Energy and protein dilution in broiler breeder pullet diets reduced offspring body weight and yield

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ABSTRACT

The objective of the current research was to evaluate transgenerational effects of maternal dietary energy and protein on growth, efficiency, and yield of broiler offspring. A factorial arrangement of treatments consisting of high and low ME and CP levels fed during the rearing and laying phases was used. The study was a final $2 \times 2 \times 2 \times 2$ factorial arrangement of treatments, including broiler sex. Ross 708 broiler breeder pullets ($n = 933$) were fed diets containing 2,736 (HEREAR) or 2,528 kcal/kg ME (LEREAR) with either 15.3% (HPREAR) or 13.7% CP (LPREAR). From 25 wk, dams were fed a 15% CP laying diet containing 2,900 (HELAY) or 2,800 kcal/kg ME (LELAY). Following artificial insemination of the dams at 35 wk, eggs were collected for 1 wk, incubated, and pedigree hatched to preserve maternal identity. Broiler offspring were placed sex-separately into 32 pens, according to laying phase maternal treatments, with rearing maternal treatments nested within pens. Individual BW and pen level feed intake were recorded weekly. Broilers were processed at 40 d of age to evaluate yield. Maternal diet effects on offspring BW were sex dependent and transient. Female LPREAR × LELAY broilers had lower pectoralis major and carcass yield than HPREAR × LELAY females. Male HPREAR × HELAY broilers had increased breast yield (19.8%) compared with 18.4% in HPREAR × LELAY broilers. Carcass yield was lower in LEREAR × HPREAR broilers (63.7%) compared with HELAY × HPREAR broilers (64.9%). LEREAR × HPREAR dams had the lowest ME to CP ratio (E: P) diets and highest rearing phase CP intake. Maternal diet did not influence offspring FCR. The most consistent contributor to increased BW was higher maternal dietary CP and ME during rearing. Low ME maternal laying phase diets increased BW of male offspring more consistently than of female offspring. Maternal nutrition also influenced broiler yield, and is thus economically important. Energy and protein dilution in broiler breeder pullet diets may have detrimental effects on offspring performance.

Key words: intergenerational effects, nutrition, progeny, caloric restriction, epigenetics

INTRODUCTION

Awareness about the importance of maternal diet on offspring health is increasing. Maternal nutrition is being studied in livestock species as a way of improving offspring growth and production (Rehfeldt et al., 2011; Long et al., 2012; van Emous et al., 2015b). The poultry industry is constantly working to increase carcass yield and obtain a fast growing broiler, and manipulation of maternal diet can be one way of increasing broiler performance (Calini and Sirri, 2007).

Peebles et al. (2002) fed broiler breeder hens diets with different ME 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 compared to BW of offspring of hens fed a high-energy diet. Spratt and Leeson (1987) reported that higher energy in the diet of broiler breeder hens increased BW in male but not in female broilers. Proudfoot and Hulan (1986) fed different combinations of CP and ME treatments to broiler breeders during rearing (12.9% CP, 2,902 kcal/kg; or 15.8% CP, 2,699 kcal/kg) and laying phases (15.3% CP, 2,746 kcal/kg; 17.6% CP, 2,746 kcal/kg; and 17.8% CP, 2,651 kcal/kg), but found no maternal dietary effects on offspring BW and FCR at processing. More recently, van Emous et al. (2015b) found no effect on broiler offspring BW and FCR when broiler breeders were fed different levels of protein during rearing.

There are few recent papers evaluating the effects of modern broiler breeder dietary energy and protein...
on offspring performance. It is possible that the increasing relative degree of feed restriction in modern broiler breeders might influence mechanisms governing offspring performance. 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 offspring growth, carcass yield, and FCR.

**MATERIALS AND METHODS**

**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 studied using a $2 \times 2 \times 2 \times 2$ factorial arrangement of treatments with 2 maternal dietary ME levels during rearing (HE$\text{REAR}$: 2,736 kcal/kg and LE$\text{REAR}$: 2,528 kcal/kg); 2 maternal dietary CP levels during rearing (HP$\text{REAR}$: 15.3% and LP$\text{REAR}$: 13.7%); 2 maternal dietary ME levels during lay (HE$\text{LAY}$: 2,900 kcal/kg and LE$\text{LAY}$: 2,800 kcal/kg), both with 15% CP and 2 broiler sexes.

**Maternal Stocks and Management**

A detailed description of the maternal broiler breeder treatments and management was reported by Moraes et al. (2014). Briefly, broiler breeder hens were artificially inseminated at 35 wk of age with 0.5 mL of pooled fresh undiluted semen. Eggs ($n = 1,250$) were collected individually, identified by hen and date laid, and incubated during the following week. All eggs were weighed individually before being isolated from the others in individual cells in the hatcher tray, thus retaining maternal treatment information of each chick upon hatching.

**Broiler Stocks and Management**

Standard broiler management procedures were used, and were the same as those reported previously (Moraes et al., 2014). Broiler chicks ($n = 933$) were individually identified and placed, 25 to 32 per pen, depending on the numbers hatched in each treatment, into 32 pens. Broiler starter diet (0 to 14 D) contained 23% CP and 3,067 kcal/kg ME; the grower diet (15 to 28 D) contained 20% CP and 3,152 kcal/kg ME; the finisher I diet (29 to 39 D) contained 19% CP and 3,196 kcal/kg ME; and the finisher II diet (40 to 54 D) contained 17.7% CP and 3,262 kcal/kg ME. Broilers were weighed weekly (Weltech BW-1050, Weltech International Ltd; St Ives, Cambridgeshire, UK), and pen level feed intake was recorded weekly by weighting back unused feed. Mortality was 4.3% overall, and did not differ between treatments. A total of 201 birds were processed at 40 D. Carcass, breast muscle, legs and wings weight were reported as percentage of live BW. Carcass weight did not include viscera, neck, feet, or abdominal fat pad.

**Statistical Analysis**

BW and dissection data were analyzed as a 4-way ANOVA using the MIXED procedure of SAS (Version 9.2. SAS Institute Inc., Cary, NC) with rearing dietary ME, rearing dietary CP, laying dietary ME, and broiler sex as main effects. Hen nested in pen was included as a random effect in the statistical model. FCR 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 to evaluate relationships among breeder BW and intake and broiler variables. Pairwise differences between means were reported, within sex, where $P \leq 0.05$.

**RESULTS AND DISCUSSION**

**Body Weight**

Significance of all effects and interactions on offspring BW was reported systematically in Table 1. There was a correlation between maternal 35 wk BW and broiler 39 d BW ($r = 0.10; P = 0.03$). At 8 and 15 d of age, female broilers had greater BW than males; however, by 39 d of age, males were 127 g heavier than females (Table 2). At hatch, male LE$\text{REAR} \times \text{HP$\text{REAR}$}$ chicks had greater BW compared with HP$\text{REAR} \times \text{HP$\text{REAR}$}$ chicks (Table 2). At 15 d of age, female HE$\text{REAR} \times \text{HP$\text{REAR}$}$ broilers were heavier than female LE$\text{REAR} \times \text{HP$\text{REAR}$}$ broilers, whereas male LE$\text{REAR} \times \text{HP$\text{REAR}$}$ broilers were heavier than male LE$\text{REAR} \times \text{LP$\text{REAR}$}$ broilers (Table 2). The first column (HP$\text{REAR} \times \text{HE$\text{REAR}$}$) and the last row (LE$\text{LAY}$) in the heat map in Table 3 show the most consistent positive effects of maternal nutritional treatments on overall broiler BW. The most consistent contributor to increased BW was the highest combination of both maternal dietary CP and ME during rearing. Hens on the LE$\text{REAR} \times \text{HP$\text{REAR}$}$ maternal diet had the highest daily maternal protein intake (8.5 g protein/kg BW$^{0.75}$). As a consequence, upon switching to laying phase diets, any increase in the protein intake for this rearing treatment would have been minimal. During lay, higher protein intake, which occurs as a result of lower maternal dietary ME level, may provide some advantage in terms of greater offspring BW, as relative BW was 1% higher across the LE$\text{LAY}$ treatment, compared with the HE$\text{LAY}$ treatment (100.5 vs. 99.5, respectively; Table 3). The data suggest that a low maternal dietary protein signal at the time of transition to the laying
Table 1. Significance of the effects of broiler age and sex, and maternal dietary treatments applied during rearing and lay on broiler BW.

| Effect                  | F Value | Prob > F |
|-------------------------|---------|----------|
| Age                     | 27.791  | <0.001   |
| Sex                     | 10.91   | 0.000    |
| ME\_REAR (ER)           | 2.79    | 0.095    |
| CP\_REAR (PR)           | 7.93    | 0.005    |
| ME\_LAY (EL)            | 2.04    | 0.15     |
| Age × sex               | 10.9    | <0.001   |
| Age × ER                | 0.82    | 0.53     |
| Age × PR                | 2.08    | 0.065    |
| Age × EL                | 1.82    | 0.11     |
| Sex × ER                | 1.23    | 0.27     |
| Sex × PR                | 0.39    | 0.53     |
| Sex × EL                | 4.33    | 0.038    |
| ER × PR                 | 2.14    | 0.14     |
| ER × EL                 | 0.02    | 0.88     |
| PR × EL                 | 0.03    | 0.87     |
| Age × sex × ER          | 0.91    | 0.47     |
| Age × sex × PR          | 0.27    | 0.93     |
| Age × sex × EL          | 1.77    | 0.12     |
| Age × ER × PR           | 0.63    | 0.68     |
| Age × ER × EL           | 0.07    | 1.00     |
| Age × PR × EL           | 0.26    | 0.94     |
| Sex × ER × PR           | 5.53    | 0.019    |
| Sex × ER × EL           | 0.55    | 0.46     |
| Sex × PR × EL           | 0.11    | 0.74     |
| Age × sex × ER × PR     | 3.14    | 0.008    |
| Age × sex × PR × EL     | 0.66    | 0.65     |
| Age × sex × ER × EL     | 0.43    | 0.82     |
| Age × ER × PR × EL      | 0.51    | 0.77     |
| Sex × ER × PR × EL      | 4.58    | 0.032    |
| ER × PR × EL            | 1.43    | 0.23     |
| Age × sex × ER × PR × EL| 1.28    | 0.27     |

ME\_REAR = maternal dietary ME treatment during rearing; CP\_REAR = maternal dietary CP treatment during rearing; ME\_LAY = maternal dietary ME treatment during lay.

Table 2. Effects of sex and maternal dietary ME and CP and broiler sex on broiler BW.

| Sex       | ME\_LAY kcal/g | ME\_REAR kcal/g | CP\_REAR kcal/g | E:P | Age (D) | BW (g) |
|-----------|----------------|-----------------|-----------------|-----|---------|--------|
|           | 0  | 8  | 15 | 22 | 29 | 39 |
| Female    |    |    |    |    |    |     |
| Male      |    |    |    |    |    |     |
| HH\_LAY   | 19.4 | 42.1 | 184 | 458 | 829 | 1.356 | 2.375 |
| LE\_LAY   | 18.5 | 41.9 | 184 | 466 | 844 | 1.386 | 2.370 |
| HH\_REAR  | 19.0 | 41.8 | 185 | 465 | 841 | 1.377 | 2.388 |
| LE\_REAR  | 17.5 | 42.1 | 185 | 469 | 852 | 1.365 | 2.358 |
| HP\_REAR  | 17.2 | 42.0 | 185 | 467 | 847 | 1.383 | 2.394 |
| LP\_REAR  | 19.2 | 41.9 | 183 | 459 | 826 | 1.360 | 2.352 |
| SEM       | 0.15 | 1.3 | 3.6 | 14.2 | 9.0 | 16.6 |

Sex × ME\_REAR × CP\_REAR × age interaction female
| Sex       | ME\_REAR kcal/g | ME\_REAR kcal/g | CP\_REAR kcal/g | E:P | Age (D) | BW (g) |
|-----------|-----------------|-----------------|-----------------|-----|---------|--------|
|           | 0  | 8  | 15 | 22 | 29 | 39 |
| Female    |    |    |    |    |    |     |
| Male      |    |    |    |    |    |     |
| HH\_REAR  | 17.9 | 42.2 | 193a | 485a | 865 | 1.402b | 2.375 |
| LP\_REAR  | 20.7 | 41.7 | 187b | 463b | 823 | 1.356b | 2.287 |
| HH\_REAR  | 16.5 | 42.1 | 185b | 459b | 828 | 1.339b | 2.286 |
| LP\_REAR  | 18.5 | 41.9b | 185b | 457b | 824 | 1.364b | 2.289 |
| SEM       | 0.30 | 2.6 | 7.2 | 28.3 | 17.9 | 33.3 |

a,bMeans within effect, age, and sex with no common superscript differ significantly (P < 0.05).

ME\_REAR = maternal dietary ME treatment during rearing; CP\_REAR = maternal dietary CP treatment during rearing; ME\_LAY = maternal dietary ME treatment during lay; HH\_REAR = high maternal dietary ME (2,736 kcal/kg) during rearing; LP\_REAR = low maternal dietary ME (2,528 kcal/kg) during rearing; HP\_REAR = high maternal dietary CP (15.3%) during rearing; LP\_REAR = low maternal dietary CP (13.7% CP) during rearing; HH\_LAY = high maternal dietary ME (2,900 kcal/kg) during lay; LP\_LAY = low maternal dietary ME (2,800 kcal/kg) during lay.

1E:P = dietary ME:CP ratio.

At the end of lay, LP\_REAR × HP\_REAR hens had lower liver weights compared with HH\_REAR × HP\_REAR hens (59.4 vs. 67.1 ± 2.3 g, respectively; P < 0.05). In rats, Muaku et al. (1995) observed that lower liver weight in protein-restricted mothers can result in reduced offspring BW. Proudfoot and Hulan (1986) did not find a maternal dietary nutrient effect (during rearing) on offspring performance; however, broiler genetics have changed a lot in the 30 yr between that time and the current study (Zuidhof et al., 2014). The current result is similar to the findings of Zhu et al. (2012), who observed that maternal diets had a transient effect on BW until 21 d of age, and disappeared by processing age in Chinese Yellow broilers. Although in the current study BW effects did not remain significant to processing age, the interaction effect of all of the maternal treatments was significant overall BW (Tables 1 and 3). Koppenol et al. (2015) reported that subtle maternal effects may not prevail through the entire broiler growout because numerous environmental and nutritional factors could overshadow maternal effects. Between the time that the hen consumes her feed and the broiler offspring are processed, many factors such as egg storage, incubation diet may reduce female offspring growth rates. Little is known about the underlying mechanisms driving incorporation of protein into tissues, and it is interesting that there are sex-specific broiler responses to broiler dietary protein levels (Eits et al., 2003). We hypothesize that the mechanisms that dictate that male broilers are more responsive to dietary amino acids may somehow also be related to this observation.
and hatching conditions, transportation, rearing conditions, feed quality, and pathogen exposure may additively or synergistically mask the effect of maternal nutrition on the broiler. In contrast with the current study, van Emous et al. (2015b) reported no effect of maternal dietary protein during rearing on offspring BW and BW gain. The current result is partially consistent with results from an earlier flock of offspring from the same maternal experiment, where female HPREAR \( \times \) LPREAR offspring had lower BW from 22 to 36 d compared with offspring from hens that consumed more CP as pullets (Moraes et al., 2014). The results from the current study confirm that maternal nutrition during the maternal pullet stage can impose a lasting influence on offspring BW and overall carcass yield compared with male broilers (Table 5). Broilers from the HPREAR \( \times \) HPREAR treatment had the highest overall carcass yield (Table 6). This was the same maternal treatment that had the most consistent increases in offspring BW (Table 3).

**Female LPREAR \( \times \) ELREAR broilers had lower pectoralis major and carcass yield than female broilers from hens fed HPREAR \( \times \) ELREAR. In female broilers, the maternal HPREAR diet increased pectoralis major yield, but only when hens were fed the LPREAR diet. In males, the opposite was true; an increase in pectoralis major yield was seen in the maternal LPREAR diet, but only when their mothers were fed the HPREAR diet (Table 5). The HPREAR had a lower energy to protein (E: P) ratio (17.2 kcal/g), compared with 19.2 kcal/g in the LPREAR treatment. A decrease in E: P ratio for LPREAR \( \times \) ELREAR upon switching from rearing to laying phase diets (ELREAR = 18.5 kcal/g) may play some role in the observed decrease in offspring breast yield, possibly related to overfeeding of protein during the laying phase. van Emous et al. (2015b) reported no effect of maternal pullet phase dietary CP on female offspring breast yield; however, a low maternal CP diet (12.5% CP) increased breast yield in males compared with a high maternal CP diet during rearing (14.1% CP). Henry and Burke (1998) described sexual dimorphism in muscle development in broiler embryos such that male broilers usually develop greater myofiber numbers (more myofibers per 30,000 \( \mu \text{m}^2 \)), while female broilers develop larger myofibers. Furthermore, myofiber number and size can be differently influenced by protein levels in maternal diet (Rehfeldt et al., 2012). Changes in E: P ratios require a metabolic adjustment by the animal (Wagle et al., 1962), which we hypothesize may

**Table 4.** Significance of the effects of sex and maternal dietary treatments on broiler carcass parts yield (% of live BW).

| Source | Pectoralis major | Pectoralis minor | Breast | Legs | Wings | Carcass |
|--------|------------------|------------------|--------|------|-------|--------|
| Sex    | 0.002            | < 0.001          | < 0.001| < 0.001| 0.81  | 0.005  |
| MEREAR (ER) | 0.93            | 0.46             | 0.96   | 0.17 | 0.21  | 0.089  |
| CPREAR (PR) | 0.45            | 0.43             | 0.64   | 0.13 | 0.046 | 0.95   |
| MEELAY (EL) | 0.29            | 0.23             | 0.24   | 0.48 | 0.52  | 0.56   |
| Sex \( \times \) ER | 0.63            | 0.58             | 0.59   | 0.71 | 0.24  | 0.35   |
| Sex \( \times \) PR | 0.31            | 0.79             | 0.34   | 0.079| 0.051 | 0.13   |
| Sex \( \times \) EL | 0.25            | 0.56             | 0.27   | 0.54 | 0.96  | 0.45   |
| ER \( \times \) PR | 0.88            | 0.39             | 0.78   | 0.33 | 0.55  | 0.036  |
| ER \( \times \) EL | 0.71            | 0.25             | 0.93   | 0.36 | 0.97  | 0.55   |
| PR \( \times \) EL | 0.87            | 0.31             | 0.97   | 0.55 | 0.29  | 0.59   |
| Sex \( \times \) ER \( \times \) PR | 0.37            | 0.75             | 0.47   | 0.24 | 0.86  | 0.44   |
| Sex \( \times \) ER \( \times \) EL | 0.18            | 0.088            | 0.15   | 0.46 | 0.53  | 0.48   |
| Sex \( \times \) PR \( \times \) EL | 0.008           | 0.061            | 0.009  | 0.35 | 0.74  | 0.038  |
| ER \( \times \) PR \( \times \) EL | 0.80            | 0.82             | 0.82   | 0.92 | 0.72  | 0.18   |
| Sex \( \times \) ER \( \times \) PR \( \times \) EL | 0.89            | 0.95             | 0.87   | 0.27 | 0.72  | 0.17   |

MEREAR = maternal dietary ME treatment during rearing; CPREAR = maternal dietary CP treatment during rearing; MEELAY = maternal dietary ME treatment during lay.

**Carcass Yield**

Significance of all treatment effects and interactions on offspring yield was reported systematically in Table 4. As a percentage of BW, female broilers had higher pectoralis major, pectoralis minor, total breast, and overall carcass yield compared with male broilers (Table 5). Broilers from the MEREAR \( \times \) HPREAR treatment had the highest overall carcass yield (Table 6). This was the same maternal treatment that had the most consistent increases in offspring BW (Table 3).
Table 5. Effects of sex and maternal dietary treatments on carcass yield.

| Sex     | MELAY | MEREAR | CPREAR | E:PREAR \(^1\) | E:PLAY \(^1\) | Pectoralis major | Pectoralis minor | Breast | Carcass |
|---------|-------|--------|--------|----------------|---------------|------------------|-----------------|--------|--------|
| **Main effects** |       |        |        |                |               |                  |                 |        |        |
| Female  |       |        |        |                |               |                  |                 |        |        |
| HE \(^{\text{ELAY}}\) | 19.0  | 16.5a  | 3.71a  | 20.0a          | 64.7a         |                  |                 |        |        |
| LE \(^{\text{ELAY}}\) | 19.2  | 15.7b  | 3.35b  | 19.8b          | 63.9b         |                  |                 |        |        |
| HEREAR | 17.5  | 16.2   | 3.56   | 19.6           | 64.4          |                  |                 |        |        |
| LEREAR | 19.2  | 16.1   | 3.55   | 19.6           | 64.0          |                  |                 |        |        |
| HPREAR | 17.2  | 16.1   | 3.55   | 19.6           | 64.3          |                  |                 |        |        |
| LPREAR | 19.2  | 16.0   | 3.55   | 19.6           | 64.3          |                  |                 |        |        |
| **SEM** | 0.17  | 0.04   | 0.20   | 0.21           |               |                  |                 |        |        |
| **MEREAR \(\times\) CPREAR interaction** |       |        |        |                |               |                  |                 |        |        |
| HE \(^{\text{PREAR}}\) | 19.4  | 16.2   | 3.50   | 19.7           | 64.4          | a                |                 |        |        |
| LE \(^{\text{PREAR}}\) | 18.5  | 16.2   | 3.51   | 19.5           | 64.2          | a,b              |                 |        |        |
| HEREAR \(^{\text{PREAR}}\) | 18.5  | 16.1   | 3.51   | 19.6           | 64.0          | b                |                 |        |        |
| LEREAR \(^{\text{PREAR}}\) | 19.2  | 16.0   | 3.51   | 19.6           | 64.3          | a,b              |                 |        |        |
| HPREAR \(^{\text{PREAR}}\) | 17.2  | 16.1   | 3.55   | 19.7           | 64.3          | b                |                 |        |        |
| LPREAR \(^{\text{PREAR}}\) | 19.2  | 16.0   | 3.55   | 19.7           | 64.3          | a,b              |                 |        |        |
| **SEM** | 0.25  | 0.06   | 0.29   | 0.30           |               |                  |                 |        |        |
| **Sex \(\times\) MELAY \(\times\) CPREAR interaction** |       |        |        |                |               |                  |                 |        |        |
| Female | HE \(^{\text{ELAY}}\) | 17.2  | 16.2   | 3.50   | 19.7           | 64.9          | a                |                 |        |        |
| LE \(^{\text{ELAY}}\) | 19.4  | 16.0   | 3.60   | 19.6           | 64.2          | b                |                 |        |        |
| HE \(^{\text{REAR}}\) | 17.2  | 16.1   | 3.51   | 19.7           | 63.7          | b                |                 |        |        |
| LE \(^{\text{REAR}}\) | 18.5  | 16.0   | 3.51   | 19.5           | 64.4          | a,b              |                 |        |        |
| **SEM** | 0.25  | 0.09   | 0.29   | 0.30           |               |                  |                 |        |        |

\(^{a,b}\)Means within column, sex, and effect with no common superscript differ significantly \((P < 0.05)\).

\(\text{MEREAR} =\) maternal dietary ME treatment during rearing; \(\text{CPREAR} =\) maternal dietary CP treatment during raring; \(\text{MELAY} =\) maternal dietary ME treatment during lay; \(\text{HEREAR} =\) high maternal dietary ME (2,736 kcal/kg) during rearing; \(\text{LEREAR} =\) low maternal dietary ME (2,528 kcal/kg) during rearing; \(\text{HPREAR} =\) high maternal dietary CP (15.3%) during raring; \(\text{LPREAR} =\) low maternal dietary CP (13.7% CP) during raring; \(\text{HELAY} =\) high maternal dietary ME (2,900 kcal/kg) during lay; \(\text{LELAY} =\) low maternal dietary ME (2,800 kcal/kg) during lay.

\(^1\)E:PREAR = energy to protein ratio for rearing diets (kcal/g); E:PLAY = energy to protein ratio for lay diets (kcal/g).

Table 6. Heat map showing relative effect of maternal rearing dietary treatments on male and female broiler breast and carcass yield.

|                | HPREAR \(\text{PREAR}\) | LPREAR \(\text{PREAR}\) |
|----------------|--------------------------|------------------------|
| **HE \(\text{ELAY}\)** | 100.6 99.4 99.4 99.4 | 100.6 99.4 99.4 99.4 |
| **LE \(\text{ELAY}\)** | 99.2 100.4 99.9 99.4 | 102.0 99.9 99.4 99.4 |
| **HE \(\text{REAR}\)** | 100.4 100.4 99.9 99.4 | 100.4 100.4 99.9 99.4 |
| **LE \(\text{REAR}\)** | 99.9 99.4 99.9 99.4 | 99.9 99.4 99.9 99.4 |
| **Prob > F** | 0.036 |

\(\text{HPREAR} =\) high maternal dietary CP (15.3%) during raring; \(\text{LPREAR} =\) low maternal dietary CP (13.7% CP) during raring; \(\text{HEPREAR} =\) high maternal dietary ME (2,736 kcal/kg) during raring; \(\text{LEPREAR} =\) low maternal dietary ME (2,528 kcal/kg) during raring.

\(^{a,b}\)Means within column with no common superscript differ \((P \leq 0.05)\).

\(^{x,y}\)Means within row with no common superscript differ \((P \leq 0.05)\).

have triggered an epigenetic effect and influenced gene expression relating to growth and breast muscle development in the offspring. However, epigenetic mechanisms were not evaluated in the current study.

Carcass yield was lower (63.8%) in LE \(^{\text{REAR}}\) \(\times\) HPREAR offspring compared with that of HE \(^{\text{REAR}}\) \(\times\) HPREAR broilers (64.9%, Table 5). Hens that received the LE \(^{\text{REAR}}\) \(\times\) HPREAR diet consumed 67.5 g/d of feed, consisting of 10.3 g/d of protein and 170.7 kcal/d. Hens fed the HE \(^{\text{REAR}}\) \(\times\) HPREAR diet consumed 61.4 g/d of feed (9.3 g of protein and 168 kcal).

HPREAR hens receiving the lower ME level had lower liver weights compared to hens on the HE \(^{\text{REAR}}\) \(\times\) HPREAR (data not shown). The liver is responsible for important metabolic functions such as lipogenesis (Taouis et al., 2001), and lipogenesis is positively correlated with E: P ratio (Donaldson, 1985). In a study conducted with rats, protein-restricted dams had a lower liver weight, resulting in lower liver weight and lower concentration of liver IGF-I in the offspring (Muaku et al., 1995). A decrease in IGF-I in the offspring 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 be economically advantageous for the poultry industry. The current study confirms that manipulation of dietary ME and CP in broiler breeders can influence broiler yield. The current study points to a positive effect from higher CP levels in pullet phase diets. This adds complexity to broiler breeder nutrition decisions since there is some consensus around the hypothesis that lower CP diets may help to faten the breeder pullet and better prepare for egg production. For example, van Emous (2015b) fed broiler breeders low or high levels of protein during rearing.
and found that birds fed the low protein diet had lower breast muscle and higher abdominal fat pad at 22 wk. Birds fed low protein during rearing also had higher hatchability and increased egg production when compared to the birds fed high protein at rearing. This is not the first broiler breeder paradox ever identified.

Feed Conversion Ratio

Broiler FCR up to 39 d of age ranged from 1.60 (HE\textsubscript{LAY}) to 1.62 (LE\textsubscript{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 \(\text{Moraes et al., 2014}\). Proudfoot and Hulan \(\text{1986}\) fed different maternal CP and ME levels during rearing \((12.9\%, 2.902 \text{ kcal/kg}; 15.8\%, 2.699 \text{ kcal/kg})\) and laying periods \((15.3\%, 2.746 \text{ kcal/kg}; 17.6\%, 2.746 \text{ kcal/kg}; \text{and} 17.8\%, 2.651 \text{ kcal/kg})\) to 3 strains of broiler breeders and found no effect on offspring FCR. \text{van Emous et al. (2015b)} also found no effect of maternal dietary treatments varying in CP during rearing \((12.5, 13.3, \text{ and} 14.1\%)\) on offspring FCR.

In conclusion, effects of maternal rearing diet on the BW of their broiler offspring were sex dependent and transient, but significant. Broiler breast and carcass yield effects were also sex dependent. High \((15.3\%)\) maternal dietary protein during rearing showed the most consistent overall greatest BW and economically important yields. The low maternal ME level during lay \((2,800 \text{ kcal/kg})\) had consistently higher BW, but may have negative effects on offspring yield, particularly in males. Maternal diet did not influence offspring FCR. Maternal nutrition influenced broiler yield, and thus may be more economically important than previously thought. Confirming previous work \(\text{Moraes et al., 2014}\), there was a significant effect related to pullet phase nutrition. A systematic and careful investigation is needed to complete our understanding of these interacting and time-confounded effects and their underlying mechanisms.

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