affects hatchability, which is the most important economic performance indicator for the hatching egg industry. Hatchability was decreased when hens were fed LE_{LAY}, a diet that resulted in higher protein intake during lay. Therefore, a high protein intake during lay should be avoided in order to achieve better hatchability.

2.4. FIGURES AND TABLES:

Figure 2-1. Broiler breeder diet treatments[1] during rearing and laying phases used for embryo development evaluation



[1]HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

Table 2-1. Composition of pullet starter diet (0 to 3 weeks)

Ingredient (%)	Starter diet
Oats	15.0
Corn	15.0
Wheat	39.41
Soybean meal (47.8%)	17.59
Canola Meal	5.0
Dicalcium phosphate	1.98
Calcium carbonate	1.58
Canola Oil	2.38
Broiler premix[1]	0.5
Choline chloride premix	0.5
Salt Fine	0.45
DL-Methionine	0.21
L-Lysine.HCl 78%	0.35
Avizyme 1302	0.05
Nutrients	
AME (kcal/kg)	2900
CP, calculated (%)	19.8
Calcium(%)	1.1
Available phosphorous (%)	0.5
Lysine (%)	1.18
Methionine (%)	0.52

[1] Premix provided per kg of diet: vitamin A (retinyl acetate): 10,000 IU; cholecalciferol: 2,500 IU; vitamin E (dl-α-tocopheryl acetate): 35 IU; vitamin K: 2.0 mg; pantothenic acid: 14 mg; riboflavin: 5.0 mg; folacin: 0.8 mg; niacin: 65 mg; thiamine: 2.0 mg; pyridoxine: 4.0 mg; vitamin B12: 0.015 mg; biotin: 0.18 mg; iodine: 0.5 mg; Mn: 70 mg; Cu: 8.5 mg; Zn: 80 mg; Se: 0.1 mg; Fe: 100 mg.

Table 2-2. Composition of pullet grower diets during rearing[1]

	Pullet Grower Diet (3 to 24 weeks)			
Ingredient (%)	LE_{REAR} x LP_{REAR}	LE_{REAR} x HP_{REAR}	HE_{REAR} x LP_{REAR}	HE_{REAR} x HP_{REAR}
Corn, Yellow	40.502	37.193	53.737	50.762
Wheat	20.0	20.0	20.0	20.0
SBM 47.8%, Dehulled	4.947	10.244	8.165	13.771
Wheat bran	25.0	22.699	8.010	5.406
Canola Meal	4.631	5.0	5.0	5.0
DiCalcium Phosphate	0.927	0.951	1.366	1.401
Limestone Fine	1.609	1.569	1.391	1.352
Canola Oil	1.000	1.0	1.0	1.0
Generic vitamins[2]	0.375	0.375	0.375	0.375
Generic minerals[2]	0.375	0.375	0.375	0.375
Salt fine	0.360	0.361	0.373	0.375
DL Methionine	0.068	0.104	0.064	0.101
Lysine. HCl 78	0.139	0.081	0.101	0.042
L-Threonine	0.028	0.006	0.003	0
Avizyme 1302	0.040	0.040	0.040	0.040
Nutrients				
Calculated AME (kcal/kg)	2,650	2,650	2,950	2,950
Analyzed AME (kcal/kg)	2,508	2,547	2,727	2,745
Calculated CP (%)	14	16	14	16
Analyzed CP (%)	13.8	15.5	13.5	15.0
Calcium (%)	0.90	0.90	0.90	0.90
Available P (%)	0.42	0.42	0.42	0.42
Lysine (%)	0.69	0.79	0.69	0.79
Methionine (%)	0.3022	0.3662	0.3082	0.3721

[1]LE_{REAR} = low dietary energy during rearing; HE_{REAR} = high dietary energy during rearing; LP_{REAR} = low dietary protein during rearing; HP_{REAR} = high dietary protein during rearing.

[2]Premix provided per kg of diet: vitamin A (retinyl acetate): 10,000 IU; cholecalciferol: 2,500 IU; vitamin E (DL-a-tocopheryl acetate): 35 IU; vitamin K: 2.0 mg; pantothenic acid: 14 mg; riboflavin: 5.0 mg; folacin: 0.8 mg; niacin: 65 mg; thiamine: 2.0 mg; pyridoxine: 4.0 mg; vitamin B12: 0.015 mg; biotin: 0.18 mg; iodine: 0.5 mg; Mn: 70 mg; Cu: 8.5 mg; Zn: 80 mg; Se: 0.1 mg; Fe: 100 mg.

Table 2-3. Composition of breeder diets during lay[1]

	Diet	
Ingredient (%)	LE_{LAY}	HE_{LAY}
Corn, Yellow	53.811	53.092
Wheat	15.0	15.0
SBM 47.8%, Dehulled	14.892	15.585
Wheat bran	1.064	0
Canola Meal	3.888	3.487
DiCalcium Phosphate	1.418	1.454
Limestone Fine	7.779	7.766
Canola Oil	0.5	1.971
Generic vitamins[2]	0.5	0.5
Generic minerals[2]	0.5	0.5
Salt fine	0.409	0.411
DL Methionine	0.167	0.169
Lysine. HCl 78	0.020	0.014
Avizyme 1302	0.050	0.050
Nutrients		
Calculated AME (kcal/kg)	2,800	2,900
Analyzed CP (%)	15.1	15
Calcium (%)	3.30	3.30
Available P (%)	0.39	0.39
Lysine (%)	0.7431	0.7417
Methionine (%)	0.4227	0.4230

[1]LE_{LAY} = low dietary energy during lay; HE_{LAY} = high dietary energy during lay.

[2]Premix provided per kg of diet: vitamin A (retinyl acetate): 12,000 IU; cholecalciferol: 3,000 IU; vitamin E (dl-α-tocopheryl acetate): 40 IU; vitamin K: 2.0 mg; pantothenic acid: 14 mg; riboflavin: 6.5 mg; folacin: 1.0 mg; niacin: 40 mg; thiamine: 3.3 mg; pyridoxine: 6.0 mg; vitamin B12: 0.02 mg; biotin: 0.2 mg; iodine: 0.5 mg; Mn: 75 mg; Cu: 15 mg; Zn: 80 mg; Se: 0.1 mg; Fe: 100 mg.

Table 2-4. Chick quality score assessment

Parameter	Score	Chick characteristics
Activity[1]	0	Quickly gets back on its feet (approximately 2 s or less)
	1	Took longer to stand up or remained in its back (> 2 s)
Hock	0	No redness in either leg
	1	Redness in one leg or both
Beak	0	No deformities or redness
	1	Redness present in punctual or large area
Navel	0	Clean and sealed navel
	1	Presence of membrane going out of the navel area or scab of blood formed over the navel

[1]Activity was assessed for each chick. Each chick was flipped on its back and the chick was timed based on how quickly it got back on its feet.

Table 2-5. Significance of effects of maternal age and diet during rearing and lay[1] on egg weight and composition

Sources of variation	Egg weight (g)	Yolk (g)	Albumen (g)	Shell (g)	Yolk (%)	Albumen (%)	Shell (%)	Shell thickness[2]	Albumen height[2]
	Probability								
Hen age (A)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
ME_{REAR} (B)	0.94	0.83	0.92	0.45	0.83	0.56	0.37	0.25	0.65
CP_{REAR} (C)	0.15	0.94	0.08	0.62	0.13	0.08	0.72	0.37	0.56
ME_{LAY} (D)	0.43	0.53	0.29	0.27	0.08	0.19	0.62	0.47	0.06
A x B	0.25	0.30	0.43	0.009	0.13	0.68	0.0003	0.009	0.41
A x C	0.29	0.52	0.26	0.70	0.85	0.49	0.54	0.11	0.33
A x D	0.35	0.07	0.55	0.10	0.27	0.78	0.002	0.25	0.87
B x C	0.77	0.49	0.44	0.80	0.18	0.09	0.58	0.20	0.91
B x D	0.41	0.56	0.44	0.59	0.66	0.64	0.98	0.92	0.04
C x D	0.23	0.08	0.69	0.02	0.48	0.13	0.10	0.20	0.06
A x B x C	0.14	0.75	0.14	0.83	0.27	0.12	0.27	0.84	0.28
A x B x D	0.48	0.0007	0.22	0.30	0.0007	0.0004	0.44	0.34	0.96
A x C x D	0.56	0.17	0.69	0.61	0.32	0.11	0.84	0.31	0.74
B x C x D	0.20	0.13	0.50	0.04	0.63	0.33	0.09	0.42	0.41
A x B x C x D	0.54	0.98	0.31	0.50	0.78	0.53	0.20	0.46	0.40

[1] ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay.
[2] Data measured in mm.

Table 2-6. Maternal age, dietary energy and protein during rearing and dietary energy during lay[1] on egg weight and composition

Age (wk)	CP_{REAR}	ME_{REAR}	ME_{LAY}	Egg weight (g)	Yolk (g)	Albumen (g)	Shell (g)	Yolk (%)	Albumen (%)	Shell (%)	Shell thickness (mm)	Albumen height (mm)
29				56.6[b]	16.0[b]	35.6[b]	5.0[b]	28.3[b]	62.8[a]	8.9[a]	0.285[b]	8.9[a]
37				62.1[a]	18.6[a]	38.1[a]	5.4[a]	30.1[a]	61.2[b]	8.7[b]	0.298[a]	8.6[b]
	HP_{REAR}			59.6	17.3	37.1	5.2	29.0	62.2	8.8	0.292	8.8
	LP_{REAR}			59.1	17.3	36.5	5.2	29.3	61.9	8.8	0.290	8.8
		HE_{REAR}		59.4	17.3	36.8	5.2	29.2	62.0	8.8	0.292	8.8
		LE_{REAR}		59.3	17.3	36.8	5.2	29.1	62.1	8.8	0.289	8.8
			HE_{LAY}	59.5	17.3	37.0	5.2	29.0	62.2	8.8	0.292	8.9
			LE_{LAY}	59.2	17.4	36.6	5.2	29.3	61.9	8.8	0.290	8.7
SEM				0.3	0.09	0.2	0.04	0.2	0.2	0.06	0.3	0.07
29		HE_{REAR}		56.5	15.9	35.5	5.1	28.2	62.7	9.0[a]	0.288[a]	8.9
		LE_{REAR}		56.6	16.0	35.6	5.0	28.3	62.9	8.8[b]	0.281[b]	9.0
37		HE_{REAR}		62.2	18.7	38.1	5.4	30.1	61.2	8.6	0.297	8.6
		LE_{REAR}		62.1	18.6	38.1	5.4	30.0	61.3	8.7	0.297	8.6
SEM				0.3	0.1	0.3	0.05	0.2	0.2	0.06	0.3	0.09
29		HE_{REAR}	HE_{LAY}	56.6	16.0	35.5	5.1	28.3[ab]	62.7[ab]	9.0	0.289	8.9
			LE_{LAY}	56.4	15.8	35.5	5.1	28.2[ab]	62.8[ab]	9.0	0.288	8.9
		LE_{REAR}	HE_{LAY}	57.0	16.0	36.0	5.0	28.0[b]	63.3[a]	8.7	0.281	9.2
			LE_{LAY}	56.3	16.1	35.2	5.0	28.7[a]	62.5[b]	8.8	0.282	8.8
37		HE_{REAR}	HE_{LAY}	62.1	18.5[b]	38.2	5.4	29.8[b]	61.5	8.7	0.298	8.6
			LE_{LAY}	62.4	19.0[a]	38.0	5.4	30.5[a]	60.9	8.6	0.286	8.7
		LE_{REAR}	HE_{LAY}	62.4	18.6[ab]	38.2	5.6	29.9[b]	61.3	8.8	0.300	8.8
			LE_{LAY}	61.7	18.5[b]	37.9	5.3	30.0[ab]	61.3	8.7	0.295	8.4
SEM				0.4	0.2	0.4	0.06	0.2	0.2	0.09	0.3	0.1

[a, b] Means within the same column, hen age and effect with no common superscript differ significantly ($P < 0.05$). [1]CP_{REAR} = crude protein during rearing; ME_{REAR} = metabolizable energy during rearing; ME_{LAY} = metabolizable energy during lay; HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

Table 2-7. Maternal age, rearing diet and dietary energy during lay[1] on broiler embryo weight and length on different embryonic ages

Sources of variation	Embryo weight (g)							Length (cm)	
	5d	7d	10d	13d	15d	18d	20d	18d	20d
Hen age (wk)									
30	0.1[b]	0.6[b]	2.5[b]	8.1[b]	14.9[b]	25.5[b]	39.5[b]	16.4[a]	18.2[a]
35	0.2[a]	0.8[a]	3.0[a]	8.8[a]	15.5[a]	27.6[a]	41.5[a]	15.9[b]	16.6[b]
SEM	0.06	0.02	0.06	0.1	0.2	0.3	0.7	0.1	0.08
Rearing diet									
HE_{REAR} x LP_{REAR}	0.1	0.6	2.7	8.5	15.3	26.3	40.4	16.2	17.6[a]
LE_{REAR} x HP_{REAR}	0.1	0.6	2.8	8.4	15.1	26.5	40.6	16.1	17.3[b]
SEM	0.06	0.02	0.06	0.1	0.2	0.3	0.7	0.1	0.07
ME_{LAY}									
HE_{LAY}	0.1	0.7	2.7	8.5	15.2	26.4	40.7	16.1	17.5
HE_{LAY}	0.1	0.7	2.7	8.4	15.2	26.6	40.2	16.2	17.3
SEM	0.06	0.02	0.06	0.1	0.2	0.3	0.7	0.1	0.07
	----------Probability----------								
Hen age (A)	<0.0001	<0.0001	<0.0001	0.0003	0.04	<0.0001	0.009	0.001	<0.0001
Rearing diet (B)	0.31	0.07	0.14	0.91	0.42	0.94	0.79	0.49	0.003
ME_{LAY} (C)	0.35	0.45	0.73	0.93	0.76	0.42	0.58	0.32	0.21
A x B	0.12	0.60	0.23	0.66	0.36	0.92	0.79	0.01	0.55
A x C	0.21	0.53	0.25	0.51	0.58	0.78	0.63	0.29	0.003
B x C	0.45	0.21	0.42	0.61	0.05	0.37	0.92	0.37	0.003
A x B x C	0.71	0.69	0.44	0.66	0.48	0.87	0.83	0.95	0.61

[a, b] Means within the same column and effect with no common superscript differ significantly ($P < 0.05$).

[1]HE_{REAR} x LP_{REAR} = high dietary energy (2,736 kcal/kg) and low dietary protein (13.7% CP) during rearing; LE_{REAR} x HP_{REAR} = low dietary energy (2,528 kcal/kg) and high dietary protein (15.3% CP) during rearing; ME_{LAY} = metabolizable energy during lay; HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

Table 2-8. Maternal age and diet during rearing and dietary energy during lay[1] on embryo length at 18 and 20 d

Hen age (wk)	Rearing diet	ME_{LAY}	18 d old embryo Length (cm)	20 d old embryo Length (cm)
	HE_{REAR} x LP_{REAR}	HE_{LAY}	16.2	17.8[a]
	HE_{REAR} x LP_{REAR}	LE_{LAY}	16.2	17.3[b]
	LE_{REAR} x HP_{REAR}	HE_{LAY}	16.0	17.2[b]
	LE_{REAR} x HP_{REAR}	LE_{LAY}	16.2	17.3[b]
SEM			0.2	0.1
30	HE_{REAR} x LP_{REAR}		16.6[a]	18.4
	LE_{REAR} x HP_{REAR}		16.2[b]	18.1
35	HE_{REAR} x LP_{REAR}		15.8	16.8
	LE_{REAR} x HP_{REAR}		16.0	16.4
SEM			0.2	0.1
30		HE_{LAY}	16.4	18.4[a]
		LE_{LAY}	16.4	18.0[b]
35		HE_{LAY}	15.8	16.5
		LE_{LAY}	16.1	16.7
SEM			0.2	0.1

[a, b] Means within the same column, hen age and effect with no common superscript differ significantly ($P < 0.05$).

[1] HE_{REAR} x LP_{REAR} = high dietary energy (2,736 kcal/kg) and low dietary protein (13.7% CP) during rearing; LE_{REAR} x HP_{REAR} = low dietary energy (2,528 kcal/kg) and high dietary protein (15.3% CP) during rearing; ME_{LAY} = metabolizable energy during lay; HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

Table 2-9. Maternal age and diet during rearing and lay[1] on hatchability

Hen age	ME_{REAR}	CP_{REAR}	ME_{LAY}	E:P[2] (kcal/g)	Hatchability (%)
28					83.3[a]
35					74.7[b]
	HE_{REAR}			19	80.4
	LE_{REAR}			17.5	79.5
		HP_{REAR}		17.2	79.8
		LP_{REAR}		19.2	80.1
			HE_{LAY}	19.4	81.9[a]
			LE_{LAY}	18.5	78.1[b]
SEM					0.06
Sources of variation				----------Probability----------	
Hen age (A)				<0.0001	
ME_{REAR} (B)				0.52	
CP_{REAR} (C)				0.83	
ME_{LAY} (D)				0.006	
A x B				0.24	
A x C				0.33	
A x D				0.72	
B x C				0.34	
B x D				0.42	
C x D				0.33	
A x B x C				0.06	
A x B x D				0.22	
A x C x D				0.23	
B x C x D				0.48	
A x B x C x D				0.06	

[a,b] Means within the same column and effect with no common superscript differ significantly ($P < 0.05$).

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]E:P = energy to protein ratio

Table 2-10. Effect of broiler sex, maternal age and diet during rearing and lay[1] on chick yield, hatch weight, yolk free BW and yolk sac weight

Sources of variation	Chick yield[2]	Hatch weight (g)	Yolk free BW (g)	Yolk sac (g)
	----------Probability----------			
Hen age (A)	<0.0001	<0.0001	<0.0001	<0.0001
Offspring sex (B)	<0.0001	0.02	0.19	0.77
ME_{REAR} (C)	0.14	0.63	0.55	0.21
CP_{REAR} (D)	0.81	0.63	0.62	0.74
ME_{LAY} (E)	0.64	0.56	0.71	0.56
A x B	0.73	0.50	0.48	0.73
A x C	0.04	0.34	0.49	0.61
A x D	0.39	0.44	0.46	0.96
A x E	0.60	0.48	0.59	0.42
B x C	0.22	0.53	0.48	0.12
B x D	0.42	0.61	0.02	0.50
B x E	0.82	0.55	0.43	0.85
C x D	0.12	0.91	0.76	0.64
C x E	0.38	0.38	0.38	0.47
D x E	0.27	0.37	0.41	0.16
A x B x C	0.18	0.04	0.38	0.16
A x B x D	0.20	0.15	0.43	0.87
A x B x E	0.47	0.86	0.15	0.48
A x C x D	0.28	0.13	0.58	0.31
A x C x E	0.35	0.50	0.07	0.44
A x D x E	0.82	0.65	0.52	0.24
B x C x D	0.18	0.13	0.40	0.70
B x C x E	0.72	0.82	0.21	0.29
B x D x E	0.69	0.52	0.42	0.21
C x D x E	0.01	0.35	0.21	0.62
A x B x C x D	0.20	0.59	0.63	0.61
A x B x C x E	0.55	0.53	0.16	0.27
A x B x D x E	0.47	0.38	0.71	0.95
A x C x D x E	0.79	0. 09	0.34	0.62
B x C x D x E	0.61	0.77	0.21	0.72
A x B x C x D x E	0.44	0.09	0.68	0.43

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]Chick weight as percentage of egg weight.

Table 2-11. Maternal age and diet[1] on chick yield, hatch weight, yolk free BW and yolk sac weight

Sex	Hen age	ME_{REAR}	CP_{REAR}	ME_{LAY}	Chick yield[2]	Hatch weight	Yolk sac	Yolk free BW
					-- % --	---------- g ----------		
Female					68.9[b]	40.2[b]	5.23	35.0
Male					69.4[a]	40.4[a]	5.26	34.8
	28				70.0[a]	38.5[b]	4.96[b]	33.5[b]
	35				68.3[b]	42.0[a]	5.53[a]	36.3[a]
		HE_{REAR}			69.1	40.2	5.20	35.0
		LE_{REAR}			69.3	40.3	5.32	34.8
			HP_{REAR}		69.2	40.3	5.27	34.8
			LP_{REAR}		69.2	40.2	5.23	35.0
				HE_{LAY}	69.2	40.3	5.28	34.9
				LE_{LAY}	69.1	40.2	5.21	35.0
SEM					0.2	0.2	0.1	0.2
	28	HE_{REAR}			69.8[b]	38.4	4.86	33.5
	28	LE_{REAR}			70.2[a]	38.6	5.06	33.5
	35	HE_{REAR}			68.3	42.0	5.48	36.5
	35	LE_{REAR}			68.4	42.0	5.59	36.2
SEM					0.2	0.2	0.1	0.3
		HE_{REAR}	HP_{REAR}	HE_{LAY}	69.2[abc]	40.2	5.09	34.8
		HE_{REAR}	HP_{REAR}	LE_{LAY}	68.7[c]	40.3	5.22	35.1
		HE_{REAR}	LP_{REAR}	HE_{LAY}	68.9[bc]	40.1	5.22	34.8
		HE_{REAR}	LP_{REAR}	LE_{LAY}	69.6[a]	40.2	5.13	35.3
		LE_{REAR}	HP_{REAR}	HE_{LAY}	69.4[ab]	40.4	5.34	34.5
		LE_{REAR}	HP_{REAR}	LE_{LAY}	69.4[ab]	40.5	5.41	34.9
		LE_{REAR}	LP_{REAR}	HE_{LAY}	69.4[ab]	40.7	5.47	35.3
		LE_{REAR}	LP_{REAR}	LE_{LAY}	69.0[abc]	39.8	5.08	34.6
SEM					0.3	0.4	0.2	0.4

[a-c] Means within the same column, hen age and effect with no common superscript differ significantly ($P < 0.05$).

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]Chick weight as percentage of egg weight.

Table 2-12. Effect of maternal age and diet during rearing and lay[1] on chick quality

Sources of variation	Activity Score 0[2]	Beak Score 0	Hock Score 0	Navel Score 0
	----------Probability----------			
Hen age (A)	<0.0001	0.02	<0.0001	0.001
ME_{REAR} (B)	0.65	0.18	0.73	0.28
CP_{REAR} (C)	0.07	0.21	0.95	0.32
ME_{LAY} (D)	0.62	0.22	0.88	0.32
A x B	0.52	0.45	0.90	0.50
A x C	0.65	0.11	0.32	0.81
A x D	0.28	0.46	0.57	0.80
B x C	0.20	0.62	0.10	0.92
B x D	0.31	0.26	0.69	0.75
C x D	0.83	0.90	0.10	0.02
A x B x C	0.49	0.91	0.57	0.64
A x B x D	0.24	0.25	0.49	0.16
A x C x D	0.20	0.29	0.28	0.84
B x C x D	0.06	0.35	0.89	0.80
A x B x C x D	0.71	0.95	0.20	0.22

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).
[2]Score 0= values measured as percentage of chicks with good quality in the specified trait

Table 2-13. Maternal diet during rearing and lay[1] on chick quality

Hen age (wk)	ME_{REAR}	CP_{REAR}	HE_{LAY}	Activity Score 0[2]	Beak Score 0	Hock Score 0	Navel Score 0
28				61.28[a]	84.10[a]	46.30[b]	47.89[a]
35				48.22[b]	80.65[b]	64.76[a]	41.30[b]
	HE_{REAR}			56.13	83.82	53.30	46.55
	LE_{REAR}			57.01	81.85	52.63	44.43
		HP_{REAR}		58.34	81.92	52.91	46.47
		LP_{REAR}		54.76	83.79	53.03	44.53
			HE_{LAY}	56.08	81.95	52.83	44.54
			LE_{LAY}	57.05	83.77	53.11	46.49
SEM				0.01	0.01	0.02	0.02
		HP_{REAR}	HE_{LAY}	58.07	81.06	55.28	47.67[a]
		HP_{REAR}	LE_{LAY}	58.60	82.79	50.54	45.27[ab]
		LP_{REAR}	HE_{LAY}	54.10	82.84	50.39	41.42[b]
		LP_{REAR}	LE_{LAY}	55.45	84.78	55.77	47.76[a]
SEM				0.02	0.02	0.02	0.02

[a,b] Means within the same column and effect with no common superscript differ significantly ($P < 0.05$).

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]Score 0= reported as percentage of chicks with good quality in the specified trait

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CHAPTER 3: Effect of maternal dietary energy and protein on live performance and yield dynamics of broiler progeny from young breeders

3.1. INTRODUCTION

Some studies have demonstrated that maternal nutrition can influence offspring BW in livestock species (Peebles et al., 2002; Micke et al., 2011; Rehfeldt et al., 2011). Mammals can influence their offspring development during pregnancy, but for birds all maternal nutritional interference is over once the egg is laid, until hatch. Therefore, maternal nutrition and metabolism during egg development are important factors influencing offspring and both can vary according to maternal body composition, age and strain. Hen age can also influence broiler performance because young hens, that are still developing their reproduction system, lay smaller eggs, with smaller proportion of yolk and have lighter offspring BW at hatch and 41 d when compared to offspring of older hens (Ulmer-Franco et al., 2010).

Interestingly, sex of progeny seems to also have an effect on how maternal diet influences offspring BW. Spratt and Leeson (1987) observed that the weight of female broilers was not affected by protein and varying energy intakes in broiler breeder diets (19 or 25 g protein and 325 or 385 or 450 kcal MEn) while higher energy diets increased BW of male broiler progeny. Male broiler BW were 575, 586 and 601 g when their dams were fed either low energy, standard energy or

high energy diets, respectively, with low and high energy diets having statistically different broiler BW at 20 d (Spratt and Leeson, 1987).

Proudfoot and Hulan (1986) observed no effect on broiler feed conversion ratio (FCR) and BW at processing when broiler breeders were fed different levels of CP and ME during rearing and laying phases. During the rearing period, these researchers fed broiler breeder pullets diets containing 12.9% CP and 2,902 kcal/kg or 15.8% CP and 2,699 kcal/kg. During the laying phase, hens were fed diets containing either 15.3% CP and 2,746 kcal/kg, or 17.6% and 2,746 kcal/kg, or 17.8% CP and 2,651 kcal/kg.

To my knowledge, there are no studies that evaluated the effect of maternal dietary energy and protein on rearing diets and dietary energy on lay diets on offspring performance of modern broilers. Broiler breeders have been selected during the years for desirable qualities as a consequence bird genetics is changing considerably over the years (Barbato, 1999) and maternal nutritional effects on progeny may have been changing as well. Therefore, the objective of this research was to evaluate the effect of different levels of ME and CP in Ross 708 broiler breeder female rearing diets and different levels of ME on early breeding diets on broiler offspring growth, FCR and carcass yield dynamics.

3.2. MATERIAL AND METHODS

3.2.1. Experimental Design

The animal protocol for the study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles

established by the Canadian Council on Animal Care Guidelines and Policies (CCAC, 1993).

The effects of maternal nutrition on broiler performance were studied using a 2 x 2 x 2 x 2 factorial arrangement of treatments with 2 sexes, 2 maternal levels of dietary energy during rearing (high ME = 2,736 kcal/kg; HE_{REAR}, or low ME = 2,528 kcal/kg; LE_{REAR}), 2 maternal levels of dietary protein during rearing (high protein = 15.3% CP; HP_{REAR}, or low protein = 13.7% CP; LP_{REAR}) and 2 maternal levels of dietary energy during lay (high ME = 2,900 kcal/kg; HE_{LAY}, or a low ME = 2,800 kcal/kg; LE_{LAY}) associated with a 15% CP.

3.2.2. Maternal Stocks and Management

The details about number of birds used, genetic stock and management are shown in Chapter 2. All broiler breeder hens were artificially inseminated at 28 wk of age with 0.5 mL of pooled fresh undiluted semen. Eggs (n=1976) were weighed, identified by hen and date laid, and incubated in a Jamesway large J incubator (PT100 Incubator, Jamesway Incubator Company Inc., Cambridge, Ontario, Canada) at 99.4 ± 0.4ºF, 84.2 ± 2% RH. Eggs were automatically turned every h in the incubator. Eggs were transferred to pedigree hatch baskets and placed in a Jamesway PT100 Hatcher **(**Jamesway Incubator Company Inc., Cambridge, Ontario, Canada) at 18 d of incubation. Each egg was isolated from the others in individual cells in the hatcher tray, thus retaining information about the source of each chick.

3.2.3. Broiler Stocks and Management

All chicks (n=1635) were weighed, sexed, individually identified by bar-coded neck tags and randomly placed sex-separately into 32 pens based on the dietary treatment that the dam received during the laying phase. Broilers received commercial diets that exceeded National Research Council (1994) requirements and water ad libitum. A starter diet containing 23% CP and 3,067 kcal/kg ME was fed from 0 to 14 d of age; a grower diet (20% CP and 3,152 kcal/kg ME) from 15 to 28 d of age, a finisher I diet (19% CP and 3,196 kcal/kg ME) from 29 to 39 d of age and a finisher II diet (17.7% CP and 3,262 kcal/kg ME) from 40 to 54 d. Broilers were exposed to a lighting program of 23L:1D with a light intensity of 30 to 40 lux from 0 to 7 d, 10 to 15 lux from 8 to 21 d, and 3 to 5 lux from 22 d until the end of the trial. Broilers were individually weighed weekly with the use of a hanging scale (Weltech BW-1050, Weltech International Ltd; St Ives, Cambs, England). Mortality was recorded daily and pen level feed intakes were recorded every week by weighing back unused feed.

At least 75 broilers at each age were randomly selected and dissected at 26, 29, 33, 36, 43, 50 and 54 d. Breast muscles (Pectoralis major and Pectoralis minor) and fat pad of birds were removed and weighed to evaluate yield dynamics. A total of 180 birds were processed at 40 d. Carcass and carcass parts were weighed and carcass yields were reported as percentage of live BW. In the current study carcass weight did not include neck or fat pads.

3.2.4. Statistical Analysis

Body weight and carcass yield data were analyzed as a 4-way ANOVA with maternal dietary energy during rearing, maternal dietary protein during rearing, maternal dietary energy during lay and broiler sex as main effects by using the MIXED procedure of SAS. Hen nested in pen was considered as a random effect in the model. Feed conversion ratio data was analyzed as a 2-way ANOVA with maternal dietary energy during lay and broiler sex as main effect. Pairwise differences between means were determined with the PDIFF option of the LSMEANS statement. Differences of means were reported within sex. Pearson correlation coefficients calculated using the CORR procedure of SAS (Version 9.2. SAS Institute Inc., Cary, NC, 2009) described relationships among breeder and broiler variables. Differences between means were considered significant at $P < 0.05$.

A nonlinear regression was performed using the serial dissection data to evaluate yield dynamics using the NLIN procedure of SAS (SAS Institute, 2009). Broiler allometric yield curves for each maternal dietary treatment were estimated using the equation $Wt = aBW^b$, where Wt is carcass part weight in g (Pectoralis major, Pectoralis minor and fat pad), BW is broiler live BW, and a and b are least squares estimated coefficients (Huxley, 1932; Zuidhof, 2005).

Using estimated coefficients obtained by NLIN procedure of SAS, curves were calculated comparing two treatments separately. The overall sum of squares of each comparison was calculated as $SS_{sep} = SS_{tmt1} + SS_{tmt2}$. Degrees of freedom was calculated as the sum of values from each treatment ($df_{sep} = df_{tmt1} + df_{tmt2}$).

Then, data from different maternal treatments were pooled to estimate a curve and the total sum of squares of the pooled data (SS_{pool}) was calculated using the df of the pooled treatments (df_{pool}). Paired F-test procedures were done and F ratio was calculated according to Motulsky and Ransnas (1987) to determine if the separated analysis was significantly better than the pooled one. A single curve for both treatments was not considered the best fit if $P < 0.05$.

$$F = \frac{(SS_{pool} - SS_{sep})/(df_{pool} - df_{sep})}{SS_{sep}/df_{sep}}$$

3.3. RESULTS AND DISCUSSION

3.3.1. Body Weight

Maternal diets had no effect on broiler BW at processing (39 d; Table 3-1). In the current study, only BW of female broilers was influenced by maternal diet during rearing. Female broilers from 22 to 36 d from hens fed HE_{REAR} x LP_{REAR} were lighter than female broilers from hens fed HE_{REAR} x HP_{REAR} and LE_{REAR} x LP_{REAR} (Table 3-2). Male and female broilers have been reported to be differentially influenced by maternal diet (Spratt and Leeson, 1987). That can be related to their different body composition (Zuidhof et al., 2005), plasma hormone levels (Gonzales et al., 2003) or differences in how their muscles develop (Henry and Burke, 1998).

A lower BW for female broilers from hens fed HE_{REAR} x LP_{REAR} may be caused by the high energy to protein ratio (E:P; 20 kcal/g protein) and low protein intake (7.3 g protein/ kg $BW^{0.75}$) in the maternal diet, while hens fed HE_{REAR} x HP_{REAR} and LE_{REAR} x LP_{REAR} had similar intermediate E:P ratios and protein intake (17.9

and 18.5 kcal/g protein, respectively, and 7.7 g protein/ kg $BW^{0.75}$ for both diets; Appendix 1). Hens that received diet with the lowest E:P ratio (16.5 kcal/g protein) and highest protein intake (8.5 g protein/ kg $BW^{0.75}$) had their female offspring BW similar to the offspring from all other maternal diets, thus a high E:P ratio (and consequently low protein intake) in maternal diet was more related to reduced female offspring BW than a lower E:P ratio (and higher protein intake). The results indicate that there may be an optimum protein intake in the maternal diet for progeny growth, because hens that had intermediate intakes of protein had numerically higher female progeny BW than hens fed the highest protein intake. That can be supported by the results of Lopez and Leeson (1995) who fed 18 wk old Hubbard broiler breeders diets containing 10, 12, 14 or 16% CP and observed that offspring from 52 wk old hens were lighter at 48 d when hens were fed 10 or 16% CP with 12% CP maternal diet resulting in heavier male and female broilers at 48 d.

Maternal dietary protein can affect and progeny growth (Rao et al., 2009). Rao et al. (2009) found that hens fed low protein (10%) had lower levels of leptin in their egg yolk and an increased offspring BW 4 wk post-hatch. The results of the current study are in contrast with what was found by Rao et al., (2009) with higher maternal protein intake resulting in heavier offspring BW. However, Rao et al. (2009) studied a different strain of bird (Langshan hens) only during the laying period. Alterations of hormone content in egg yolk induced by maternal nutrition during rearing were not found in the literature and the genetic

mechanisms in which leptin changes due to maternal diet influences offspring are very elusive and were not evaluated in the current research.

3.3.2. Carcass Yield

Effects of maternal diet on carcass yield are shown in Table 3-3. When only rearing diet is considered it was observed that hens fed HE_{REAR} had offspring with lower breast yield (20.3%) than offspring from hens fed LE_{REAR} (20.8%; Table 3-4). The maternal diet with lower offspring breast yield (HE_{REAR}) was the diet with highest E:P ratio and lower protein intake (19 kcal/g protein and 7.5g/$BW^{0.75}$). Hens fed LE_{REAR} consumed more feed and consequently more methionine, which is a methyl donor.

It has been reported that increases in methyl donors in the diet influences epigenetic regulation by increasing the occurrence of DNA methylation (Choi and Friso, 2010). It is known that myogenesis is under the influence of epigenetic mechanisms during embryogenesis and adult life (Saccone and Puri, 2010), therefore dietary manipulations in maternal diets may have provided internal environmental cues to the developing embryo to induce a specific transcriptional reprogramming of myogenic genes leading to a different carcass yield. The mechanism could involve DNA methylation causing a decreased expression of proteolytic-related genes, which has been associated with increased myogenesis in chick cultured cells (Nakashima et al., 2011). However, DNA methylation and gene expression were not assessed in the current study; therefore further investigation would be needed.

An interaction of maternal dietary energy during the rearing and laying phases affected offspring carcass yield (Table 3-3). Broilers from HE_{REAR} x LE_{LAY} hens had lower breast and carcass yields than broilers from all other maternal dietary energy combinations (Table 3-4). Energy to protein ratio typically increased from rearing to laying diets. However, E:P ratio decreased from 19 kcal/g to 18.5 kcal/g within the maternal HE_{REAR} x LE_{LAY} treatment (Appendix 1). Energy to protein ratio can influence fat deposition, growth and nitrogen retention (Wagle et al., 1962; Gous, 1972). As a consequence changes in E:P ratio require a metabolic adjustment (Wagle et al., 1962). The decrease in E:P ratio observed in the current study may have acted as an environmental factor that induced an epigenetic mechanism that resulted in lower carcass and breast yields in the offspring. However, with the data collected, we cannot confirm that an epigenetic effect actually occurred and, if it did, the epigenetic mechanism that may have caused the decrease in offspring yield is unknown as it was not evaluated in the current study.

Pearson correlation analysis showed a significant positive correlation between maternal cumulative feed intake and broiler breast yield (P=0.04, r=0.17, data not shown). It was observed that the cummulative intake of breeders was mainly related to the energy level of the diet, because hens receiving a lower energy diet had to consume more feed to reach the same BW target.

3.3.3. Breast Muscles and Fat Pad

As previously observed, sex of the offspring influenced breast muscles and fat pad weight (Table 3-5), with females having more breast and fat pad (Zuidhof et al., 2005). There was no effect of maternal diet on offspring breast muscles dynamics (data not shown). However, abdominal fat pad weight was higher in offspring of hens fed HE_{REAR} diet when compared to offspring of hens fed LE_{REAR} diet (Figure 3-1). Body composition analysis were performed in a few of the hens and it was found that at 27 wk of age hens fed a HE_{REAR} diet had a heavier fat pad weight than breeder hens fed LE_{REAR} diets (Mba et al., unpublished), which may have influenced offspring of hens fed HE_{REAR} to also develop more fat pad.

The amount of adipose tissue in an individual is an indication of its nutritional state and energy reserves. Studies in mammal models showed that fat metabolism and adiposity of the mother can influence the same parameters in the offspring; females exposed to obesity/overnutrition generated offspring with increased fat mass (Drake and Reynolds, 2010). These effects might be the result of reprogramming of appetite and also genetic reprograming of adipogenic genes expression (Bayol et al., 2008).

An increase in fat pad is not desired as it can suggest an increase in broiler BW without increasing the amount of edible, lean meat. Based on the results of the current study dietary energy during lay did not influence fat pad in the progeny, which indicates that dietary energy during rearing has a more permanent influence in lipid deposition in the progeny.

3.3.4. Feed Conversion Ratio

A decrease in feed conversion ratio is desired as it reduces feed costs in broiler production. However, maternal dietary energy during lay (P = 0.13), sex of the offspring (P = 0.51) and interaction of maternal dietary energy and sex of offspring (P = 0.52) did not influence the FCR of the broilers up to 36 d (Data not shown). This is in agreement with previous results in Hubbard broiler breeders that received different daily intakes of protein and energy (varying from 13 to 23.7 kcal/g protein) and the FCR of their offspring did not differ (Spratt and Leeson, 1987). It seems that broiler FCR is not influenced by nutritional changes in maternal diet.

3.3.5. Conclusions

Maternal diets HE_{REAR} x HP_{REAR} and LE_{REAR} x LP_{REAR} increased BW in female offspring from 22 to 36 d of age when compared to female offspring of hens fed HE_{REAR} x LP_{REAR} diet. Male offspring BW was not influenced by maternal diet. Broiler carcass and breast yields decreased when E:P ratio (kcal/g) in maternal diet decreased upon transition from rearing to laying diet. Maternal diet did not influence FCR of broilers. Overall, a higher protein intake per unit of metabolic hen BW resulted in higher progeny BW and yield. The influence of maternal diet on broiler offspring performance could have been due to changes in methylation of genes due to a higher intake of methyl donor by hens or an increased deposition of leptin in egg yolk, or other unknown physiological responses of tissue deposition in the offspring due to protein intake per unit of metabolic hen BW.

However, we did not analyze DNA methylation, gene expression or leptin content in yolk in the current research, therefore further investigation is needed. Knowing the exact mechanisms that trigger epigenetic regulation through diet may become an important tool to the poultry industry in order to achieve the desired phenotype through genetic reprogramming in broilers from maternal dietary manipulation.

3.4. FIGURES AND TABLES

Table 3-1. Effect of maternal diet during rearing and lay[1] and broiler sex on broiler BW (g) at several ages

Sources of variation	BW 0 d	BW 8d	BW 15 d	BW 22 d	BW 29 d	BW 36 d	BW 39 d	BW 43 d	BW 50 d	BW 54 d
	----------Probability----------									
Sex (A)	0.12	0.02	0.83	0.11	0.04	<0.0001	0.11	<0.0001	<0.0001	0.01
ME_{REAR} (B)	0.06	0.86	0.63	0.84	0.88	0.46	0.58	0.77	0.74	0.18
CP_{REAR} (C)	0.08	0.63	0.38	0.62	0.70	0.98	0.11	0.64	0.23	0.48
ME_{LAY} (D)	0.42	0.23	0.16	0.81	0.97	0.31	0.64	0.20	0.15	0.16
A x B	0.81	0.91	0.76	0.59	0.78	0.97	0.88	0.97	0.65	0.58
A x C	0.06	0.80	0.57	0.79	0.68	0.35	0.78	0.78	0.47	0.08
A x D	0.88	0.41	0.27	0.44	0.74	0.84	0.87	0.06	0.14	0.26
B x C	0.25	0.68	0.70	0.69	0.46	0.12	0.10	0.19	0.86	0.14
B x D	0.17	0.90	0.41	0.20	0.14	0.17	0.39	0.10	0.86	0.36
C x D	0.41	0.20	0.11	0.18	0.20	0.28	0.20	0.21	0.12	0.17
A x B x C	0.14	0.08	0.18	0.001	0.0004	0.019	0.32	0.33	0.26	0.06
A x B x D	0.49	0.88	0.17	0.06	0.06	0.19	0.66	0.010	0.81	0.25
A x C x D	0.35	0.92	0.64	0.50	0.36	0.46	0.37	0.16	0.07	0.03
B x C x D	0.89	0.72	0.82	0.60	0.51	0.75	0.79	0.98	0.31	0.26
A x B x C x D	0.32	0.62	0.81	0.47	0.41	0.72	0.75	0.65	0.30	0.66

[1] ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay

Table 3-2. Broiler sex and maternal diet during rearing and lay[1] on progeny BW

Sex	ME_{LAY}	ME_{REAR}	CP_{REAR}	E:P[2]	Age			
					22 d	29 d	36 d	39 d
					----------g----------			
Female					789.5	1312.6[b]	1849.9[b]	2124.3
Male					802.9	1344.0[a]	1951.0[a]	2211.2
	HE_{LAY}			19.4	795.2	1328.1	1887.7	2180.3
	LE_{LAY}			18.5	797.2	1328.5	1913.1	2155.1
		HE_{REAR}		19	797.0	1327.2	1891.4	2152.5
		LE_{REAR}		17.5	795.3	1329.4	1909.5	2182.9
			HP_{REAR}	17.2	798.2	1331.2	1900.2	2124.4
			LP_{REAR}	19.2	794.1	1325.4	1900.6	2211.0
SEM					6.1	11.1	18.0	39.8
Female		HE_{REAR}	HP_{REAR}	17.9	806.8[a]	1348.5[a]	1901.1[a]	2134.4
			LP_{REAR}	20	769.3[b]	1270.2[c]	1781.3[b]	2091.8
		LE_{REAR}	HP_{REAR}	16.5	778.4[ab]	1288.9[bc]	1821.6[ab]	2012.3
			LP_{REAR}	18.5	803.4[a]	1342.8[ab]	1895.4[a]	2258.6
Male		HE_{REAR}	HP_{REAR}	17.9	794.7	1323.0	1919.4	2174.0
			LP_{REAR}	20	817.3	1367.1	1963.6	2210.0
		LE_{REAR}	HP_{REAR}	16.5	813.0	1364.5	1958.8	2177.0
			LP_{REAR}	18.5	786.5	1321.4	1962.2	2283.6
SEM					12.5	22.7	37.6	82.8

[a-c] Means within column, sex and effect with no common superscript differ significantly ($P < 0.05$).

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]E:P = energy to protein ratio.

Table 3-3. Effects of broiler sex and maternal diet during rearing and lay[1] on progeny yield (% of BW)

Sources of variation	Pectoralis major	Pectoralis minor	Breast	Legs	Wings	Carcass
	----------Probability----------					
Sex (A)	0.14	<0.0001	0.03	0.002	0.61	0.21
ME_{REAR} (B)	0.02	0.25	0.03	0.63	0.35	0.13
CP_{REAR} (C)	0.43	0.58	0.46	0.47	0.55	0.26
ME_{LAY} (D)	0.13	0.01	0.05	0.37	0.04	0.11
A x B	0.18	0.72	0.32	0.42	0.22	0.12
A x C	0.94	0.45	0.84	0.20	0.01	0.93
A x D	0.83	0.50	0.67	0.13	0.70	0.67
B x C	0.55	0.59	0.57	0.69	0.11	0.75
B x D	0.001	0.35	0.001	0.57	0.81	0.044
C x D	0.91	0.29	0.67	0.23	0.75	0.83
A x B x C	0.95	0.22	0.79	0.82	0.19	0.18
A x B x D	0.05	0.65	0.06	0.17	0.97	0.06
A x C x D	0.26	0.06	0.18	0.61	0.79	0.06
B x C x D	0.80	0.64	0.69	0.48	0.38	0.48
A x B x C x D	0.78	0.79	0.80	0.78	0.10	0.55

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay

Table 3-4. Broiler sex and maternal diet during rearing and lay[1] on broiler breast and carcass yield

Sex	CP_{REAR}	ME_{REAR}	ME_{LAY}	$E:P_{REAR}$[2]	$E:P_{LAY}$[2]	Pectoralis major	Pectoralis minor	Breast	Carcass
Female						16.9	3.8[a]	20.8[a]	64.7
Male						17.0	3.6[b]	20.3[b]	64.4
	HP_{REAR}			17.2		16.7	3.7	20.5	64.5
	LP_{REAR}			19.2		16.9	3.7	20.6	64.7
		HE_{REAR}		19		16.6[b]	3.7	20.3[b]	64.4
		LE_{REAR}		17.5		17.0[a]	3.8	20.8[a]	64.8
			HE_{LAY}		19.4	17.0	3.8[a]	20.8	64.8
			LE_{LAY}		18.5	16.7	3.7[b]	20.3	64.4
SEM						0.14	0.04	0.16	0.17
		HE_{REAR}	HE_{LAY}	19	19.4	17.1[a]	3.8	20.9[a]	64.8[a]
			LE_{LAY}	19	18.5	16.2[b]	3.6	19.8[b]	64.0[b]
		LE_{REAR}	HE_{LAY}	17.5	19.4	16.9[a]	3.8	20.7[a]	64.7[a]
			LE_{LAY}	17.5	18.5	17.2[a]	3.7	20.9[a]	64.8[a]
SEM						0.20	0.06	0.24	0.25

[a,b] Means within the same column and effect with no common superscript differ significantly ($P < 0.05$).

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]$E:P_{REAR}$ = energy to protein ratio for rearing diets (kcal/g); $E:P_{LAY}$ = energy to protein ratio for lay diets (kcal/g).

[3]Measured as percentage of live broiler BW

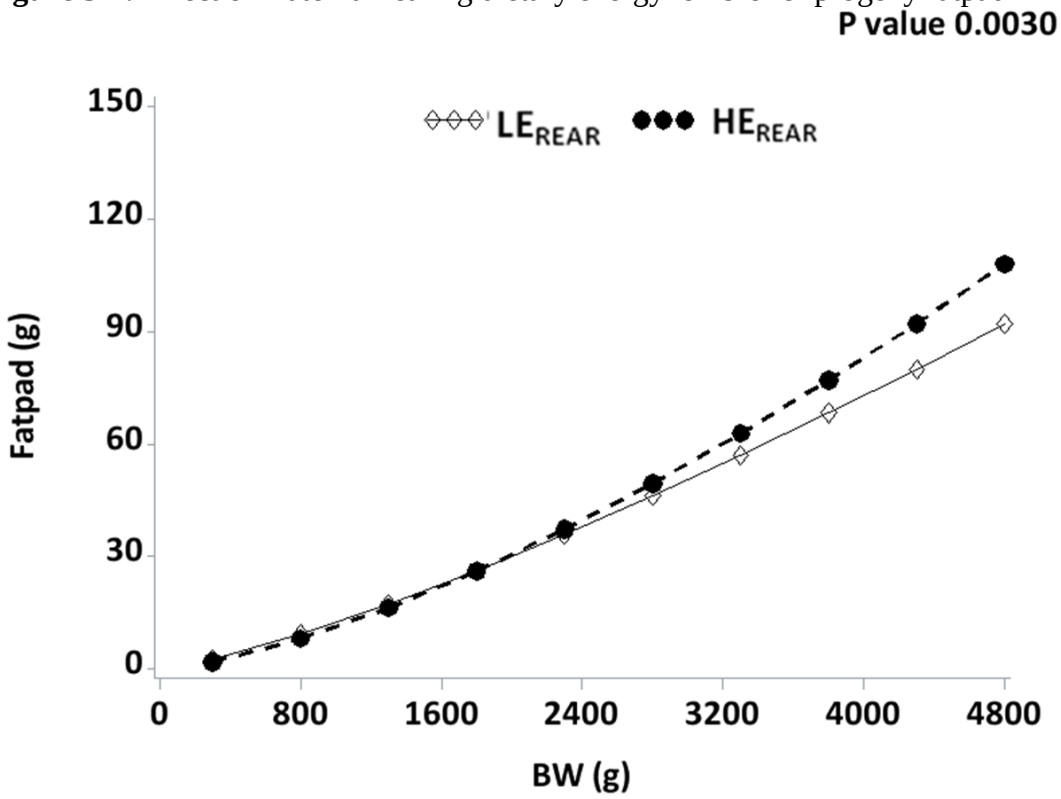
Table 3-5. Coefficients[1] for Pectoralis major, Pectoralis minor and fat pad of female and male broilers

	Female		Male		P[2]
	a	b	a	b	
Pectoralis major	0.0524	1.1602	0.0523	1.1564	0.0006
Pectoralis minor	0.0438	0.9955	0.0347	1.0139	<0.0001
Fatpad	0.00004	1.7734	0.0001	1.6078	<0.0001

[1]Coefficients for the model $Wt = aBW^b$, where Wt is carcass part weight in grams, BW is broiler live body weight, and a and b are least squares estimated coefficients.

[2]Probability that the yield curves are best explained by a single function. The alternative hypothesis is that the yield curves for females and males are different.

Figure 3-1. Effect of maternal rearing dietary energy[1] on broiler progeny fatpad



[1]HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg). Standard error of the mean for HE_{REAR} was 1.24. Standard error of the mean for LE_{REAR} was 1.15. Data showed based on the model $Wt = aBW^b$, where Wt is carcass part weight in grams, BW is broiler live body weight, and a and b are least squares estimated coefficients. For HE_{REAR}, a=0.00051 and b=1.446; for LE_{REAR}, a=0.00174 and b=1.283.

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CHAPTER 4: Effect of maternal dietary energy and protein on broiler live performance and yield

4.1. INTRODUCTION

Awareness about the importance of maternal diet on offspring health is increasing lately. Maternal diet is also being studied in livestock species as a way of improving offspring growth and production (Peebles et al., 2002; Micke et al., 2011; Rehfeldt et al., 2011; Choe et al., 2010; Long et al., 2012). The poultry industry is constantly working to improve carcass yield and obtain a fast growing broiler and manipulation of maternal diet can be one way of improving broiler performance (Calini and Sirri, 2007).

Peebles et al. (2002) fed broiler breeder hens diets with different energy levels (2,709, 2,826 or 2,940 kcal/kg) and observed that broiler BW at 43 d was higher for offspring of hens fed a low energy diet in comparison with BW of progeny of hens fed a high energy diet. Spratt and Leeson (1987), however, observed that higher energy in the diet of broiler breeder hens increased BW in male but not in female broilers. When different combinations of CP and ME treatments were fed to broiler breeders during rearing (12.9% CP and 2,902 kcal/kg or 15.8% CP and 2,699 kcal/kg) and laying phases (15.3% CP and 2,746 kcal/kg, or 17.6% and 2,746 kcal/kg, or 17.8% CP and 2,651 kcal/kg), progeny feed conversion ratio (FCR) and BW at processing were not affected by maternal diet (Proudfoot and Hulan, 1986).

Studies evaluating effect of maternal nutrition on progeny performance were done a long time ago. To my knowledge, there are no recent papers evaluating effects of modern broiler breeder dietary energy and protein on progeny. Therefore, the objective of this research was to evaluate the effect of different dietary energy and protein levels in broiler breeder female rearing diets and different dietary energy levels during lay on progeny growth, carcass yield and FCR.

4.2. MATERIAL AND METHODS

4.2.1. Experimental Design

The protocol for the current study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles established by the Canadian Council on Animal Care Guidelines and Policies (CCAC, 1993).

The effect of maternal nutrition on broiler performance was conducted using a 2 x 2 x 2 x 2 factorial arrangement of treatments with 2 broiler sexes, 2 levels of maternal dietary energy during rearing (high ME = 2,736 kcal/kg; HE_{REAR}, or low ME = 2,528 kcal/kg; LE_{REAR}), 2 levels of maternal dietary protein during rearing (high protein = 15.3% CP; HP_{REAR}, or low protein = 13.7% CP; LP_{REAR}) and 2 levels of maternal dietary energy during lay (high ME = 2,900 kcal/kg; HE_{LAY}, or a low ME = 2,800 kcal/kg; LE_{LAY}) and 15% CP.

4.2.2. Maternal Stocks and Management

Information about broiler breeder management as well as the number of birds used and the genetic stock can be found in Chapter 2. Broiler breeder hens were artificially inseminated at 35 wk of age with 0.5 mL of pooled fresh undiluted semen. Eggs (n=1250) were collected, identified, weighed, incubated and hatched according to the procedure explained in Chapter 3.

4.2.3. Broiler Stocks and Management

Broiler chicks (n = 604) management details can be found in Chapter 3. Broilers were individually weighed weekly with the use of a hanging scale (Weltech BW-1050, Weltech International Ltd; St Ives, Cambs, England). Mortality was recorded daily and pen level feed intakes were recorded every wk by weighting back unused feed. At total of 201 birds were processed at 40 d. Carcasses, breast muscles, legs and wings were weighed and reported as percentage of live BW. Carcass weight did not include neck or fat pads.

4.2.4. Statistical Analysis

Body weight and dissection data were analyzed as a 4-way ANOVA using MIXED procedure of SAS (Version 9.2. SAS Institute Inc., Cary, NC, 2009) with dietary energy during rearing, dietary protein during rearing, dietary energy during lay, and broiler sex as main effects. Hen nested in pen was considered as a random effect in the model. Feed conversion ratio data was analyzed as a 2-way ANOVA with dietary energy during lay and broiler sex as main effects. Pearson

correlation coefficients were calculated using the CORR procedure of SAS in order to evaluate the relationships among breeder BW and intake and broiler variables. Pairwise differences between means were determined with the PDIFF option of the LSMEANS statement. Differences of means were reported within sex. Significance was assessed at the < 0.05 level.

4.3. RESULTS AND DISCUSSION

4.3.1.Body Weight

Pearson correlation analysis showed a 1% correlation between maternal BW at 35 wk and broiler BW at 39 d ($P=0.03$ $r=0.10$). Effects of maternal diet on broiler BW can be observed in Table 4-1. At 15 and 22 d of age, female broilers from hens fed HE_{REAR} x HP_{REAR} were heavier than female broilers from hens fed LE_{REAR} x HP_{REAR}, while male broilers from LE_{REAR} x HP_{REAR} maternal diet were heavier than male broilers from hens fed LE_{REAR} x LP_{REAR} (Table 4-2). For female broilers, the maternal diets with different offspring BW only differed in the energy level (HE_{REAR} x HP_{REAR} and LE_{REAR} x HP_{REAR}) while for male broilers the maternal diets with different offspring BW only differed in protein level (LE_{REAR} x HP_{REAR} and LE_{REAR} x LP_{REAR}). Maternal diet LE_{REAR} x HP_{REAR} was the experimental diet with highest daily protein intake (8.5g protein/kg $BW^{0.75}$) as consequence when diets changed for the lay there was almost no increase or even a decrease in the protein intake depending to the laying diets each hen was assigned to and that may have affected negatively BW of female offspring (Appendix 1). Similarly, maternal diet LE_{REAR} x LP_{REAR} had the highest feed intake (56.1g/kg $BW^{0.75}$) with almost no

increase or even a decrease in the feed intake when diets where changed in lay which may have affected negatively BW of male offspring. It is interesting to observe that the maternal diet that had lighter female progeny BW was the one that originated the heaviest male progeny (LE_{REAR} x HP_{REAR}). The reason for this difference is still not completely understood but it may be associated to their sexual dimorphism. Hens fed LE_{REAR} x HP_{REAR} had lower liver weight when compared to hens fed HE_{REAR} x HP_{REAR} (Mba et al., unpublished) and it was previously observed in protein restricted mammals that lower liver weight in the mother can result in lighter progeny weight (Muaku et al., 1995). Proudfoot and Hulan (1986) did not find any effect of nutrient levels of maternal diets during rearing on offspring performance. To our knowledge no other studies have evaluated effects of dietary energy and protein on maternal nutrition during rearing on progeny performance. The result from the current study indicates that maternal diet during rearing has more influence in BW of progeny that maternal diet during the laying phase, therefore manipulation of pullet diet has long term effects in hen metabolism that is able to influence its progeny.

4.3.2. Carcass Yield

Effect of maternal diet on broiler breast yield was sex-dependent (Table 4-3). Female broilers from hens fed LP_{REAR} x LE_{LAY} had lower Pectoralis major and carcass yield than female broilers from hens fed HP_{REAR} x $LE_{LAY.}$ Male broilers from hens fed HP_{REAR} x HE_{LAY} had 19.8% breast yield while male broilers from hens fed HP_{REAR} x LE_{LAY} had 18.4% breast yield (Table 4-4). Maternal diets that

resulted in different Pectoralis major yield in female broilers only differed in the protein level during rearing (both had low ME during lay), with HP_{REAR} having lower energy to protein ratio (E:P; 17.2 kcal/g) than LP_{REAR} treatment (19.2 kcal/g; Appendix 1). A decrease in E:P ratio for LP_{REAR} x LE_{LAY} when the diet changed between the rearing and the laying phase (LE_{LAY} =18.5 kcal/g) may have caused this decrease in progeny breast yield. The reason why a decrease in E:P ratio decreased yield in female progeny is still not clear and more studies have to be done for clarification. Changes in E:P requires a metabolic adjustment by the animal (Wagle et al., 1962). Therefore, it is hypothesized that a decrease in E:P ratio may have required a metabolic readjustment in the broiler breeder metabolism and that adjustment may have acted as an environmental factor influencing the offspring epigenetically. However, that cannot be assured as the occurrence of an epigenetic effect was not evaluated in the current study. For male broilers, Pectoralis major yield only differed in response to maternal energy level during lay (HP_{REAR} x LE_{LAY} and HP_{REAR} x HE_{LAY}) with LE_{LAY} having lower E:P ratio (18.5 kcal/g) than HE_{LAY} treatment (19.4 kcal/g). Differences between male and female broilers that came from hens fed the same dietary treatments are still not clarified but it may be due to the difference on how differently their muscles develop. A study showed sexual dimorphism in muscle development in broiler embryos and observed that male broilers usually develop more myofiber numbers (more myofibers per 30,000 μm^2) while female broilers develop larger myofibers (Henry and Burke, 1998), and myofiber number and size can be differently influenced by protein levels in maternal diet (Rehfeldt et al., 2012)

Carcass yield was lower in offspring of hens fed LE_{REAR} x HP_{REAR} (63.8%) when compared to the carcass yield of broilers from hens fed HE_{REAR} x HP_{REAR} (64.9%, Table 4-4). Hens that received the LE_{REAR} x HP_{REAR} diet consumed 67.5 g of feed daily with a daily intake of 10.3g of protein and 170.7 kcal/bird while hens fed HE_{REAR} x HP_{REAR} consumed 61.4 g of feed daily, 9.3 g of protein and 168 kcal/bird, on average. Differences of carcass yield could also be due to changes in E:P ratio when diets changed from rearing to lay. Hens from LE_{REAR} x HP_{REAR} diet had 20 kcal/g which decrease for 18.5 kcal/g if they were fed LE_{LAY} or 19.4 kcal/g if they were fed HE_{LAY}. Hens fed LE_{REAR} x HP_{REAR} had lower liver weight when compared to hens fed HE_{REAR} x HP_{REAR} (Mba et al., unpublished). The liver is responsible for important metabolic functions such as lipogenesis (Taouis et al., 2001) and lipogenesis is positivity correlated with E:P ratio (Donaldson, 1985). In a study done in rats, protein restricted dams had lower liver weight, resulting in lower liver weight and lower concentration of liver IGF-I in the progeny (Muaku et al., 1995). A decrease in IGF-I in the progeny could result in a decreased carcass yield because IGF-I is a regulator of muscle development (Duclos, 2005).

An increase in carcass or breast yield generated by changes in dietary energy and protein level in broiler breeder diets can bring huge economic advantage for the poultry industry as an increase in yield means a increase in the amount of saleable meat. It was observed that manipulation of dietary energy and protein in broiler breeders can influence broiler yield, therefore the results of the current study are only an initial step to understand how yield can be influenced by maternal diet as there are other influencing factors such as broiler sex.

4.3.3.Feed Conversion Ratio

Broiler feed conversion ratio up to 39 d of age ranged from 1.60 (HE_{LAY}) to 1.62 (LE_{LAY}) but was not significantly influenced by maternal dietary energy during lay (P = 0.65), broiler sex (0.86) or the interaction of maternal dietary energy during lay and broiler sex (P = 0.59). This result concurs with previous work that did not find any influence of maternal diet on FCR of the offspring. Proudfoot and Hulan (1986) fed different levels of protein and energy in the grower (15 to 20 wk; 12.9% CP and 2,902 kcal/kg or 15.8% CP and 2,699 kcal/kg) and adult diet (21 to 60 wk; 15.3% CP and 2,746 kcal/kg or 17.6% and 2,746 kcal/kg or 17.8% CP and 2,651 kcal/kg) of 3 strains of broiler breeders and no effect was observed in FCR of the progeny. Feed conversion ratio of the offspring was also not influenced when Spratt and Leeson (1987) fed Hubbard broiler breeders with 6 different diet treatments varying in their energy and protein intake (19 or 25 g protein and 325, 385 or 450 kcal MEn).

A reduction in FCR would be of economic value for the poultry industry because it would decrease the amount of feed needed to raise broilers to the market BW. The current study did not find any influence of maternal diet during lay on FCR. The above literature agrees with our findings as it seems that broiler FCR is not influenced by maternal nutrition. Effects of maternal diet during rearing on FCR were not evaluated because feed intake was measured based on pen level and there were physical limitations to allocate all the 16 interactions (8 treatments and 2 sexes) in isolated pens.

4.3.4. Conclusions

Effects of maternal rearing diet on the BW of their broiler offspring were sex-dependent and transient, only being observed at 15 and 22 d of age. Broiler breast and carcass yield effects were also sex-dependent, with the maternal dietary protein during rearing and dietary energy during lay affecting breast yield in male offspring and carcass yield in female offspring. Maternal rearing diet with lower E:P ratio and higher protein intake during rearing had lower carcass yield in both broiler sexes (LE_{REAR} x HP_{REAR}). Maternal diet did not influence FCR of broiler offspring. Maternal nutrition may influence broiler yield, and thus may be more economically important than previously thought, because based on our findings we verified that is possible to affect broiler yield through manipulation of maternal diet already in the pullet phase.

4.4. FIGURES AND TABLES

Table 4-1. Effects of broiler sex and maternal diet during rearing and lay[1] on broiler BW (g) at different ages

Sources of variation	BW 0 d	BW 8d	BW 15 d	BW 22 d	BW 29 d	BW 39 d
	----------Probability----------					
Sex (A)	0.38	<0.0001	0.008	0.56	0.51	<0.0001
ME_{REAR} (B)	0.07	0.61	0.21	0.15	0.35	0.21
CP_{REAR} (C)	0.78	0.32	0.19	0.07	0.17	0.15
ME_{LAY} (D)	0.50	0.80	0.07	0.09	0.05	0.99
A x B	0.28	0.13	0.23	0.84	0.32	0.36
A x C	0.50	0.47	0.58	0.37	0.38	0.84
A x D	0.47	0.24	0.44	0.96	0.42	0.40
B x C	0.39	0.62	0.99	0.71	0.50	0.34
B x D	0.88	0.94	0.85	0.77	0.62	0.72
C x D	0.70	0.47	0.62	0.88	0.82	0.88
A x B x C	0.39	0.19	0.01	0.045	0.25	0.54
A x B x D	0.98	0.50	0.29	0.87	0.80	0.34
A x C x D	0.64	0.48	0.39	0.63	0.74	0.43
B x C x D	0.07	0.69	0.88	0.74	0.57	0.30
A x B x C x D	0.86	0.52	0.28	0.30	0.17	0.10

[1] ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay.

Table 4-2. Maternal diet during rearing and lay[1] and broiler sex on progeny BW

Sex	ME_{LAY}	ME_{REAR}	CP_{REAR}	E:P[2] (kcal/g)	BW (g) 15 d	BW (g) 22 d	BW (g) 29 d	BW (g) 39 d
Female					469.4[a]	839.6	1366.5	2312.0[b]
Male					455.7[b]	833.9	1377.0	2433.3[a]
	HE_{LAY}			19.4	457.9	828.5	1355.8	2372.5
	LE_{LAY}			18.5	467.2	845.0	1387.7	2372.7
		HE_{REAR}		19	465.8	843.8	1379.3	2388.5
		LE_{REAR}		17.5	459.3	829.8	1364.2	2356.7
			HP_{REAR}	17.2	465.9	845.9	1382.7	2390.5
			LP_{REAR}	19.2	459.2	827.6	1360.8	2354.8
SEM					3.7	7.2	11.7	18.3
Female		HE_{REAR}	HP_{REAR}	17.9	484.2[a]	864.1[a]	1400.4	2,374.2
			LP_{REAR}	20	467.3[ab]	831.0[ab]	1363.5	2,304.5
		LE_{REAR}	HP_{REAR}	16.5	458.4[b]	824.6[b]	1340.2	2,280.6
			LP_{REAR}	18.5	467.7[ab]	838.7[ab]	1361.8	2,288.7
Male		HE_{REAR}	HP_{REAR}	17.9	454.1[ab]	845.4[ab]	1391.0	2,474.3
			LP_{REAR}	20	457.6[ab]	834.6[ab]	1362.4	2,413.5
		LE_{REAR}	HP_{REAR}	16.5	466.8[a]	849.6[a]	1399.1	2,445.1
			LP_{REAR}	18.5	444.2[b]	806.2[b]	1355.6	2,412.4
SEM					7.8	15.1	24.3	39.2

[a,b] Means within column, sex and effect with no common superscript differ significantly ($P < 0.05$).

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).

[2]E:P = energy to protein ratio.

Table 4-3. Effects of broiler sex and maternal diet during rearing and lay[1] on broiler carcass parts yield (% BW)

Sources of variation	Pectoralis major	Pectoralis minor	Breast	Legs	Wings	Carcass
	----------Probability----------					
Sex (A)	0.003	<0.0001	0.0001	<0.001	0.89	0.009
ME_{REAR} (B)	0.98	0.42	0.90	0.16	0.15	0.08
CP_{REAR} (C)	0.34	0.43	0.52	0.12	0.04	0.90
ME_{LAY} (D)	0.35	0.21	0.28	0.47	0.50	0.68
A x B	0.62	0.48	0.57	0.70	0.29	0.45
A x C	0.51	0.83	0.55	0.08	0.05	0.11
A x D	0.21	0.42	0.21	0.54	0.96	0.32
B x C	0.96	0.42	0.91	0.32	0.59	0.02
B x D	0.44	0.31	0.63	0.36	0.95	0.41
C x D	0.91	0.24	0.90	0.55	0.31	0.58
A x B x C	0.39	0.63	0.50	0.23	0.70	0.35
A x B x D	0.25	0.07	0.19	0.45	0.54	0.50
A x C x D	0.008	0.05	0.009	0.34	0.80	0.03
B x C x D	0.53	0.69	0.56	0.92	0.79	0.11
A x B x C x D	0.62	0.65	0.62	0.27	0.74	0.11

[1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay

Table 4-4. Maternal diet during rearing and lay[1] and broiler sex on progeny carcass yield (% BW)

Sex	ME_{REAR}	CP_{REAR}	ME_{LAY}	$E:P_{REAR}$[2]	$E:P_{LAY}$[2]	P. major	P. minor	Breast	Carcass
Female						16.4[a]	3.7[a]	20.2[a]	64.7[a]
Male						15.8[b]	3.3[b]	19.1[b]	63.9[b]
	HE_{REAR}			19		16.1	3.5	19.7	64.6
	LE_{REAR}			17.5		16.1	3.5	19.6	64.1
		HP_{REAR}		17.2		16.2	3.5	19.7	64.3
		LP_{REAR}		19.2		16.0	3.5	19.5	64.3
			HE_{LAY}		19.4	16.2	3.6	19.8	64.4
			LE_{LAY}		18.5	16.0	3.5	19.5	64.2
SEM						0.2	0.04	0.2	0.2
	HE_{REAR}	HP_{REAR}		17.9		16.2	3.5	19.7	64.9[a]
		LP_{REAR}		20		16.0	3.6	19.6	64.2[ab]
	LE_{REAR}	HP_{REAR}		16.5		16.2	3.5	19.7	63.8[b]
		LP_{REAR}		18.5		16.0	3.5	19.5	64.4[ab]
SEM						0.3	0.06	0.3	0.3
Female		HP_{REAR}	HE_{LAY}	17.2	19.4	16.3[ab]	3.7	20.0	64.8[ab]
			LE_{LAY}	17.2	18.5	17.0[a]	3.7	20.7	65.1[a]
		LP_{REAR}	HE_{LAY}	19.2	19.4	16.6[ab]	3.8	20.3	65.0[a]
			LE_{LAY}	19.2	18.5	16.0[b]	3.7	19.7	63.9[b]
Male		HP_{REAR}	HE_{LAY}	17.2	19.4	16.4[a]	3.5	19.8[a]	63.9
			LE_{LAY}	17.2	18.5	15.2[b]	3.2	18.4[b]	63.6
		LP_{REAR}	HE_{LAY}	19.2	19.4	15.7[ab]	3.3	19.0[ab]	63.8
			LE_{LAY}	19.2	18.5	15.8[ab]	3.4	19.2[ab]	64.5
SEM						0.4	0.1	0.5	0.5

[a,b]Means within column, sex and effect with no common superscript differ significantly ($P < 0.05$). [1]ME_{REAR} = metabolizable energy during rearing; CP_{REAR} = crude protein during rearing; ME_{LAY} = metabolizable energy during lay; HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg). [2]$E:P_{REAR}$ = energy to protein ratio for rearing diets (kcal/g); $E:P_{LAY}$ = energy to protein ratio for lay diets (kcal/g).

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CHAPTER 5: Effect of male broiler breeder weight on semen quality and fertility

5.1. INTRODUCTION

Broiler breeder fertility can be negatively affected by sexual behavior such as reduced completed mating frequency, or physiological aspects such as reduced semen production and quality. Reduction in fertility as a consequence of decreased mating activity and semen production can occur if broiler breeder males are over or underfed (Leeson and Summers, 2005). The BW currently considered optimum for maximum fertility in naturally-mated Ross males is 3.6 kg for a 25 wk old male and 4.8 kg for a 60 wk old male (Aviagen, 2007). Similar to the problem in commercial turkey breeders, in high BW males, depressed fertility can be caused by anatomical inability to successfully mate (Hocking and Duff, 1989). This could also be from the development of musculoskeletal diseases in roosters as they age (Hocking and Duff, 1989). Rooster fertility normally decreases after 37 wk of age as a consequence of decreased plasma testosterone levels (Weil et al., 1999) which may decrease libido and a reduction of the number of sperm cells ejaculated (Rosenstrauch et al., 1994).

Romero-Sanchez et al. (2008) suggested that a decrease in male fertility can be caused by a deficiency in metabolizable energy intake, because the rooster would not have enough energy for semen production and mating activity. Bramwell et al. (1996) mentioned that a decrease in male BW would indicate that energy intake is not enough for the maintenance requirements which would result in poor

reproductive performance. Romero-Sanchez et al. (2008) suggested that reproductive dysfunction would be greater in high BW males within a flock because the bigger males would have higher maintenance requirements with less dietary energy being used for reproduction. Cerolini et al. (1995) fed Ross broiler breeder males with a diet containing 12% CP and approx. 2,746 kcal ME/kg from 23 to 54 wk of age with 110, 120, 130 g/bird/d or ad libitum (corresponding to 302, 329.5, 357, 483.3 kcal ME/d, respectively), and found that feeding roosters 357 kcal ME/male/d resulted in the highest percentage of males producing semen and overall best reproductive performance when hens were artificially inseminated.

Fertility is affected by semen quality because if semen has less or deformed sperm cells that is going to decrease its ability to fertilize the egg. Some predictors for semen quality are sperm concentration, mobility, ratio of live-to-dead spermatozoa and morphological evaluation of the sperm cells (Alkan et al., 2002). Semen quality can be affected by male BW. Bowling et al. (2003) verified that roosters with lower mobility, lower fertility and higher percentages of sperm with abnormal mitochondria from 29 to 32 wk of age were the heaviest roosters in the flock. The objective of this research was to investigate the effect of BW of broiler breeder males near peak production on semen quality, fertility and duration of fertility in eggs from artificially inseminated hens.

5.2. MATERIAL AND METHODS

5.2.1. Stocks and Management

The animal protocol for the study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles established by the Canadian Council on Animal Care Guidelines and Policies (CCAC, 1993).

At 203 d of age, a total of 36 Ross 344 (Aviagen Inc., Huntsville, Alabama) males managed to breeder recommended BW targets were divided into 3 treatment groups. Roosters on the CONTROL treatment continued to be fed to BW targets, while males on the LOW treatment were fed to BW that were 5% lower, and males on the HIGH treatment were fed to BW that were 10% higher than target BW (Figure 5-1). All males received a diet containing 2,800 kcal/kg and 15.3% CP. To achieve BW targets, males were individually weighed bi-weekly and feed allocations were adjusted for each male based on its BW.

In total, 144 White Leghorn hens (25 to 35 wk old) were artificially inseminated with semen collected when the males were 210, 230, 257 and 284 d of age. Fresh undiluted semen from each male was used to inseminate the same 4 hens on each insemination day (0.5 mL/hen). Following insemination, eggs from inseminated hens were cracked open every day for 21 d for a fresh egg breakout determination of fertility. Eggs were considered fertile if the blastoderm was observed on the egg yolk (Wilson, 1995).

Semen was collected from all males at 211, 238, 266 and 294 d of age. The complete semen analysis procedure was performed according to Froman (2006).

Sperm concentration and mobility were evaluated using a 596a Chicken Mobility Analyzer (Animal Reproduction Systems®, Chino, California). Concentration was measured and mobility was estimated using a mobility index, a grading scale proportional to the number of sperm cells that enter the Accudenz solution during an incubation period of 5 minutes. Accudenz is a biologically inert solution used as a medium to evaluate sperm motility (Froman and Feltmann, 1998). To measure sperm mobility a standard polystyrene cuvette containing 6% (wt/vol) Accudenz was warmed to mimic conditions in the body of the hen. Immobile and slow sperm cells will not be able to penetrate the Accudenz solution, motile sperm cells will penetrate and move to the bottom of the solution and then mobility will be measured by the analyzer (Froman, 2006).

After 230 d of age, 1 male from LOW treatment and 1 male from CONTROL treatment produced watery semen resulting in less than 10% fertility and these data were discarded from the experiment.

5.2.2. Statistical Analysis

Body weight, feed intake, fertility, duration of fertility and sperm concentration were submitted to analyses of variance using the MIXED procedure of SAS (Version 9.2. SAS Institute Inc., Cary, NC, 2009). To account for correlated repeated measures, individual males were included in the model as a random effect for BW, feed intake and sperm concentration analyses. Individual males and inseminated females were considered random terms in the fertility and duration of fertility analysis. Pairwise differences between means were

determined with the PDIFF option of the LSMEANS statement. Differences between means were considered significant at $P < 0.05$. Sperm mobility data was not normally distributed according to the Kolmogorov-Smirnov test at a significance level of 0.05. As a result, effect of male treatment on sperm mobility was analyzed as a 1-way non-parametric Kruskal-Wallis test in SAS using the NPAR1WAY procedure.

5.3.RESULTS AND DISCUSSION

5.3.1. Male Body Weight and Feed Intake

Following our experimental design, roosters from HIGH treatment were heavier than rooster from CONTROL treatment, which were heavier than roosters from LOW treatment (Table 5.1, Figure 5-1.). Overall, roosters from the HIGH BW treatment consumed more feed (137.4 g/d, 384.7 kcal/day) on average than males from CONTROL (117.6 g/bird/d, 329.3 kcal/day) or LOW (109.4 g/d, 306.3 kcal/day) treatments (Table 5.1).

5.3.2. Fertility and Duration of Fertility

Fertility results found in Leghorns hens are relevant for broiler breeders, because according to Kirby et al. (1998), duration of fertility and fertility for 21 d after insemination did not differ between Leghorn hens and most broiler breeder lines.

Effects of treatments on fertility were age-dependent. Fertility of males at 210 d of age was similar in all treatments (Table 5-2). Male treatment did not influence fertility up to 257 d, however at 284 d fertility was significantly higher in males

from the CONTROL treatment (73%) than males from LOW BW treatment (63.7%; Table 5-2).

Cerolini et al. (1995) found that increasing the daily quantity of feed increased overall fertility. They fed Ross broiler breeder males 110, 120, or 130 g/d, or ad libitum (corresponding to 120.10, 128.22, 136.02, and 184.15 kcal/kg$^{0.75}$, respectively) and observed fertility every 28 d from 182 to 378 d of age. They found that roosters fed 130 g/d or ad libitum achieved 79% average fertility compared with males fed 110 g/d that had 59% fertility average. In the present study, average fertility was highest (70%) in the CONTROL treatment but no differences were observed statistically.

Duration of fertility was not influenced by the treatment but it was influenced by age. In younger roosters (210 d of age) duration of fertility was 18.4 d. However, the duration of fertility decreased to 16, 15.5, and 15.8 d for older males (230, 257 and 284 d of age, respectively).

5.3.3. Sperm Concentration and Mobility

Sperm concentration and mobility were not affected by rooster BW treatment or the interaction of age and treatment. This result is in contrast with Cerolini et al. (1995) who evaluated the effect of different feed intake for broiler breeder males on semen quality and concluded that increasing the daily quantity of feed from 110 to 130 g/d increased the mobility and percentage live spermatozoa in the semen. The discrepancy may be due to the difference in the way the experiment was conducted (feeding a fixed amount of feed vs. feeding to a specific BW),

male genetics or the way sperm concentration and mobility were measured. Cerolini measured sperm concentration with spectrophotometry and sperm mobility had a subjective evaluation (Cerolini et al., 1995); whereas in the current research sperm concentration and mobility were measured with an objective analysis using an instrument specialized to analyze semen quality in poultry species, the 596a Chicken Mobility Analyzer.

5.3.4. *Conclusions*

Sperm concentration and mobility were not affected by male age or BW profile. Treatment effects on male fertility were age-dependent. Males that were in the CONTROL BW treatment had better fertility at 284 d of age than feed restricted males (LOW treatment). It suggests that broiler breeder males in the target or high BW have better fertility, and an increase in feed intake in males used for artificial insemination did not negatively affect fertility. This implies that when artificial insemination is used, any anatomical or behavioral problems due to heavy BW of males in the flock do not occur because of the absence of a natural mating process and, as a consequence, heavier males can still obtain good fertility levels while lighter males have decreased fertility due to physiological problems.

5.4. FIGURES AND TABLES

Table 5-1. Feed intake and male BW according to treatment[1]

Treatment	Feed intake (g/d)	BW (kg)
LOW	109.4[b]	3.95[c]
CONTROL	117.6[b]	4.10[b]
HIGH	137.4[a]	4.44[a]
SEM	4.9	19.7
Probability	0.001	<0.0001

[a-g] Means within column with no common superscript differ significantly ($P < 0.05$).
[1]LOW = BW target - 5%; CONTROL = BW target; HIGH = BW target + 10%.

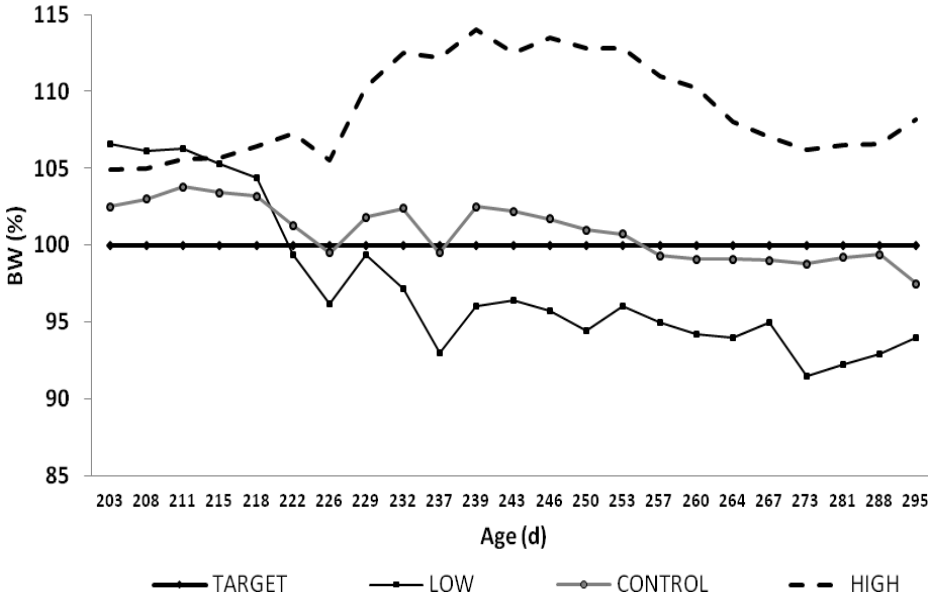
Table 5-2. Effect of age and BW profile of males[1] on fertility and duration of fertility

	Treatment		
Age (d)	LOW	CONTROL	HIGH
	Fertility (%)		
210	74.5^{abc}	71.9^{acde}	75.4^{ab}
230	62.2^{fg}	68.0^{abcdefg}	62.4^{g}
257	63.2^{fg}	67.0^{bfg}	64.6^{defg}
284	63.7^{efg}	72.9^{acd}	68.9^{cdef}
SEM	3.03	3.08	2.95
	Duration of fertility (d)		
210	18.8	18.1	18.4
230	15.9	16.4	15.6
257	15.2	15.9	15.3
284	15.1	16.5	16.1
SEM	0.48	0.49	0.46

Sources of variation	Probability	
	Fertility	Duration of fertility
Treatment	0.54	0.62
Age	<0.001	<0.001
Treatment * Age	0.01	0.13

[a-g] Means within dependent variable with no common superscript differ significantly ($P < 0.05$).
[1]LOW = BW target - 5%; CONTROL = BW target; HIGH = BW target + 10%.

Figure 5-1. Male BW treatments[1] relative to Aviagen BW target



[1]LOW = BW target - 5%; CONTROL = BW target; HIGH = BW target + 10%.

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CHAPTER 6: General Discussion and Conclusions

Normal embryonic development depends on maternal nutrition because all nutrients available to the embryo have to be deposited in the egg by the hen. Several studies have shown that maternal diet influences broiler performance (Spratt and Leeson, 1987; Peebles et al., 2002; Rao et al., 2009) including changes to gene expression (Rao et al., 2009). Studies evaluating the effects of maternal rearing diets on offspring were done decades ago (Proudfoot and Hulan, 1986; Spratt and Leeson, 1987) and since then considerable changes have been made to the genetics of birds which might have changed the way they react to maternal diets. It is not known how modern broilers respond to maternal dietary energy and protein manipulation.

To evaluate the effects of maternal dietary manipulation on offspring we fed pullets diets containing high ME or low ME combined with either high CP or low CP. During lay the same birds were reallocated to a different diet and fed either a high ME or low ME diet. Eggs were collected from hens at two different ages and effects of maternal diet on offspring were evaluated.

It was hypothesized that maternal diet manipulation would impact offspring performance. More specifically, that diets resulting in higher feed intake (such as low energy diets) and less deposition of breast muscles (such as diets with lower protein intake) by the hen would result in heavier offspring due to higher maternal intake of vitamins and minerals, and reduced maintenance needs in the hen. It was also hypothesized that rearing diets would have more effect on progeny of

younger hens due to the higher temporal proximity between the rearing diet and early lay.

The results showed that broiler breeder hen diet can significantly influence the performance of the offspring. Hens with high protein intake during rearing had higher broiler progeny yield as long as maternal protein intake/$BW^{0.75}$ did not decrease when diets changed for the laying phase. Breeder age and sex of the offspring affected how the broilers reacted to the maternal diet. Maternal diet only influenced BW of female progeny of young hens, however in mature hens BW of male and female offspring were differently influenced by maternal diet. Due to the complexity of the results, more details about the interaction between maternal effects and sex of the progeny are presented on Chapters 3 and 4. Previous papers have shown that broiler sex (Spratt and Leeson, 1987; Lopez and Leeson, 1994a; Lopez and Lesson, 1995) and broiler breeder age (Lopez and Leeson, 1995; Barreto et al., 1999) can change how offspring is influenced by maternal diet.

It was expected more influence of the rearing diet on the offspring from younger hens than from older hens but rearing nutrition also affected the offspring of 35 wk old hens. This suggests that pullet nutrition exerts a long term influence on offspring performance. The mechanism of how rearing diets influenced offspring is still unknown. Maternal rearing diet may change hen metabolism and act as an environmental factor able to influence the epigenomic programming during embryo development of offspring.

Because macronutrients deposited in the egg do not change with the breeder`s diet (Lopez and Leeson, 1994a), maternal influence on the offspring can be an

epigenetic effect. The most common epigenetic mechanism is DNA methylation. Maternal diets with increased intake of methyl donors (methionine, folate, vitamin B-12, choline, and betaine) can increase the occurrence of DNA methylation (Choi and Friso, 2010), and as consequence offspring performance could be affected through changes in gene expression. In the current research, changes induced by maternal diet observed in the offspring yield or fat pad mass could have an epigenetic origin. In that case, epigenetic mechanisms such as methylation could have been induced and affected genes involved in biological processes such myogenesis and adipogenesis impacting gene expression of the broilers and consequently their BW and yield. However, we did not analyze DNA methylation or gene expression in the current research, therefore further investigation is needed.

Epigenetic studies are new in bird species and only very few papers relating maternal diet and offspring growth are found in the literature. The pathways through which maternal nutrition influences the offspring and the genes affected in the developing avian embryo are still being studied (Rao et al., 2009). It has been reported that leptin (Rao et al., 2009) and thyroid hormones (Wilson and McNabb, 1997) can influence offspring development in proportion to the amount of these hormones that are transferred to the yolk. It is still not known how changes in yolk hormones influences progeny performance, but it is known that changes in hormones in the egg can influence endocrine system (Lamosová et al., 2003) and gene expression (Rao et al., 2009) in the embryo, which could change embryonic metabolism and development with long term effects. As an example,

it was observed that a decrease in yolk leptin associated to a decrease in protein intake in Langshan breeder hens resulted in an up-regulated expression of IGF-I and an increased offspring BW and breast weight at 4 wk of age (Rao et al, 2009). Previous studies did not find any significant effect of maternal diet on broiler BW or yield (Wilson and Harms, 1984; Proudfoot and Hulan, 1986; De Brum et al., 1996). Effects of maternal diets on offspring are hard to compare between experiments because they are often subtle and can be influenced by genotype, hen age, offspring age, offspring sex and treatments used (Figure 6-1, Figure 6-2, Figure 6-3). Using a random regression to analyze the data from several studies (Aitken et al., 1969; Wilson and Harms, 1984; Proudfoot and Hulan, 1986; Lopez and Leeson, 1994b; Rao et al., 2009; CHAPTER 3; CHAPTER 4), we found little evidence of any general maternal effects on progeny BW or yield. Although offspring BW slightly increased, and progeny breast yield slightly decreased with increase in maternal E:P ratio, these effects were not statistically significant.

The effect of maternal nutrition on offspring performance is a complex phenomenon. Research into this area may be of economic benefit to the poultry industry globally. In the current research, overall maternal diets with higher intakes of protein resulted in increased offspring weight and yield, but a reduction in protein intake ($g/BW^{0.75}$) when diets changed for the laying period was detrimental for the offspring. It was also observed that a decrease in E:P ratio from rearing to lay was detrimental to offspring performance. It seems that the transition from pullet to sexually mature hen is a critical period for the hen metabolism and a mistake in management during the transition (such as decrease

in protein or feed intake/$BW^{0.75}$) can have long term effects in the progeny. Therefore, careful attention should be paid to maternal diet during rearing and its transition to the laying phase by producers as it can influence broiler performance bringing huge financial benefits to the poultry industry.

A brief economic analysis done with data of the current research suggests that the 1.1% absolute increase in breast yield in broilers from mothers fed high energy diets during rearing and lay (CHAPTER 3) translates to an increase of over 1,000,000 kg of breast meat per year in Alberta when compared to the offspring of hens fed low energy during lay resulting in an increase of over $9,000,000 in profit. The current work contributes to the broiler breeder and broiler industries by re-examining nutrition for the hen to provide modern broiler chicks an optimal start to support ever-increasing growth and performance potentials.

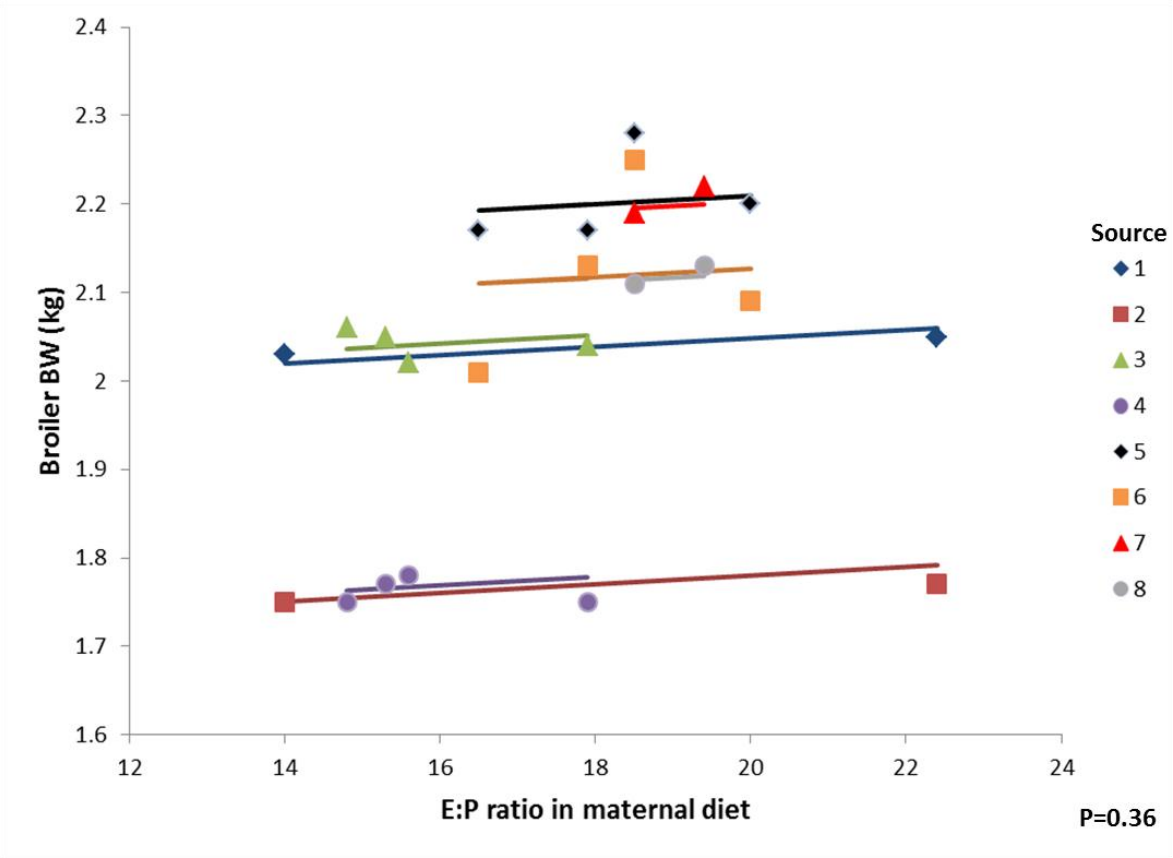
There are still a lot of questions to be answered. To try to get a better understanding of maternal diet influence on the offspring, further studies could be done using the same dietary energy and protein levels during both rearing and laying phases in order to reduce the number of influencing factors. Age and strain of broiler breeder used in the research can also act as confounding factors, making results harder to interpret and inconsistent from one study to the other.

The physiological mechanism responsible for the influence of maternal nutrition on broiler performance is still unknown. It would be interesting to analyze yolk hormones and gene expression in the offspring to try to confirm an epigenetic effect caused by maternal nutrition at each hen age.

It is also unclear how much difference in protein or energy levels from the commercial standard will have an influence on the progeny performance. In the current research, for example, laying diets only influenced offspring performance when in interaction with the rearing diet, and it is unknown if this occurred because the different treatments of energy during lay only differ in 100 kcal. Further research can be done using greater ranges of CP and ME to get a broader understanding of maternal nutrition effects on progeny performance. The challenge is to find the appropriate amount of nutrients that should be fed to broiler breeder birds bringing benefits to both broiler sexes and for most of the productive maternal ages.

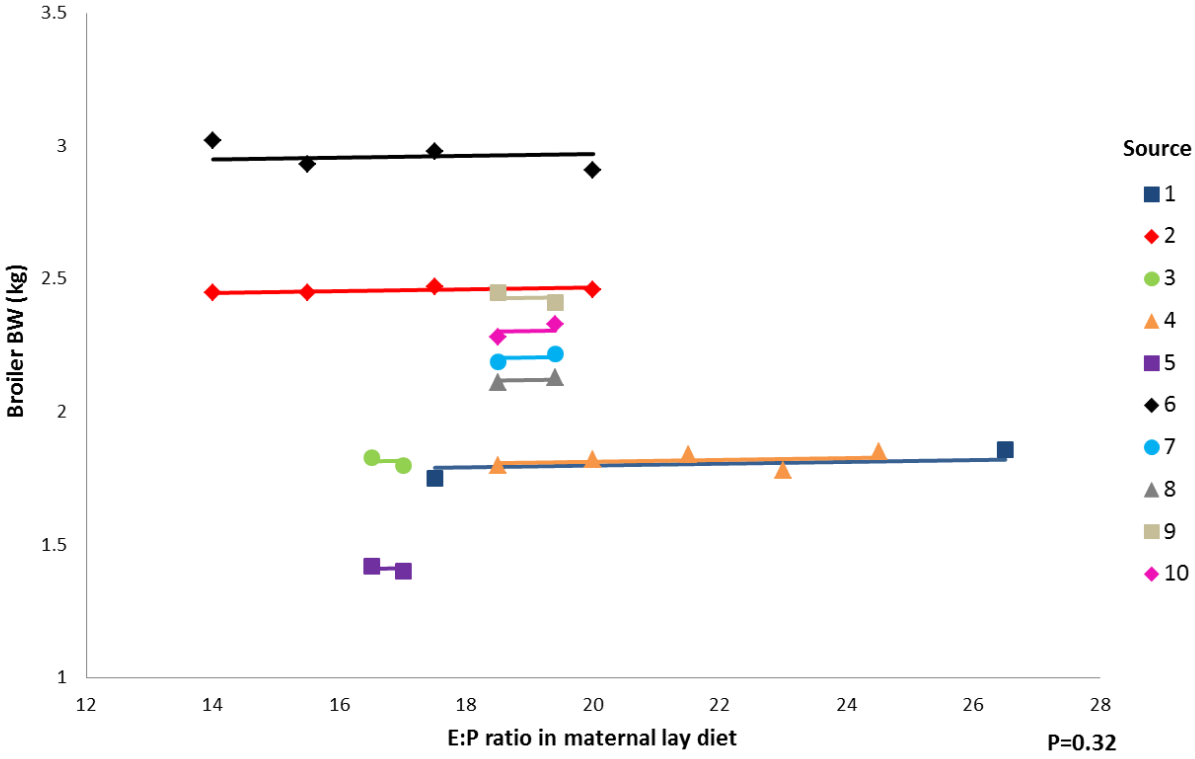
6.1. FIGURES AND TABLES

Figures 6-1. Random regression[1] of broiler BW and maternal dietary E:P[2] from 2 different experiments[3] during rearing or lay



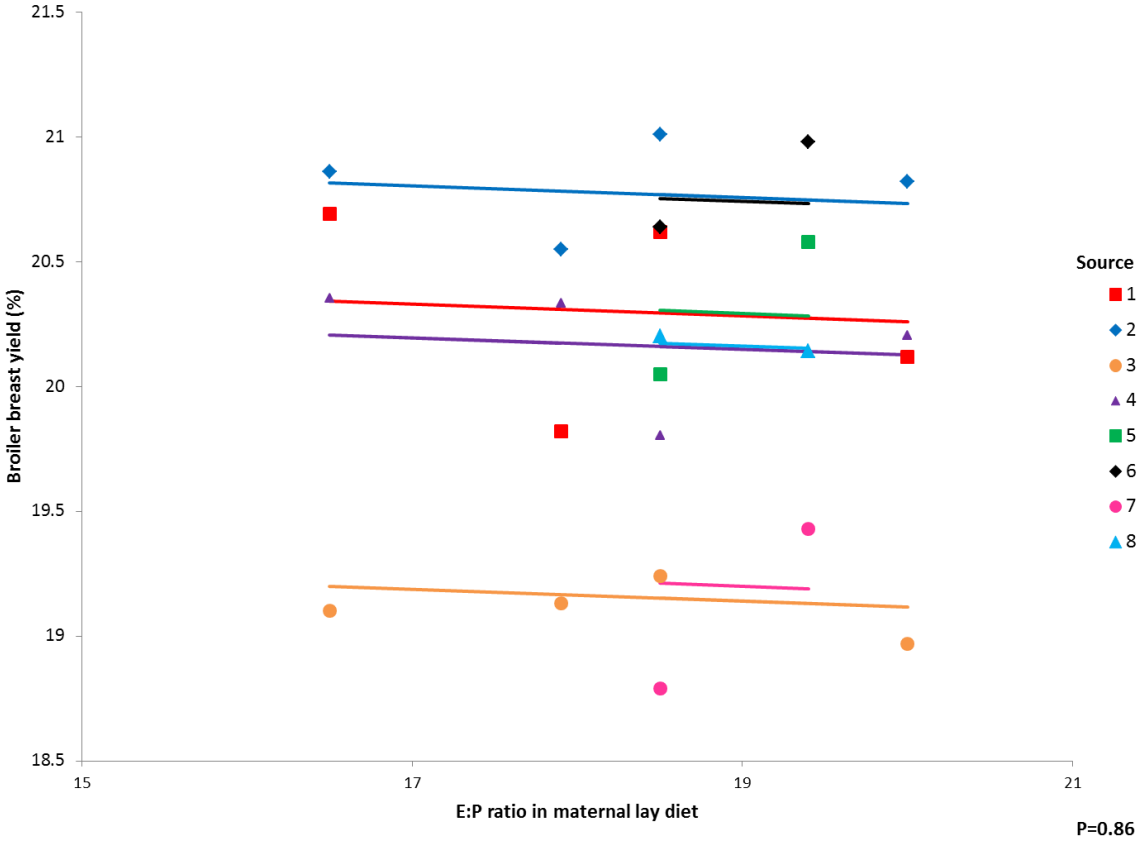
[1]This figure shows results of a random regression done using the mixed procedure of SAS. The slope of the regression line is 0.024kg/E:P (P=0.36).
[2]E:P = energy to protein ratio.
[3]Values obtained from the current research with Ross broiler (2012) and Proudfoot and Hulan (1987). Potentially confounding variables that could influence BW (broiler age and sex, maternal and age and year) were categorized as source and considered random effects in the model.
Sources:
1= Males from 3 strains at 42 d (1987): maternal rear diet
2= Females from 3 strains at 42 d (1987): maternal rear diet
3= Males from 3 strains at 42 d (1987): maternal lay diet
4= Females from 3 strains at 42 d (1987): maternal lay diet
5= Male Ross at 40d: maternal rear diet, young hens
6= Female Ross at 40d: maternal rear diet, young hens
7= Male Ross at 40d: maternal lay diet, young hens
8= Female Ross at 40d: maternal lay diet, young hens

Figure 6-2. Random regression[1] of broiler BW and maternal E:P[2] during lay from 5 different experiments[3]



[1]This figure shows results of a random regression done using mixed procedure of SAS. The slope of the regression line is 0.035kg/E:P (P=0.32).
[2]E:P = energy to protein ratio.
[3]Values obtained from the current research with Ross broiler (2012), Aitken et al. (1969), Wilson and Harms (1984), Lopez and Leeson (1994b), Rao et al. (2009). Potentially confounding variables that could influence BW (broiler age and sex, maternal and age and year) were categorized as source and considered random effects in the model.
Sources:
1= Langshan breed at 28 d
2= Females Arbor Acres (1994) at 49 d
3= Males from 9 meat genotypes (1969) at 63 d
4= Cobb (1984) at 49 d
5= Females from 9 meat genotypes (1969) at 63 d
6= = Males Arbor Acres (1994) at 49 d
7= Male Ross at 40d: young hens
8= Female Ross at 40d: young hens
9= Male Ross at 40d: mature hens
10= Female Ross at 40d: mature hens

Figure 6-3. Random regression[1] of broiler breast yield (%) and maternal dietary E:P[2] from the current research[3] during rearing and lay



[1]This figure shows results of a random regression done using mixed procedure of SAS. The slope of the regression line is -0.022%/E:P (P=0.86).
[2]E:P = energy to protein ratio.
[3]Values obtained from the current research with Ross broilers (2012). Potentially confounding variables that could influence broiler yield (broiler age and sex, maternal and age and year) were categorized as source and considered random effects in the model.
Sources:
1= Male Ross: maternal rear diet, young hens
2= Female Ross: maternal rear diet, young hens
3= Male Ross: maternal rear diet, mature hens
4= Female Ross: maternal rear diet, mature hens
5= Male Ross: maternal lay diet, young hens
6= Female Ross: maternal lay diet, young hens
7= Male Ross: maternal lay diet, mature hens
8= Female Ross: maternal lay diet, mature hens

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APPENDIX

Appendix 1. E:P ratio[1] and protein, energy and feed intake of broiler breeders based on their metabolic BW ($BW^{0.75}$)

Diet[2]	E:P ratio	Protein intake	Energy intake	Feed intake
		$g/BW^{0.75}$	$kcal/BW^{0.75}$	$g/BW^{0.75}$
HE_{REAR}	19	7.47	141.30	51.64
LE_{REAR}	17.5	8.09	141.18	55.83
HP_{REAR}	17.2	8.10	139.10	52.93
LP_{REAR}	19.2	7.47	143.37	54.53
HE_{REAR} x HP_{REAR}	17.9	7.70	137.71	50.33
HE_{REAR} x LP_{REAR}	20	7.25	144.89	52.95
LE_{REAR} x HP_{REAR}	16.5	8.50	140.48	55.56
LE_{REAR} x LP_{REAR}	18.5	7.69	141.87	56.11
HE_{LAY}	19.4	8.06	155.89	53.76
LE_{LAY}	18.5	8.58	159.11	56.83

[1]E:P ratio = energy to protein ratio

[2]HE_{REAR} = high dietary energy during rearing (2,736 kcal/kg); LE_{REAR} = low dietary energy during rearing (2,528 kcal/kg); HP_{REAR} = high dietary protein during rearing (15.3% CP); LP_{REAR} = low dietary protein during rearing (13.7% CP); HE_{LAY} = high dietary energy during lay (2,900 kcal/kg); LE_{LAY} = low dietary energy during lay (2,800 kcal/kg).