Energy partitioning by broiler breeder hens in conventional daily-restricted feeding and precision feeding systems

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ABSTRACT An empirical linear mixed model was derived to describe metabolizable energy (ME) partitioning in broiler breeder hens. Its coefficients described ME used for total heat production (HP), growth (ADG), and egg mass (EM). A total of 480 Ross 308 hens were randomly and equally assigned to 2 treatments: precision feeding (PF) and conventional daily-restricted feeding (CON) from 23 to 34 wk of age. The PF system allowed birds to enter feeding stations voluntarily at any time, weighed them, and provided access to feed for 60 s if their BW was less than the breeder-recommended target BW. The CON birds were fed daily each morning. Energetic efficiency of hens was evaluated using residual feed intake (RFI), defined as the difference between observed and predicted ME intake (MEI). The energy partitioning model predicted ($P < 0.05$): MEI = A $\times$ BW$^{0.67}$ + 1.75 $\times$ ADG + 0.75 $\times$ EM + ε. The coefficient *A*, a vector of age-specific HP, was 142 kcal/kg$^{0.67}$/d; the energy requirement for growth and EM was 1.75 and 0.75 kcal/g, respectively. For the CON and the PF hens, respectively, MEI was 366 and 354 kcal/d ($P = 0.006$); RFI was −5.9 and 6.7 kcal/d ($P = 0.009$); HP% was 85.5 and 87.7 ($P < 0.001$); hen-day egg production (HDEP) was 65.5 and 55.2% ($P < 0.001$). Although the CON hens had higher MEI, the model predicted lower HP%; thus, CON hens had more nutrients available for egg production, increased egg production, and were more energetically efficient than the PF hens. The decreased egg production by the PF hens was likely due to these hens receiving production-related feed increases after an egg was laid. However, feed allocation increases for the CON hens resulted in increasing MEI for all CON hens at the same time. Therefore, the PF hens had lower MEI and lower HDEP than the CON hens.

Key words: caloric restriction, precision livestock farming, maintenance requirements, body composition, meat-type chicken

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INTRODUCTION

Broiler BW at 56 D of age has increased by over 450% due to intensive genetic selection from 1957 to 2005 (Zuidhof et al., 2014), whereas the target BW for broiler breeders has remained almost constant (Renema et al., 2007b). Thus, the gap between the growth potential of broilers and broiler breeder target BW is increasing and as a result, the degree of feed restriction in broiler breeders became more severe and modern broiler breeders have reduced fat deposition (Renema et al., 2007b; Zuidhof, 2018). It was reported that modern broiler breeders had abdominal fat pad weights of only 0.44% of BW at 20 wk of age (van Emous, 2015) compared with 2.8% in 1989 (Bowmaker and Gous, 1989) and 1993 (Fattori et al., 1993). Zuidhof et al. (2014) demonstrated that in 2005, broiler chickens, the offspring of broiler breeders, had less body fat and more body protein compared with broiler chickens in 1957 and 1978. Broiler breeder hens from a line unselected since 2000 and 2.65% of abdominal fat pad delayed onset of sexual maturation 19.2 D compared with hens from a line unselected since 1980 that their abdominal fat pad was 5.38% (Eitan et al., 2014). These results suggest that modern broiler breeders are reducing body fat due to severe feed restriction and this can reduce egg production during the laying period. A relaxation in the severity of feed restriction can increase fat pad deposition and egg production in broiler breeders (Zuidhof, 2018).

de Beer and Coon (2007) reported that daily-restricted broiler breeder hens produced more eggs than skip-a-day-fed hens (fed on alternate days). The reason was probably due to more frequent availability of dietary nutrients in a daily-restricted feeding program, since deposition and mobilization of nutrients are not completely efficient processes (de Beer and Coon, 2007). On the other hand, broiler breeder hens fed on a 5–2

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feeding program (feeding 5 consecutive days and off for 2 consecutive days) had larger eggs than those fed according to a daily-restricted feeding program (de Beer and Coon, 2007). Repeated fasting and refeeding cycles in 5–2 birds caused conversion of dietary carbohydrates to lipid and deposition of lipid in the carcass (de Beer and Coon, 2007). Some of the lipid is mobilized during fasting period to meet the energy requirement and some is stored in the carcass (de Beer and Coon, 2007). There is probably an increase in hepatic lipogenesis and the deposition of more carcass fat which may result in larger eggs in feeding programs that include off-feed days (de Beer and Coon, 2007).

Metabolizable energy intake is partitioned to maintenance, growth, and egg production in broiler breeders (Sakomura, 2004). The maintenance requirement (**ME_m**) includes energy required for basal metabolism, thermal regulation, immune responses, and activity (NRC, 1981); since the ME_m is the sum of all unretained ME, it is the same as total heat production (**HP**) (Zuidhof, 2019). Predicting total HP will help nutritionists to precisely match energy supply (available energy in feed) to energy needed for maintenance, growth, and production (Zuidhof, 2019). Empirical ME intake models quantify the amount of dietary ME partitioned to maintenance (HP), ME retained in the body (ADG), and egg mass produced by broiler breeder hens (Romero et al., 2009b; Pishnamazi et al., 2015). Residual feed intake (**RFI**), the difference between observed and model-predicted ME intake, can be used to identify efficient animals and differences due to management or feeding system (Luiting and Urff, 1991; Romero et al., 2009a).

To increase efficiency, ensure equitable feed distribution for every individual bird, and increase consistency in supply of nutrients to increase egg production, new feed restriction methods or new feeding technologies may be needed for modern broiler breeders. A novel precision feeding (**PF**) system was developed at the University of Alberta to provide the right amount of feed to each bird, increase BW uniformity, and increase efficiency through increasing consistency in nutrient supply because it provides several small meals in a day for an individual bird (Zuidhof et al., 2016, 2017). The PF system individually weighs broiler breeders and makes decisions in real time about whether or not to feed them after comparing their actual BW with their target BW.

The first objective for the current experiment was to develop an ME intake model whose coefficients quantified the amount of ME partitioned to total HP, ADG, and egg mass of broiler breeder hens. The second objective was to use this model to compare energetic efficiency between a conventional daily-restricted feeding program and the PF system. The third objective was to evaluate the effect of a conventional daily restricted feeding program and the PF system on egg production, egg mass, total HP, ADG, carcass composition, and age at 50% production as an indicator of sexual maturation. It was hypothesized that precision-fed broiler breeders hens would be more energetically efficient because of a higher feeding frequency and would partition more energy toward egg production compared with the hens in the conventional daily restricted feeding program.

MATERIALS AND METHODS

Experimental Design

The current study was approved by Animal Care and Use Committee Livestock at the University of Alberta and followed the Canadian Council on Animal Care guidelines (CCAC, 2009). A total of 480 Ross 308 broiler breeder hens were randomly and equally assigned to 2 treatments (8 pens of 30 hens in each treatment): 1) precision feeding system (PF) and 2) conventional daily restricted feeding (**CON**) in a randomized complete block design. Eight environmentally controlled chambers (blocks) were used, and each block contained 1 replicate pen of each treatment. Prior to the current experiment, in the rearing period from 10 to 23 wk of age, PF hens were fed using the PF system, and CON hens were fed using a skip-a-day feeding program (Hadinia et al., 2018). The PF and the CON hens were reared to achieve the breeder-recommended Ross 308 BW target (Aviagen, 2011), and the interpolated BW target was updated hourly in the PF treatment by the PF system. In the CON treatment, pullets were fed each morning and feed allocation decisions for the CON treatment were made based on weekly BW measurements, to maintain breeder recommended BW targets. The BW CV for the CON and the PF pullets at 23 wk of age were 13% ± 0.11 and 8% ± 0.11, respectively ($P < 0.001$, data not shown). For the laying period, broiler breeder pullets were randomly reassigned to new pens within the same treatment.

Precision and Conventional Feeding Treatments

The PF hens in each pen (n = 30) were fed using one feeding station per pen, the design and function of which are fully disclosed elsewhere (Zuidhof et al., 2016, 2017). Briefly, each PF hen was identified by a unique radio frequency identification (**RFID**) tag and weighed by a built-in platform scale when she entered the PF station. If her BW was equal to or greater than the target BW, the PF hen was gently ejected by the station. However, if her BW was lower than the target BW, access to approximately 25 g of feed was provided for 1 min, after which the hen was ejected from the station. Before and after feeding, the feeder that was mounted on a load cell was weighed; feed intake for each feeding bout was calculated as the initial minus the final feed weight. After weighing the feed at the end of each bout, the feeder was topped up to provide approximately 25 g of feed for the next feeding bout. For each visit, RFID, BW, and initial and final feed weight data were written to a database with a date and time stamp. Monochromatic green LED lights (525 nm wavelength) mounted above the feeder provided a light intensity of 1.9 lux at the feeder position. The green wavelength was strategically chosen to help pullets to see well enough to enter the feeding stations and eat during the scotophase without stimulating hypothalamic photoreceptors (Rodriguez, 2017). Thus, PF hens could access feed 24 h per day and consume several small meals over a day, whereas the CON hens received a single large meal per day. Each week, all hens in both treatments were individually weighed manually. The ADG was calculated for each experimental unit (pen).

Management

Each experimental pen contained pine shavings litter at a depth of approximately 5 cm. Two suspended nipple drinkers (4.4 birds per nipple) provided water ad libitum throughout the experiment. The stocking density was 7.4 birds/m^2. There were 3 hanging tube feeders in each CON pen, providing 10 cm of feeder space per hen. The feeder in each PF station was 4.8 cm wide, and only one bird at a time was allowed access to feed. Temperature was 21 ± 0.36°C during the entire experimental period. Photoperiod was gradually increased by 1 h per week from 8L:16D to 14L:10D at 23 wk of age, and was accompanied by an increase in light intensity from 10 to 30 lux in one step. A single broiler breeder layer diet (Table 1) was formulated according to the Ross 308 recommendations (Aviagen, 2013) and was provided in pellet form to both treatments for the duration of the study.

Table 1. Composition and calculated analysis of broiler breeder diet provided from 23 to 34 wk of age.

Ingredient	g/kg
Corn	367
Wheat	350
Soybean meal	158
Canola oil	17
Ground limestone	78
Dicalcium phosphate	14
Choline chloride premix	5
Vitamin premix[1]	2.5
Mineral premix[2]	2.5
NaCl	3.7
D, L-methionine	1.5
L-lysine	0.3
Enzyme[3]	0.5
Total:	1,000
Analyzed composition, as fed basis	
AME (kcal/kg)	2,715
CP (g/kg)	156
Calculated composition, as fed basis	
AME (kcal/kg)	2,909
CP (g/kg)[4]	157
Calcium (g/kg)	33.9
Nonphytate phosphorous (g/kg)	3.7
Available lysine (g/kg)	7.3
Available methionine (g/kg)	4.1
Available methionine + cysteine (g/kg)	6.9

[1]Premix provided per kilogram of diet: vitamin A (retinyl/acetate), 12,500 IU; cholecalciferol, 3,125 IU; vitamin E (DL- α-tocopheryl acetate), 40.0 IU; vitamin K, 2.50 mg; pantothenic acid, 12.5 mg; riboflavin, 7.50 mg; folacin, 0.63 mg; niacin, 37.50 mg; thiamine, 2.55 mg; pyridoxine, 5.00 mg; vitamin B_{12}, 0.02 mg; biotin, 0.15 mg.

[2]Premix provided per kilogram of diet: iodine, 1.65 mg; Mn, 88 mg; Cu, 15.0 mg; Zn, 100 mg; Se, 0.30 mg; Fe, 80.0 mg.

[3]Avizyme 1302 feed enzyme for use in poultry diets containing at least 20% wheat (Danisco Animal Nutrition, Marlborough, Wiltshire, UK); minimum activity: 5,000 U/g endo-1,4-beta-xylanase, 1,600 U/g subtilisin (protease).

[4]Analyzed N using Leco TruMac (Leco Corporation, St. Joseph, MI)

Measurement of AME

Two percent of an acid-insoluble ash marker (Celite 281, Lompoc, CA) was added to the diet for 4 consecutive days beginning at each of 23, 28, and 32 wk of age to allow calculation of AME content of the diet. In total, 16 hens per treatment (2 hens per pen) were randomly selected after 4 D on the celite containing feed, and euthanized by cervical dislocation. Ileal digesta samples were collected from Meckel's diverticulum to the ileal–cecal–colon junction of the intestinal tract. Digesta samples were pooled within each pen and frozen at −20°C until further analysis. Diet and ileal digesta samples were oven-dried at 60°C for 48 h and then ground. Samples were digested with 4 N HCl and then the residues were ashed at 500°C (Vogtmann et al., 1975). Using bomb calorimetry, gross energy (**GE**) of feed and digesta samples was measured. The AME values were calculated as described by Scott and Boldaji (1997):

$$AME = GE_{diet} - GE_{digesta} \times \frac{Marker_{diet}}{Marker_{digesta}}$$

where GE = gross energy (kcal/kg of sample); and Marker = concentration of acid insoluble ash in sample. Because the diet did not contain the acid insoluble ash marker at all times, a 2% correction factor was applied to the dietary AME values. The AME values were not corrected for nitrogen retention and were expressed on an as-fed basis. Nitrogen content of feed was determined by the combustion method using a Leco TruMac N machine (Leco Corporation, St. Joseph, MI), and dietary CP was estimated using a factor of 6.25 (Hossain et al., 2012; Mutucumarana et al., 2015).

Carcass Traits

Breast Muscle and Fat Pad For carcass characteristics, 42 birds per treatment were euthanized at each of 23, 28, 32, and 34 wk of age, and the weights of breast muscle (pectoralis major + pectoralis minor) and abdominal fat pad were recorded. The weights of fat pad and breast muscle were reported as a percentage of live BW.

Oviduct and Ovarian Morphology At each dissection age, the ovarian stroma and oviduct were weighed and expressed as a percentage of BW. Each large yellow follicle (**LYF**, greater than 10 mm) was individually weighed at 34 wk of age and the number of hierarchical LYF was counted.

Age at 50% Production

Eggs were collected daily and average egg weight was determined for each pen. The number of normal eggs was calculated by deducting the number of abnormal eggs (double yolks, deformed and eggs with shell problems such as soft shelled eggs or shell-less eggs) from the number of total eggs. Hen-day egg production (**HDEP**) for each pen was calculated by dividing the number of normal eggs produced per day by the number of hens alive on that day. The egg mass (g/d) per hen for each pen was calculated as laying percentage multiplied by the average egg weight. To evaluate sexual maturation (from photostimulation to 50% egg production), age at 50% production was estimated for the CON and the PF treatments. Age at 50% production (parameter μ in the following model) was estimated using a nonlinear model as described by Renema et al. (2007a):

$$\text{Hen-day egg production}$$
$$\text{HDEP} \times \left(1 + \exp^{-\frac{\pi}{3\sigma} \times (\text{age}-\mu)}\right) = 100 \quad (1)$$

where HDEP was calculated for each treatment per day (%); π to 4 decimal points was 3.1416; σ was the SD in age at 50% production; *age* was age of hens in days; μ was the average age (d) at 50% production. The parameters σ and μ were estimated directly using the NLIN procedure of SAS (SAS 9.1, SAS Institute Inc., Cary, NC). Equation 1 was predicted under the assumption that sexual maturation follows a normal distribution (Yang et al., 1989).

Metabolizable Energy Partitioning Model A linear mixed model (Equation 2) was used to derive ME requirements for total HP, ADG, and egg mass of broiler breeder hens from 23 to 34 wk of age. The model was estimated with the MIXED procedure of SAS (version 9.4; SAS Inst. Inc.) and pen was a random effect:

$$\text{Observed MEI} = \text{Predicted MEI} + \varepsilon$$
$$\text{Predicted MEI} = \text{A} \times \text{BW}^{0.67} + \text{c} \times \text{ADG} + \text{d} \times \text{EM}$$
$$\text{Observed MEI} = \text{A} \times \text{BW}^{0.67} + \text{c} \times \text{ADG} + \text{d} \times \text{EM} + \varepsilon \quad (2)$$

where MEI was ME intake (kcal/d); observed MEI for each pen was calculated weekly by multiplying the energy of the diet (kcal/kg) by observed feed intake (kg); A was a vector of estimated age-specific (weekly) total HP coefficients (kcal/kg$^{0.67}$/d); BW was the average BW (kg) of each experimental unit during the week in which total HP was estimated; BW$^{0.67}$ was metabolic BW; c was the estimated coefficient of ADG (g/d),

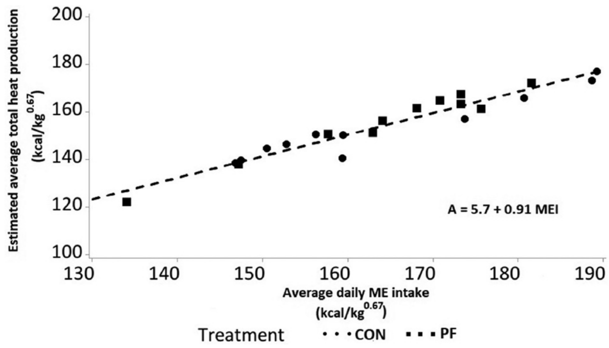

Figure 1. Regression of average total heat production [A] versus ME intake (R^2 = 0.98; $P < 0.001$). Average daily ME intake (MEI; kcal/kg$^{0.67}$) from 23 to 34 wk of age was calculated for precision feeding (PF) and conventional daily-restricted feeding (CON) treatments. Intercept and slope SEM were 9.30 and 0.06, respectively.

which defined the ME cost for each g of BW gain ($\mathbf{ME_g}$, kcal/g); EM was egg mass and d was the estimated coefficient of egg mass (g/d), which defined the ME cost for each g of egg mass ($\mathbf{ME_e}$, kcal/g); and ε was the residual or unexplained error (RFI) and was used to evaluate energetic efficiency.

Partitioning of ME Intake to Growth, Total HP, and Egg Mass To partition ME intake to total HP, ADG, and egg mass in broiler breeder hens from 23 to 34 wk of age, the percentage of total HP to observed ME intake (Total HP%), the percentage of ADG to observed ME intake (Growth%), and the percentage of egg mass (EM) to observed ME intake (Egg mass%), respectively were calculated weekly:

$$\text{Total HP\%} = \left[\frac{\text{A} \times \text{Metabolic BW}}{\text{Observed ME intake}}\right] \times 100$$

$$\text{Growth\%} = \left[\frac{\text{c} \times \text{ADG}}{\text{Observed ME intake}}\right] \times 100$$

$$\text{Egg mass\%} = \left[\frac{\text{d} \times \text{EM}}{\text{Observed ME intake}}\right] \times 100$$

Regression Analysis Between ME Intake and Weekly Total HP The relationship between total HP and ME intake from 23 to 34 wk of age was estimated by a linear regression, modified from Romero et al. (2009b) such that ME intake was expressed per unit of metabolic BW:

$$\text{A} = \text{intercept} + \text{slope} \times \text{MEI} + \varepsilon$$

where A was the total HP coefficient estimated for each pen (kcal/kg$^{0.67}$); MEI was ME intake (kcal/kg$^{0.67}$); slope ((kcal/kg$^{0.67}$)/(kcal/kg$^{0.67}$)) was the coefficient defining the linear rate of change of weekly total HP with respect to ME intake; and ε was the error term. Since the units for the slope coefficient cancel, the slope can be directly interpreted as the proportion of dietary energy lost by the hens as heat (Figure 1).

Egg Composition

In the current study, egg composition was not measured. However, to understand whether the result of the estimation for the coefficient d (ME_e = 0.75 kcal/g) in the Equation 2 was biologically feasible, a set of calculations and estimations were simply carried out using Excel (Microsoft, 2010). It was assumed that a 55 g egg consists of 10% eggshell (0.08 kcal/g), 60% albumen (0.47 kcal/g), and 30% of yolk (3.01 kcal/g; Gilbert, 1971; Radu-Rusu et al., 2012; Abeyrathne et al., 2013; McLeod et al., 2014). Weight and energy content of shell, albumen, and yolk were calculated for a 55 g egg:

$$\text{Yolk energy} = 30\% \times 55\,\text{g} \times 3.01\,\text{kcal/g} = 49.7\,\text{kcal}$$

$$\text{Albumen energy} = 60\% \times 55\,\text{g} \times 0.47\,\text{kcal/g} = 15.5\,\text{kcal}$$

$$\text{Shell energy} = 10\% \times 55\,\text{g} \times 0.08\,\text{kcal/g} = 0.44\,\text{kcal}$$

ME_e = 1.19 kcal/g at the 55 g egg was calculated by dividing the total energy content of the egg (65.6 kcal) by the weight of the egg (55 g). Next, using Excel Solver Add-in and the ME_e = 1.19 kcal/g, yolk weight (6.91 g) and albumen weight (42.6 g) for ME_e = 0.75 kcal/g at the 55 g egg were estimated. Lastly, yolk and albumen percentage in broiler breeder hens from 24 to 34 wk of age were calculated:

$$\text{Yolk\%} = \left[\frac{\text{Yolk Weight for } ME_e = 0.75 \text{ at } 55 \text{ g Egg}}{\text{Average Egg Weight in the Current Study}}\right] \times 100$$

$$\text{Albumen\%} = \left[\frac{\text{Albumen Weight for } ME_e = 0.75 \text{ at } 55 \text{ g Egg}}{\text{Average Egg Weight in the Current Study}}\right] \times 100$$

Statistical Analysis

Analysis of Variance Metabolizable energy intake, BW, ADG, egg weight, ovary and oviduct weights, and total HP ($A \times BW^{0.67}$) were evaluated as a 2-way ANOVA using MIXED procedure in SAS where age and treatment considered as source of variations, and pen was a random effect. Egg mass, total HP%, growth%, egg mass%, RFI, and LYF weight were analyzed using the MIXED procedure as a 1-way ANOVA, with feeding treatment as the main effect. Least significant difference test was applied to multiple mean comparisons. The PDIFF option of the LSMEANS statement used to estimate pairwise differences between means and least significant difference test was applied to multiple mean comparisons. Differences between means were reported as significant where $P \leq 0.05$. Trends were reported where $0.05 < P < 0.1$.

RESULTS AND DISCUSSION

Metabolizable Energy Intake, BW, and Average Daily Gain

The CON hens had a 3% higher ME intake (366 kcal/d) compared with the PF hens (354 kcal/d) from 23 to 34 wk of age (Table 2). Metabolizable energy intake of CON hens was higher than PF hens from 23 to 28 wk of age, after which the ME intake of PF hens was higher than the CON hens. After 25 wk of age, CON hens were heavier than PF hens (Table 2) and after 27 wk of age CON hens were above the breeder-recommended target BW. The ADG of CON hens was higher than PF hens from 23 to 28 wk of age, after which ADG did not differ between treatments (Table 2).

The lower ME intake for the PF hens during the first 5 wk of the experiment than for the CON hens could have been due to several factors. First, the CON hens were weighed only once per week and the feed allocation decisions were made weekly, considering their BW and desired rate of gain for the subsequent week. The BW of CON hens at the start of the laying period was lower than the PF hens (2,477 vs. 2,602 g respectively); thus, the feed allocation for the CON hens was increased compared with PF hens which resulted in their higher ME intake. Because the feed allocation decisions for the CON hens were made much less frequently, they were more prone to error than the real-time feed allocation decisions for the PF hens. If the CON hens reached the target BW earlier than expected or delayed their achievement to the target BW, there was no chance of revising the feed allocation until the next feed allocation decision since they were weighed only once per week. Second, the feed allocation decisions for the PF treatment were based on the individual BW of each hen. If, for example, a PF hen laid a 50 g egg, her BW would be reduced by 50 g. Since she would then be lower than the target BW, she would continue to receive feed until her BW matched the target BW. This would effectively increase her feed allocation on any day she laid an egg. Conversely, feed increases for the CON treatment allowed for all hens to increase feed intake simultaneously. Therefore, a PF hen that did not lay an egg did not receive the same feed increase as a PF hen that did lay an egg. The current PF protocol provided feed increases after an egg was laid in each individual hen, but did not provide feed increases before the onset of egg production in the same manner as the conventional feeding protocol. Therefore, the PF hens had lower ME intake than the CON hens from 23 to 28 wk of age. Lower ADG of PF hens compared with CON hens from 23 to 28 wk of age was due to their lower ME intake from 23 to 28 wk of age. The CON hens had lower ME intake than the PF hens from 29 to 34 wk of age. The reason was due to decreasing the feed allocations to match the BW with the target BW because the BW of the CON hens exceeded the

Table 2. Metabolizable energy intake (MEI), average daily gain (ADG), and body weight (BW) of broiler breeder hens on precision feeding (PF) and conventional daily-restricted (CON) feeding treatments from 23 to 34 wk of age.

	MEI		ADG			BW		
Period (wk)	PF	CON	PF	CON	Age (wk)	PF	CON	Ross 308 recommended target BW
	– kcal/hen/d –		g/d			g		
	354^{s}	366^{r}	12.6^{s}	16.9^{r}		$3{,}094^{s}$	$3{,}284^{r}$	–
					23	$2{,}602^{a,Q}$	$2{,}477^{b,Q}$	2,660
23 to 24	$300^{b,M,N}$	$359^{a,K\text{-}M}$	$13.3^{b,K\text{-}M}$	$23.9^{a,J}$	24	$2{,}611^{Q}$	$2{,}610^{P}$	2,820
24 to 25	$318^{b,L}$	$372^{a,I\text{-}K}$	$23.2^{b,I,J}$	$30.6^{a,I,J}$	25	$2{,}718^{P}$	$2{,}768^{O}$	2,975
25 to 26	$357^{b,K}$	$375^{a,I,J}$	28.5^{I}	$29.7^{I,J}$	26	$2{,}885^{b,O}$	$2{,}979^{a,N}$	3,120
26 to 27	$310^{b,L,M}$	$378^{a,I,J}$	$16.3^{b,J\text{-}L}$	$31.9^{a,I}$	27	$3{,}041^{b,N}$	$3{,}194^{a,M}$	3,245
27 to 28	$289^{b,N}$	$364^{a,J\text{-}L}$	$19.5^{b,J,K}$	$35.0^{a,I}$	28	$3{,}140^{b,M}$	$3{,}428^{a,L}$	3,340
28 to 29	361^{K}	346^{M}	$7.7^{M\text{-}O}$	$9.4^{K,L}$	29	$3{,}245^{b,L}$	$3{,}588^{a,K}$	3,395
29 to 30	$380^{a,J}$	$349^{b,M}$	$3.5^{N,O}$	$7.6^{K\text{-}M}$	30	$3{,}303^{b,K,L}$	$3{,}621^{a,J,K}$	3,435
30 to 31	$376^{a,J}$	$357^{b,L,M}$	$4.0^{N,O}$	$2.5^{L,M}$	31	$3{,}324^{b,K}$	$3{,}637^{a,J,K}$	3,465
31 to 32	$409^{a,I}$	$365^{b,J\text{-}L}$	$10.2^{L\text{-}N}$	$3.5^{K\text{-}M}$	32	$3{,}362^{b,J,K}$	$3{,}669^{a,I,J}$	3,490
32 to 33	$396^{a,I}$	$383^{b,I}$	$11.3^{L,M}$	10.2^{K}	33	$3{,}428^{b,I,J}$	$3{,}709^{a,I}$	3,510
33 to 34	$399^{a,I}$	$377^{b,I,J}$	1.5^{O}	1.7^{M}	34	$3{,}466^{b,I}$	$3{,}727^{a,I}$	3,530
Source of variation	SEM	*P*-value	SEM	*P*-value		SEM	*P*-value	
Treatment	2.6	0.006	0.8	0.001		14.9	<0.001	
Age	4.0	<0.001	1.8	<0.001		19.1	<0.001	
Treatment x age	5.6	<0.001	2.6	<0.001		27.1	<0.001	

[a,b]Means within row within each variable with no common superscript differ ($P < 0.05$).
[I-Q]Means within column with no common superscript differ ($P < 0.05$).
[r,s]Means within row within overall treatment effect with no common superscript differ ($P < 0.05$).

target BW after 27 wk of age. However, the CON hens still had higher BW than the PF hens until wk 34. Obviously, feed allocation decisions are difficult and this challenge for the research team underscores this difficulty. Precision-fed broiler breeder hens compared with conventionally daily fed grandparent had lower average daily feed intake from 22 to 52 wk of age and it was hypothesized that feed restriction should be relaxed for precision-fed broiler breeders by increasing the target BW (Zuidhof, 2018).

Carcass Traits

Breast muscle as a percentage of BW did not differ between the CON and the PF hens at any age (Table 3). At 23 and 28 wk of age, hens in the CON treatment had increased fat pad compared with hens in the PF treatment. However, there was no difference in fat pad percentage after 28 wk of age. The CON hens had higher ME intake than the PF hens from 23 to 28 wk and this explained the higher fat pad percentage in the CON hens than the PF hens during that period. Less frequent feeding (skip-a-day) in comparison with more frequent feeding (daily restricted) increased expression of genes involved in hepatic lipogenesis 12 and 24 h after feeding (de Beer et al., 2007). The CON feeding program used in the current study that involved less frequent feeding probably provided just such a scenario. The less frequency of feeding in the CON hens would likely have increased hepatic lipogenesis compared with the PF hens. In addition, the higher ME intake of the CON hens than the PF hens from 23 to 28 wk of age would likely have provided sufficient energy for the CON hens to store some energy in the abdominal fat pad. Abdominal fat pad weight is linked directly to total body fat content in avian species; thus, it is a reliable indicator for judging total body fat content (Becker et al., 1979; Thomas et al., 1983). In the current study, the CON hens deposited more energy in the fat pad; thus, they had more energy available for reproductive development and egg production.

Sexual Maturation and Egg Production

Overall, HDEP from 24 to 34 wk of age was higher for the CON hens (65.5%) compared with the PF hens (55.2%; Table 4). The peak of HDEP for the CON treatment was 87.6% from 32 to 33 wk of age, compared with 82.0% for the PF treatment from 33 to 34 wk of age. The PF hens likely did not peak by 34 wk of age. Age at 50% production was estimated to be 192.7 d ± 0.56 for the CON hens, 8.5 d earlier than the PF hens (201.2 d ± 0.75; $P < 0.05$).

From 23 to 28 wk of age, the CON hens had 14.8% higher ME intake and at 23 and 28 wk of age, the CON hens had 29.4 and 20.8% higher fat pad weights respectively than the PF hens. Moreover, the CON hens were 7% heavier than the PF hens from 26 to 34 wk of age. Thus, the CON hens had more energy available in the body and they increased HDEP compared with the PF hens from 25 to 33 wk of age. Broiler breeder hens utilize body lipid reserves as an energy source for egg production (Nonis and Gous, 2012). Body fat content affects yolk synthesis because incorporation of lipids originating from diet, lipoproteins from liver, and release of lipids from adipose tissue contributes to yolk synthesis (Yang et al., 2013). Renema et al. (2007a) reported that hens with higher fat pad content reached 50% production 7 d earlier than hens with lower fat pad content ($P < 0.05$). The CON hens likely had more lipid resources available in the body, which may have advanced the age at 50% production and increased egg production relative to the PF hens. Age at 50% production was delayed in the PF hens because

Table 3. Carcass characteristics in broiler breeder hens on precision feeding (PF) and conventional daily-restricted (CON) feeding treatments at 23, 28, 32, and 34 wk of age.

	Breast				Fat pad			
	PF	SEM	CON	SEM	PF	SEM	CON	SEM
	% of live BW							
	19.6	0.39	19.6	0.39	1.8^{s}	0.07	2.0^{r}	0.07
Age (wk)								
23	19.7	0.48	19.9^{I,J}	0.41	1.2^{b,J}	0.17	1.7^{a,J}	0.14
28	20.0	0.58	19.1^{J}	0.58	1.9^{b,I}	0.16	2.4^{a,I}	0.16
32	19.1	0.62	19.9^{I,J}	0.62	1.9^{I}	0.16	2.0^{I,J}	0.16
34	19.4	0.33	20.1^{I}	0.43	2.0^{I}	0.06	2.1^{I}	0.11
Source of variation	*P*-value							
Treatment		0.86				0.003		
Age		0.79				<0.001		
Treatment × age		0.046				0.220		

[a,b]Means within row within each variable with no common superscript differ ($P < 0.05$).
[I,J]Means within column with no common superscript differ ($P < 0.05$).
[r,s]Means within row within overall treatment effect with no common superscript differ ($P < 0.05$).

Table 4. Hen-day egg production and egg weight of broiler breeder hens on precision feeding (PF) and conventional daily-restricted (CON) feeding treatments from 23 to 34 wk of age.

	Hen-day egg production		Egg weight	
	PF	CON	PF	CON
	%		g	
	55.2^{s}	65.5^{r}	57.6	57.4
Period (wk)				
24 to 25	3.8^{P}	6.4^{N}	48.5^{O}	49.6^{O}
25 to 26	9.3^{b,O}	17.4^{a,M}	52.3^{N}	51.8^{N}
26 to 27	27.2^{b,N}	48.7^{a,L}	53.7^{N}	53.9^{M}
27 to 28	52.0^{b,M}	74.1^{a,K}	56.3^{M}	57.6^{L}
28 to 29	69.5^{b,L}	82.4^{a,J}	58.3^{L}	58.5^{K,L}
29 to 30	73.4^{b,K,L}	85.5^{a,I,J}	59.2^{K,L}	58.1^{L}
30 to 31	75.6^{b,J,K}	85.0^{a,I,J}	60.4^{J,K}	60.8^{I,J}
31 to 32	79.1^{b,I,J}	85.3^{a,I,J}	61.7^{a,I,J}	60.2^{b,J,K}
32 to 33	80.6^{b,I,J}	87.6^{a,I}	62.4^{I}	61.3^{I,J}
33 to 34	82.0^{I}	82.9^{I,J}	62.8^{I}	62.0^{I}
Source of variation	SEM	*P*-value	SEM	*P*-value
Treatment	1.31	<0.001	0.25	0.610
Age	1.57	<0.001	0.47	<0.001
Treatment × age	2.22	<0.001	0.66	0.360

[a,b]Means within row within each variable with no common superscript differ ($P < 0.05$).
[I-O]Means within column with no common superscript differ ($P < 0.05$).
[r,s]Means within row within overall treatment effect with no common superscript differ ($P < 0.05$).

the feed allocation increases for the PF hens was provided after the hen had laid an egg. Thus, the PF hens had limited nutrients to form the egg unlike the CON hens, which received feed increases prior to laying the egg. The CON hens reached 50% production earlier, indicating the rate of pubertal growth was faster for them and they advanced sexual maturation than the PF hens. The hypothalamic–pituitary–gonadal (**HPG**) axis controls sexual maturation (Bédécarrats et al., 2009). Advancing sexual maturation in the CON hens relative to the PF hens suggested that the higher ME intake and greater fat pad deposition could advance the activation of the HPG axis. Although the PF hens at the end of study (week 34) attained approximately the target BW, they delayed sexual maturation and also did not have increased egg production relative to CON hens. Precision-fed broiler breeder hens compared with conventionally fed grandparent hens had lower egg production from 22 to 52 wk of age and 1.2 times greater breast muscle weight at week 22; however, abdominal fat pad weight did not differ between both groups of hens at 22 wk (Zuidhof, 2018). van der Klein et al. (2018a, b) demonstrated that total egg production from 20 to 55 wk of age and fat pad weight at 55 wk of age respectively were lower for the hens in the standard breeder-recommended target BW (92.8 and 1.6%) relative to the hens in the high BW treatment reaching the standard 21 wk BW at 18 wk (129.4 and 2.2%). Therefore, the target BW for the PF hens would likely have to be increased before the laying period and also around the time of sexual maturation to provide a sharp increase in feed intake and help the PF birds to increase their ME intake, and body fat deposition to advance the activation of the HPG axis likely leading to advance sexual maturation and higher production.

Egg Weight and Egg Mass

Egg weight did not differ between the CON and the PF treatments except at 31 wk of age. At 31 wk of age, the PF hens had 1.5 g greater egg weight than the CON hens (Table 4), likely due to their higher ME intake from 29 to 34 wk of age. The CON hens had higher egg mass (38.6 g/d ± 0.69) than the PF hens (33.1 g/d ± 0.69) from 24 to 34 wk of age ($P < 0.001$). Hen-day egg production was higher for the CON hens than the PF hens from 25 to 33 wk of age. Romero et al. (2009b) reported that egg mass was 4.3 g lower in hens with low target BW (standard × 0.9) compared with hens with high target BW (standard × 1.1). This result and the result of the current study are consistent with the hypothesis that egg production was limited by ME intake for hens with lower BW which resulted in a decrease in the egg mass. Therefore, in the current

Table 5. Carcass characteristics in broiler breeder hens on precision feeding (PF) and conventional daily-restricted (CON) feeding treatments at 23, 28, 32, and 34 wk of age.

	Ovary and stroma				Oviduct			
	PF	SEM	CON	SEM	PF	SEM	CON	SEM
	of live BW							
	1.10^{s}	0.10	1.27^{r}	0.10	1.40^{s}	0.08	1.51^{r}	0.08
Age (wk)								
23	0.02^{L}	0.12	0.02^{K}	0.13	0.01^{K}	0.11	0.01^{K}	0.10
28	$1.02^{b,K}$	0.14	$1.39^{a,J}$	0.14	$1.34^{b,J}$	0.12	$1.72^{a,J}$	0.12
32	$1.41^{b,J}$	0.15	$1.73^{a,I}$	0.15	2.16^{I}	0.12	2.18^{I}	0.12
34	1.96^{I}	0.08	1.95^{I}	0.10	2.08^{I}	0.07	2.13^{I}	0.09
Source of variation	*P*-value							
Treatment		0.009				0.040		
Age		<0.001				<0.001		
Treatment × age		0.060				0.090		

[a,b]Means within row within each variable with no common superscript differ ($P < 0.05$).
[I-K]Means within column with no common superscript differ ($P < 0.05$).
[r,s]Means within row within overall treatment effect with no common superscript differ ($P < 0.05$).

Table 6. Large yellow follicle numbers (LYF), hierarchical follicle weight, hierarchical follicle diameters of breeder hens on precision feeding (PF), and conventional daily-restricted (CON) feeding treatments at 34 wk of age.

	LYF				
	PF	SEM	CON	SEM	*P*-value
LYF (n) > 10 mm	6.20	0.12	5.86	0.23	0.18
Hierarchical follicle weight, g					
F1	17.48	0.20	17.34	0.38	0.75
F2	14.68	0.19	14.85	0.36	0.68
F3	11.36	0.22	11.52	0.42	0.74
F4	8.07	0.22	8.09	0.42	0.97
F5	4.93	0.20	5.42	0.38	0.26
F6	2.58	0.14	3.04	0.28	0.14
F7	1.53	0.11	1.60	0.19	0.77

study, the higher production levels resulted in higher egg mass for the CON hens than the PF hens.

Ovarian Morphology

The CON hens had higher relative ovary and stroma weights than the PF hens at 28 and 32 wk of age (Table 5). Moreover, the CON hens had a higher relative oviduct weight compared with the PF hens at 28 wk of age (Table 5). The greater weights of ovary and stroma and oviduct for the CON hens relative to the PF hens suggested a more advanced ovary development in the CON hens, resulting in advancing sexual maturation for the CON hens, which is consistent with the age at 50% production for the CON hens being 8.5 D earlier than the PF hens. Weight and number of LYF (F1 to F7) did not differ between the CON and the PF hens at 34 wk of age (Table 6). The average number of LYF was 6.03 at 34 wk of age. Similarly, Joseph et al. (2002) reported 6.16 LYF at 32 wk of age for Cobb 500 broiler breeder hens and Hocking et al. (1987) reported 5.6 LYF in dwarf breeders at 30 wk of age. Although the growth potential for modern broiler breeders has increased during the last 30 yr and feed restriction has become more severe (Renema et al., 2007b), the number of LYF does not appear to have changed.

Metabolizable Energy Partitioning

The ME partitioning model was ($P < 0.001$):

$$\mathrm{MEI} = \mathrm{A} \times \mathrm{BW}^{0.67} + 1.75 \times \mathrm{ADG} + 0.75 \times \mathrm{EM} + \varepsilon \quad (3)$$

The ME Requirement for BW Gain The estimated ME_g was c = 1.75 kcal/g using the linear model, Equation 3. A value of 2.13 was reported for ME_g kcal using non-linear models in Ross 708 broiler breeder hens from 25 to 41 wk of age (Pishnamazi et al., 2015). Romero et al. (2009b) estimated 2.94 kcal/g for ME_g in Ross 708 broiler breeder hens using a non-linear model and the interaction of metabolic BW and ADG ($1.18\mathrm{BW}^{0.60}\mathrm{ADG}^{1.10}$) from 20 to 60 wk of age. It is possible that ME_g estimates might differ in part due to modeling methodology, but may also vary due to differences in strain and composition of gain. To have an understanding of body compositions of broiler breeders using the estimated ME_g, a simple system of equations was used:

$$1.38\,X + 9.1\,Y = ME_g$$
$$X + Y = 1$$

where 1.38 was the ME requirement per g of lean tissue (kcal/g; Claus and Weiler, 1994; Hadinia et al., 2018); X was the lean tissue as a proportion of total gain; 9.1 was the ME requirement per gram of fat tissue (kcal/g; Johnston, 1970); Y was the fat tissue as a proportion of total gain (kcal/g); and ME_g was ME requirement per gram of ADG (kcal/g). These formulas predicted broiler breeders in the study by Romero et al. (2009b, ME_g = 2.94 kcal/g) deposited 21 and 79% fat and lean tissues, respectively. Moreover, these formulas predicted broiler breeders in the study by Pishnamazi et al. (2015, ME_g = 2.13 kcal/g) deposited 10 and 90% fat and lean

Table 7. Total heat production (HP), growth and egg mass (EM), and residual feed intake (RFI) of broiler breeder hens on precision feeding (PF) and conventional daily-restricted (CON) feeding treatments from 23 to 34 wk of age.

	PF	CON	SEM	*P*-value
HP (%)[1]	87.7	85.5	0.3	<0.001
Growth (%)[2]	5.6	7.1	0.3	0.008
EM (%)[3]	6.7	7.4	0.1	0.005
RFI (kcal/d)[4]	6.7	–5.9	2.9	0.009

The following linear model was fitted to derive ME requirements for HP, growth, and hen-day egg production:

Observed MEI = $A \times BW^{0.67} + c \times ADG + d \times EM + \varepsilon$,

where MEI was ME intake (kcal/d); *A* was a vector of age-specific (weekly) total HP coefficients (kcal/kg$^{0.67}$/d); BW was the average BW (kg) of each pen; BW$^{0.67}$ was metabolic BW; *c* was the coefficient of ADG (g/d); EM was egg mass and *d* was the coefficient of egg mass (g/d) and the following factors were calculated using the estimates from the above model:

[1]Total HP% $= [\frac{A \times \text{Metabolic BW}}{\text{Observed ME intake}}] \times 100$

[2]Growth% $= [\frac{c \times ADG}{\text{Observed ME intake}}] \times 100$

[3]Egg mass% $= [\frac{d \times EM}{\text{Observed ME intake}}] \times 100$

[4] Calculated using the above model:

RFI = ε = [observed MEI] – [$A \times BW^{0.67} + c \times ADG + d \times EM$]

Table 8. The coefficient of age-specific (A; weekly) total heat production (HP)[1] and the total HP ($A \times BW^{0.67}$)[1] of breeder hens on precision feeding (PF) and conventional daily-restricted (CON) feeding treatments from 23 to 34 wk of age.

	A		$A \times BW^{0.67}$	
	Estimate	SEM	PF	CON
	kcal/kg$^{0.67}$/d		kcal/d	
			305^{s}	318^{r}
Period (wk)				
23 to 24	156^{I}	4.3	297^{N}	297^{O}
24 to 25	$151^{I,J}$	4.9	295^{N}	299^{O}
25 to 26	$151^{I,J}$	5.0	$307^{b,M}$	$314^{a,N}$
26 to 27	$134^{J,K}$	5.9	$282^{b,O}$	$292^{a,P}$
27 to 28	123^{K}	8.6	$265^{b,P}$	$281^{a,Q}$
28 to 29	$134^{I\text{-}K}$	9.8	$295^{b,N}$	$315^{a,N}$
29 to 30	$139^{I\text{-}K}$	10.2	$310^{b,M}$	$329^{a,M}$
30 to 31	$141^{I\text{-}K}$	10.6	$315^{b,L}$	$335^{a,L}$
31 to 32	$145^{I\text{-}K}$	10.8	$327^{b,J}$	$346^{a,J}$
32 to 33	$141^{I\text{-}K}$	11.0	$322^{b,K}$	$339^{a,K}$
33 to 34	$147^{I\text{-}K}$	11.0	$338^{b,I}$	$355^{a,I}$
Source of variation	*P*-value		SEM	*P*-value
Treatment	–		1.0	<0.001
Age	<0.001		1.0	<0.001
Treatment × age	-		1.5	<0.001

[1] *A* was a vector of age-specific (weekly) total HP coefficients and was estimated using a linear model:

MEI = $A \times BW^{0.67} + 1.75 \times ADG + 0.75 \times EM + \varepsilon$

Next, *A* was multiplied by metabolic BW (BW$^{0.67}$) and eventually total HP was estimated using the mixed procedure.

where MEI was observed ME intake (kcal/d); BW was the average BW (kg) of each experimental unit; BW$^{0.67}$ was metabolic BW; *c* was the coefficient of ADG (g/d), which defined the ME cost for each g of BW gain (kcal/g); EM was egg mass and *d* was the coefficient of egg mass (g/d), which defined the ME cost for each g of egg mass, and ε was the residual or unexplained error (RFI) and was used to evaluate energetic efficiency.

[a,b]Means within row within each variable with no common superscript differ ($P < 0.05$).

[I-Q]Means within column with each variable with no common superscript differ ($P < 0.05$).

[r,s]Means within row within overall treatment effect with no common superscript differ ($P < 0.05$).

tissues, respectively. These formulas predicted broiler breeders in the current study (ME_g = 1.75 kcal/g) deposited 5 and 95% fat and lean tissues, respectively. The coefficient c = 1.75 kcal/g estimated in the current experiment is close to the value of retained energy of lean tissue (1.38 kcal/g), and it is consistent with the observation that modern broiler breeders deposit primarily lean tissue under conventional feed restriction (van Emous, 2015; Hadinia et al., 2018). A greater ME_g is expected at higher BW because broiler breeders increase body fat with age (Sakomura, 2004). Because of continued selection for broiler traits, broiler breeders deposit less fat as a proportion of total gain and therefore ME_g is continually being reduced.

Total Heat Production The CON and the PF hens partitioned ME intake differently from 23 to 34 wk of age. The CON and the PF hens, respectively, partitioned 85.5 and 87.7% of their total ME intake toward maintenance, which eventually was lost as total HP (Table 7). The CON and the PF hens, respectively, partitioned 7.1 and 5.6% of their ME intake toward growth (Table 7). Additionally, the CON hens partitioned more ME intake into egg mass than the PF hens (7.4 vs. 6.7% respectively; Table 7). The age-specific total HP (*A*) was reduced from 156 kcal/kg$^{0.67}$/d at week 23 to 123 kcal/kg$^{0.67}$/d at week 28 (Table 8). Total HP ($A \times BW^{0.67}$) was higher for the CON hens than the PF hens from 25 to 34 wk of age (Table 8).

The first priority of animals is to satisfy the maintenance energy requirement, after which energy can be partitioned to growth and egg production (Pishnamazi et al., 2015). The CON hens had higher ME intake from 23 to 28 wk of age, higher BW from 26 to 34 wk of age, and higher total HP ($A \times BW^{0.67}$) from 25 to 34 wk of age. However, the model predicted that the CON hens would partition less energy toward maintaining their body (total HP%) and more energy toward growth (growth%) and egg mass (egg mass%) from 23 to 34 wk of age than the PF hens. Since the CON hens partitioned more energy toward egg mass, they increased hen-day egg production and eventually became more energetically efficient than the PF hens.

Physical activity accounted for about 22% of total HP in laying hens (Saiful et al., 2002), and about 20% in broiler breeders (Sakomura, 2004). In the current study, the activity levels of the hens were not estimated. However, there may have been differences in the level of activity which we did not observe. It was possible that the CON hens had a higher level of activity from 25 to 34 wk of age because they had higher total HP during that period. It was suggested that ME_m (total HP) was lower in fat animals than lean animals because fat tissue contributes little to HP compared with protein (Close, 1990). In the current experiment, the increased fat pad weight from 23 to 34 wk of age could be reason for the reduction in the age-specific total HP (*A*) from 156 kcal/kg$^{0.67}$ at week 23 to 123 kcal/kg$^{0.67}$ at week 28. Protein synthesis accounted for between 16 and 26% of total HP in pigs, and lipid synthesis accounted for between 1 to 3% of total HP in rats (Reeds et al., 1982). In poultry, there is lack of information about the proportion of total HP accounted for by protein and lipid synthesis. Although the CON hens had greater fat pad weight than the PF hens at 23 and 28 wk of age, the CON hens were allocated higher ME intake than the PF hens during that period because their BW was lower than the target BW until 27 wk of age. Increasing feed intake increases diet-induced thermogenesis (the energy expended to digest feed; Pishnamazi et al., 2008). Moreover, the CON hens had higher BW than PF hens from 26 to 34 wk of age which resulted in their higher total HP from 25 to 34 wk of age. Larger broiler breeders have higher total HP than smaller broiler breeders (Leeson and Summers, 2000). Thus, diet-induced thermogenesis and BW likely contributed at least in part to the higher total HP ($A \times BW^{0.67}$) by the CON hens from 25 to 34 wk of age. Regression analysis between ME intake and weekly total HP defined the following equation ($P < 0.001$; Figure 1):

$$A = 5.7 + 0.91\,\text{MEI}$$

Thus, total HP (A) increased linearly with increasing ME intake (MEI) within the ranges reported for A (123 to 177 kcal/$BW^{0.67}$) and MEI (134 to 189 kcal/$BW^{0.67}$). Specifically, the model predicted that 91% of every additional kcal of ME consumed within the reported intake range was lost as heat. Although the estimation of 91% was different than the estimations of 85.5 and 87.7% for the ME partitioned toward total HP in the CON and PF hens, respectively, the values are close to each other. The differences between these values could be related to the differences in the methodology. Moreover, the estimate of 91% focused on the upper part of the intake range vs. the total observed ME intake.

The ME Requirement for Egg Mass The ME_e in the current study was d = 0.75 kcal of ME per gram of egg mass at the mean egg mass 38.6 and 33.1 g/d for the CON and the PF treatments respectively from 24 to 34 wk of age. Cobb 500 broiler breeder hens needed 2.30 kcal ME for each gram of egg mass and their average egg mass was 50.47 g/d from 32 to 42 wk of age (Reyes et al., 2012). These researchers reported a greater value for the ME_e compared with the estimated values in the current experiment. These researchers determined the ME_e from the energy content of eggs, in contrast with the empirical linear model used in the current study. It is possible that ME requirement estimates might differ in part due to modeling methodology, but may also vary due to differences in egg mass and egg composition. Increasing egg mass increased ME_e (Pishnamazi et al., 2015) because there is an increased energy cost with increasing egg mass production (Chwalibog, 1992). Romero et al. (2009b) reported a positive correlation ($r = 0.85$) between egg mass production and yolk deposition. Reyes et al. (2012) reported each egg in their study contained 29.5% yolk and 61% albumen. In the current study, with ME_e = 0.75 kcal/g and the average egg weight of 57.5 g, each egg contained 12% yolk and 74% albumen and the ratio of yolk: albumen was 0.16. Nangsuay et al. (2011) reported that yolk: albumen ratio varied between 0.38 and 0.44 at week 29 and between 0.55 and 0.57 at week 53 in Ross 308 broiler breeders. This indicated that the estimated value for the ME_e (0.75 kcal/g) using the empirical model was biologically infeasible. Moreover, the estimation of the ratio of yolk to albumen showed that the empirical ME intake model probably underestimated the ME_e. This is one of the main flaws of mathematical models that there is absence of a way to describe energy balance to incorporate energy intake-related changes in maintenance requirement (Romero et al., 2009b) and in production requirement. The predicted model (Equation 3) did not appear to work well and the major limitation for that was probably the relatively small number of experimental units (16 pens). Moreover, the small sample size for egg collections (10 wk) could be another limitation for the predicted model which led to an inaccurate prediction by the model. If eggs were collected for a longer period, including after peak production, the model would have a larger sample size.

Energetic Efficiency

In the current study, the CON hens had lower RFI compared with the PF hens (–5.9 and 6.7 kcal/d, respectively, Table 7); thus, they were more energetically efficient than the PF hens. Several authors reported animals having a lower maintenance requirement (total HP) had lower RFI and were more efficient compared with animals having a higher total HP (Luiting and Urff, 1991; Basarab et al., 2003; Swennen et al., 2007; Sharma et al., 2018). Adult cockerels genetically selected for high RFI (inefficient) had 40% higher ME intake and 31% higher diet-induced thermogenesis (as a percentage of ME intake) than cockerels genetically selected for low RFI (efficient; Gabarrou et al., 1997).

The CON hens had higher ME intake from 23 to 28 wk of age, higher BW from 26 to 34 wk of age, and higher total HP (A × $BW^{0.67}$) from 25 to 34 wk of age. However, the model predicted that the CON hens partitioned more ME intake toward ADG and egg mass and less ME intake toward total HP than the PF hens. Moreover, the greater ovary and stroma weight at 28 and 32 wk of age and the greater oviduct weight at 28 wk of age for the CON hens showed that they partitioned more energy toward developing reproductive tissues than the PF hens. In addition, the CON hens had higher abdominal fat pad than the PF hens at 23 and 28 wk of age, indicating that the CON hens were in a state of higher energy balance, and likely had more resources available for egg production. These results indicated that the CON hens partitioned ME intake more efficiently than the PF hens.

In conclusion, the CON hens had higher ME intake from 23 to 28 wk of age, higher BW from 26 to 34 wk of age, and higher total HP (A × $BW^{0.67}$) from 25 to

34 wk of age than the PF hens. The feed allocation decisions for the PF treatment were based on the individual BW of each hen, and the increase in feed allocation was provided after the hen laid the egg; thus, the PF hens had limited nutrients to form the egg. Conversely, feed increases for the CON treatment allowed for all hens to increase feed intake simultaneously prior to lay an egg. Thus, the PF hens had lower ME intake than the CON hens from 23 to 28 wk of age. Increased diet-induced thermogenesis and body size likely contributed at least in part to the higher total HP by the CON hens. However, the model predicted that the CON hens compared with the PF hens would partition less energy toward total HP and more energy toward growth and egg mass and eventually they increased egg production. This resulted in the higher energetic efficiency of the CON hens than the PF hens. The CON hens compared with the PF hens had higher fat pad content at 23 and 28 wk of age, greater ovary and stroma weight at 28 and 32 wk of age, and greater oviduct weight at 28 wk of age. These results showed that the CON hens likely had more resources available for egg production and partitioned more energy toward developing reproductive tissues which advanced the age at 50% production. To provide the practical conclusion whether use the PF system in the industry for the maximum egg production in broiler breeders, the results of the current study should be taken in the context of other research results that used the PF system to feed broiler breeders. The PF system can be used for increasing egg production in broiler breeders. Because it was shown by the previous research in our group that increasing the target BW for 22% compared with the standard breeder-recommended target BW increased egg production. Therefore, we hypothesized that the target BW for the PF birds should be increased before the laying period and around the time of sexual maturation to help the PF birds to increase their ME intake and the body fat deposition to increase their productivity. The ME_e (0.75 kcal/g) predicted from the ME intake model did not have biological meaning which showed that the predicted ME intake model was not great. The reasons could be due to the relatively small sample size for the number of experimental units and the short duration of the egg collection.

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