Energy partitioning by broiler breeder pullets in skip-a-day and precision feeding systems

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ABSTRACT An empirical nonlinear mixed model was derived to describe metabolizable energy (ME) partitioning in Ross 308 broiler breeder pullets. Its coefficients described ME used for total heat production (HP) and growth. A total of 630 pullets were randomly and equally assigned to 2 treatments: precision feeding (PF) and conventional skip-a-day feeding (CON) from 10 to 23 wk of age. The PF system allowed birds to enter voluntarily at any time, weighed them, and provided access to feed for 60 s if their BW was less than the target BW. Birds in the CON treatment were fed as a group on alternate days. Energetic efficiency of pullets was evaluated using residual total heat production (RHP), defined as the difference between observed and predicted total HP. Additionally, ME intake (MEI), ADG, HP, and cumulative feed conversion ratio (FCR) were calculated for the entire experimental period. The energy partitioning model ($P < 0.05$) predicted MEI = (120+u)BW$^{0.68}$ + 1.52(ADG) + ε. Total HP was (120 kcal/kg$^{0.68}$ + u); the energy requirement for each g of BW gain was 1.52 kcal/d. The random variable u $\sim$ N (0, σ_u^2) indicated a pen level HP standard deviation σ_u = 12.1 kcal/kg$^{0.68}$. Over the experimental period, for CON and PF treatments, respectively, MEI was 194 and 174 kcal/d ($P < 0.001$); ADG was 15.3 and 15.4 g/d ($P = 0.94$); HP was 129 and 111 kcal/kg$^{0.68}$ ($P < 0.001$); FCR was 4.888 and 4.057 ($P < 0.001$); and RHP was 0.12 and –0.12 kcal/kg$^{0.68}$ ($P = 0.73$). The CON pullets had similar ADG, but higher MEI relative to PF, consistent with levels of heat production predicted by RHP. The PF pullets had lower cumulative FCR compared to CON pullets. The PF pullets lost less energy as heat, likely because they were fed continuously, reducing the need to store and mobilize nutrients compared to CON pullets. Thus, increased feeding frequency likely increased PF pullet efficiency.

Key words: precision livestock feeding, caloric restriction, energy partitioning, maintenance requirement, residual feed intake

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INTRODUCTION

In the past decades, residual feed intake (**RFI**) has been used in animal nutrition studies as a biological estimate of feed utilization efficiency (Aggrey and Rekaya, 2013). Residual feed intake is an efficiency indicator that can account for variations in maintenance requirements and growth (Koch et al., 1963). Residual feed intake is the difference between observed and expected ME intake (**MEI**; Romero et al., 2009a). Metabolizable energy intake models can be used to estimate RFI as an efficiency indicator. The error term of MEI models is referred to RFI. Moreover, MEI models have been used to determine ME requirements for broiler breeders (Sakomura et al., 2003; Sakomura, 2004; Pishnamazi et al., 2015). Coefficients in these models are used to describe ME requirements for maintenance (**ME$_m$**), which is equivalent to total heat production (**HP**), and growth and egg production (retained energy) of broiler breeders. Residual maintenance ME requirement (**RME$_m$**) is another energetic efficiency factor and is defined as the difference between observed and expected ME$_m$ (Romero et al., 2011). Residual maintenance ME requirement is calculated by the residual of the linear relationship between total HP and MEI (Romero et al., 2009a). Since the ME$_m$ is the sum of all unretained ME, it is the same as total HP (NRC 1981; Zuidhof, 2018); RME$_m$ can also be termed residual total HP (**RHP**).

It is important to control feed intake (including energy intake) of broiler breeders during rearing to reduce reproductive problems during the production phase

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(Richards et al., 2010). Various methods have been used to restrict feed intake of broiler breeders (Mench, 2002) to optimize their BW for reproductive performance (Renema and Robinson, 2004). Skip-a-day feeding and limited everyday feed restriction methods are practical, and therefore commonly used by the broiler breeder industry. In the skip-a-day program, a feed allotment for 2 d is combined and fed to broiler breeders every second day. When feed intake rate of the most aggressive birds slows or they leave the feeder, the amount of feed remaining is sufficient for less aggressive birds to receive an adequate amount of feed. It was hypothesized that reducing competition for feed by providing more feed less frequently might improve BW uniformity (Bartov et al., 1988). Skip-a-day feeding improved flock uniformity relative to everyday feeding during severe feed restriction (de Beer and Coon, 2007). Moreover, it was observed that daily fed broiler breeders were more efficient compared to skip-a-day birds due to consistency in the supply of nutrients (de Beer et al., 2007; Zuidhof et al., 2015). On the other hand, overdrinking and stereotypic pecking are the result of feed restriction in broiler breeders (Hocking et al., 1997) and it brings up the concern that welfare of broiler breeder pullets may be compromised during rearing (Savory et al., 1993; Tolkamp et al., 2005).

To allocate feed of broiler breeders they are typically weighed weekly (once or twice) and feed allocation decisions are based on their BW and rate of gain. However, a precise feed allocation requires weighing birds frequently, which requires labor (Schneider et al., 2005) or automated weighing equipment. Both of these increase the cost of hatching egg production. Although a major concern with automated data systems is the cost, it is conceivable that automation might eventually increase profitability through increased chick production, which in many parts of the world is currently well below broiler breeders' genetic potential.

To the best of our knowledge, there has not been a practical method to weigh broiler breeders and allocate required feed based on their BW in real time. To provide a more stable energy balance and consistency in the supply of nutrients in broiler breeders, a novel precision feeding system was developed at the University of Alberta (Zuidhof et al., 2016, 2017). The precision feeding system weighs individual broiler breeders and makes decisions in real time about whether or not to feed them after comparing their observed BW with their target BW. The implications of such a feeding approach for energy efficiency in broiler breeders have not been explored previously.

The first objective of the current study was to develop a model whose coefficients describe ME cost for total HP and growth in broiler breeder pullets. Most previous literature assessed partitioning MEI during lay (Rabello et al., 2006; Reyes et al., 2011). However, partitioning MEI by modern broiler breeders has not been assessed as comprehensively during the rearing period. Additionally, using an energy partitioning model to measure energetic efficiency has not been studied thoroughly. The second objective was to evaluate energy efficiency and feed conversion rate of broiler breeder pullets fed using precision feeding and skip-a-day feeding systems. Efficiency was calculated using RFI, RHP, and feed conversion ratio (**FCR**). It was hypothesized that precision-fed broiler breeder pullets would be more efficient compared to pullets fed using conventional skip-a-day feeding method because of a higher feeding frequency.

MATERIALS AND METHODS

Experimental Design

All procedures in the present study were approved by the Animal Care and Use Committee for Livestock at the University of Alberta. A total of 630 Ross 308 broiler breeder pullets were reared using pan feeders from 0 to 9 wk of age in floor pens. From 10 to 23 wk of age, they were randomly allocated to 2 treatments (7 pens of 45 birds in each treatment): precision feeding system (**PF**) and conventional skip-a-day feeding (**CON**) in a randomized complete block design. Seven environmentally controlled chambers (blocks) were used, and each block contained 1 replicate pen of each treatment.

Precision and Conventional Feeding Treatments

Birds in the PF treatment were fed using 1 feeding station per pen, the design and function of which are fully disclosed elsewhere (Zuidhof et al., 2016, 2017). Briefly, each PF pullet was identified by a unique radio frequency identification 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 pullet was gently ejected by the station. However, if her BW was lower than the target BW, the PF station provided access to approximately 25 g of feed for 1 min, after which the pullet was ejected from the station. A feeder was mounted on a load cell so that feed could be weighed. Before feeding the feed was weighed and after feeding the remaining feed was weighed again. Feed intake was calculated as the initial minus the final feed weight. After weighing, the feeder was topped up to provide approximately 25 g of feed for the next feeding bout. For each visit, radio frequency identification, BW, and initial and final feed weight data were written to a database with a date and time stamp. Target BW was interpolated hourly for the PF treatment. Monochromatic green LED lights (525 nm wavelength) were mounted above the entry door and the feeder with a light intensity of 1.9 lux at the position of feeder. The intensity was measured using a light meter in all experimental pens during the scotophase when the only source of light was from the LED light of the

PF station. The wavelength was strategically chosen to help pullets to enter the feeding stations and see feed during the scotophase without stimulating hypothalamic photoreceptors (Rodriguez, 2017). Thus, PF pullets could access feed 24 h/d and sequentially received several small meals over a full 24 h/d rather than 1 large meal. During the first 3 wk of the study (10, 11, and 12 wk), PF pullets required training to become familiarized with the feeding stations. They had to learn that they would receive a small meal as a reward for voluntarily entering the feeding station. During week 10, pullets were daily encouraged to enter PF system voluntarily, by guiding them to the feeder inside the station. The PF pullets that were slower to learn to use the PF stations were identified from the database records by low visit frequencies. These birds were remedially trained every second day during week 11 and 12. During this time, all PF pullets with BW less than 70% of their target BW were trained. Training continued or was reinstated when pullets voluntarily entered the PF station less than 4 times for 2 consecutive days or when the BW of pullet was less than 70% of the target BW. It was decided a priori to remove any of PF birds from the experiment that were not able to learn the principle of individual feeding by the end of week 12. However, all birds were able to learn to use the PF stations. Thus, none of the PF birds were removed from the experiment.

Because the initial BW of the largest birds exceeded the target BW, and to ensure that heavy PF pullets would receive feed and not be immediately ejected, the BW of the heaviest PF pullet was initially assigned as the PF target BW. This BW was maintained as the target BW until 13 wk, after which an hourly interpolated breeder-recommended Ross 308 BW target (Aviagen, 2011) was adopted. In the CON treatment, pullets were fed on alternate mornings. Feed allocation for the CON treatment was based on weekly BW recording, to maintain breeder recommended BW targets. At the end of each week in the morning, all pullets in both treatments were individually weighed manually. The CON pullets were weighed before feeding and the PF pullets were weighed while PF stations were working. The nature of PF system was about providing continuously small amount of feed to PF pullets throughout the day. Thus, the PF stations were not shut down before weighing birds to avoid stopping naturally feeding the PF pullets. There was a small amount of feed in gut of PF pullets, which may have had a minimal effect on their BW. The ADG was calculated for each experimental unit (pen). The cumulative FCR for each experimental unit was calculated weekly by dividing the total feed intake to the total ADG.

Management

Each experimental pen contained pine shavings as litter at a depth of approximately 5 cm. Two suspended nipple drinkers (3.2 pullets per nipple) provided water ad libitum throughout the experiment. The stocking density was 5.4 birds/m^2. There were 3 round hanging feeders in each CON pen, providing 10 cm of feeder space per pullet. The feeder in each PF station was 4.8 cm wide, and only 1 bird was provided access at a time. Temperature was 20.8 ± 0.34°C during the entire experimental period. Photoperiod was 10L:14D with a light intensity of 10 lux. A single broiler breeder grower diet (Table 1) was formulated according to breeder recommendations (Aviagen, 2013) and provided in pellet form to all treatments for the duration of the study.

Table 1. Composition and calculated analysis of broiler breeder pullet grower diet provided from 10 to 23 wk of age.

Ingredient	g/kg
Corn	250
Wheat	470
Soybean meal	50
Oats	97.6
Canola meal	90
Ground limestone	10.8
Dicalcium phosphate	15.3
Choline chloride premix	5
Vitamin premix[1]	2.5
Mineral premix[2]	2.5
NaCl	4.5
D, L-methionine	0.9
L-lysine	0.4
Enzyme[3]	0.5
Total:	1,000
Analyzed composition, as fed basis	
AME (kcal/kg)	2,744
CP (g/kg)[4]	158
Calculated composition, as fed basis	
AME (kcal/kg)	2,900
CP (g/kg)	155
Calcium (g/kg)	9
Non-phytate phosphorous (g/kg)	4.2
Available lysine (g/kg)	6.8
Available methionine (g/kg)	3.7
Available methionine + cysteine (g/kg)	6.5

[1]Premix provided per kilogram of diet: vitamin A (retinyl/acetate), 10,000 IU; cholecalciferol, 4,000 IU; vitamin E (DL- α-tocopheryl acetate), 50.0 IU; vitamin K, 4.00 mg; pantothenic acid, 15.0 mg; riboflavin, 10.0 mg; folacin, 2.00 mg; niacin, 65 mg; thiamine, 4.00 mg; pyridoxine, 5.00 mg; vitamin B12, 0.02 mg; biotin, 0.20 mg.

[2]Premix provided per kilogram of diet: iodine, 1.65 mg; Mn, 120 mg; Cu, 20.0 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).

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

Diet Composition

The AME content of the diet was determined by adding 2% acid-insoluble ash marker (Celite, Celite 281, Lompoc, CA) for 4 d in the diet at both 16 and 23 wk of age. Two birds in each pen (14 per treatment) were randomly selected at 16 and 23 wk of age and euthanized by cervical dislocation 4 h after the CON treatment birds were fed. Ileal digesta samples were collected by gently squeezing the intestinal tract from Meckel's diverticulum to the ileal-cecal-colon junction. Digesta samples were pooled for each experimental pen, and stored at –20°C until analysis. Samples were later oven-dried at 60°C for 48 h and ground prior to analysis. Insoluble ash content of diet and digesta samples was determined. Briefly, acid insoluble ash remained after digesting the digesta samples with 4 N HCL and ashing the residue at 500°C (Vogtmann et al., 1975). Gross energy (**GE**) was measured using bomb calorimetry for feed and digesta samples. The AME values were calculated using the following equation (Scott and Boldaji, 1997):

$$\mathrm{AME} = \mathrm{GE}_{\mathrm{feed}} - \mathrm{GE}_{\mathrm{digesta}} \times \frac{\mathrm{Marker}_{\mathrm{feed}}}{\mathrm{Marker}_{\mathrm{digesta}}}$$

where GE = gross energy (kcal/kg of sample) and Marker = concentration of acid insoluble ash in the sample. After AME determination, a 2% correction was applied to the analyzed AME values for each treatment to correct AME to the energy content of the diet that was free of the acid insoluble ash marker. The AME values were not corrected for nitrogen. Apparent ME values were expressed on an as fed basis. Nitrogen content was determined by the combustion method using a Leco TruMac N determinator (Leco Corporation, St. Joseph, MI), and CP was estimated using a factor of 6.25.

Carcass Traits

At 16 and 23 wk of age, 28 birds per treatment were euthanized and breast muscle and fat pad weights were recorded. Fat pad weight and breast muscle weight as a percentage of live BW were calculated for both treatments.

Statistical Analysis

Analysis of Variance The nonlinear MEI model was fit for the overall experimental period from 10 to 23 wk of age using the NLMIXED procedure of SAS (version 9.4; SAS Inst. Inc., Cary, NC). Linear regression between (a+u) and MEI was conducted using the MIXED procedure. Treatment effects for RFI and total HP (a + u) were subsequently evaluated using the MIXED procedure as a 1-way ANOVA. Treatment effects for MEI, BW, ADG, cumulative FCR, partitioning of MEI toward total HP and BW gain, and carcass traits were evaluated using 2-way ANOVA using the MIXED procedure in SAS, with age and treatment as sources of variation. The PDIFF option of the LSMEANS statement used to estimate pairwise differences between means and differences were reported where $P \leq 0.05$. Trends were considered where $0.05 < P \leq 0.10$.

ME Partitioning Model A nonlinear mixed model (Eq. 1) was used to derive ME requirements for total HP and gain of broiler breeder pullets from 10 to 23 wk of age:

$$\begin{aligned} &\text{Observed MEI} = \text{Expected MEI} + \varepsilon \\ &\text{Expected MEI} = (\mathrm{a}+\mathrm{u}) \times \mathrm{BW}^{\mathrm{b}} + \mathrm{c} \times \mathrm{ADG} \\ &\text{Observed MEI} = (\mathrm{a}+\mathrm{u}) \times \mathrm{BW}^{\mathrm{b}} + \mathrm{c} \times \mathrm{ADG} + \varepsilon \end{aligned} \qquad (1)$$

where MEI was ME intake (kcal/d); a was $\mathrm{ME_m}$ or the average total HP for all pens for the entire experimental period (kcal/kg^b); $u \sim \mathrm{N}(0, \sigma_u^2)$ (kcal/d) was the pen-associated deviation from a such that $a + u_i$ was the total HP estimate for each unique experimental pen i; BW was the average BW (kg) of each experimental unit during each week, which was used to estimate total HP; $\mathrm{BW^b}$ was metabolic BW; c (kcal/g) was the coefficient of ADG (g/d) that defined the ME cost for each g of BW gain; and ε was the residual or unexplained error (RFI; kcal/d).

From 10 to 23 wk of age, the percentage of MEI partitioned to ADG ($\mathrm{G_p}$) and the percentage of MEI partitioned to total HP ($\mathrm{HP_p}$) were calculated weekly as:

$$G_p = \left[\frac{c \times \mathrm{ADG}}{\text{Observed MEI}}\right] \times 100\%$$

$$\mathrm{HP}_p = \left[\frac{[a+u] \times \text{Metabolic BW}}{\text{Observed MEI}}\right] \times 100\%$$

Residual Total HP The relationship between total HP and MEI from 10 to 23 wk of age was estimated by a linear regression (2), modified from Romero et al. (2009b) such that MEI was expressed per unit of metabolic BW:

$$E\,(a+u) = \text{intercept} + \text{slope} \times \mathrm{MEI} + \varepsilon \qquad (2)$$

where $E\ (a+u)$ was the total HP coefficient estimated for each pen (kcal/kg^b); slope (kcal/kg^b/kcal/kg^b) was the coefficient defining the linear rate of change of total HP with respect to MEI (kcal/kg^b); and ε was the RHP (kcal/kg^b). On the resulting graph (see Figure 1), RHP is represented by the vertical distance between every point and the regression line. Since the units for the slope coefficient cancel, the slope can be directly interpreted as the proportion of dietary energy lost by the pullets as heat.

RESULTS AND DISCUSSION

ME Intake

Overall, MEI increased from 148 at wk 10 to 196 kcal/d at wk 23 ($P < 0.001$, Table 2). The BW of pullets also increased from 1,005 to 2,517 g from 10 to 23 wk of age ($P < 0.001$, Table 3). Moreover, ADG increased from 10.7 to 23.1 g from 10 to 23 wk of age ($P < 0.001$, Table 4). Overall MEI for both treatments

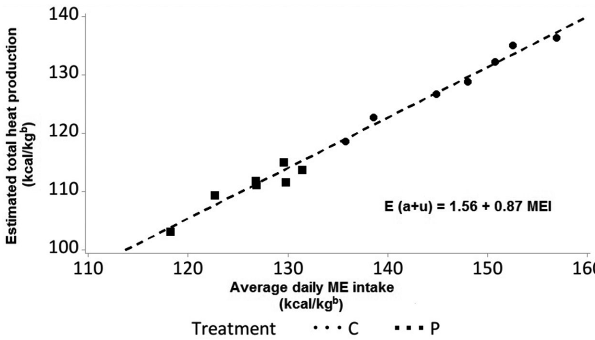

Figure 1. Regression of pen-specific total heat production [E(a + u)] vs. ME intake (R^2 = 0.99; $P < 0.001$). The coefficient b for metabolic BW (kg^b) was independently estimated in the first stage (nonlinear) regression (b = 0.68). Average daily ME intake (MEI; kcal/kg^b) from 10 to 23 wk of age was calculated for each pen. Intercept and slope SEM were 3.96 and 0.028, respectively.

Table 2. Metabolizable energy intake of breeder pullets on precision feeding (PF) and conventional skip-a-day (CON) feeding treatments from 10 to 23 wk of age.

	Treatment × age effect		Age effect
	PF	CON	Overall
Age (wk)		kcal/d	
10 to 11	174[a]	122[b]	148[g]
11 to 12	156	127	141[g]
12 to 13	157	147	152[g]
13 to 14	128	150	139[g]
14 to 15	122[b]	159[a]	140[g]
15 to 16	157	153	155[g]
16 to 17	142[b]	221[a]	182[f]
17 to 18	210	182	196[f]
18 to 19	166[b]	277[a]	222[e]
19 to 20	174[b]	213[a]	193[f]
20 to 21	236	257	246[d]
21 to 22	274	287	280[c]
22 to 23	166[b]	227[a]	196[f]
Treatment effect	174[s]	194[r]	-
Source of variation	DF	SEM	*P*-value
Treatment	1	3.23	<0.001
Age	12	8.23	<0.001
Treatment × age	12	11.64	<0.001

[a,b]Means within row within treatment × age effect with no common superscript differ ($P < 0.05$).
[c–g]Means within age effect with no common superscript differ ($P < 0.05$).
[r,s]Means within treatment effect with no common superscript differ ($P < 0.05$).

increased from 10 to 23 wk of age primarily because BW increased with age and broiler breeder pullets needed more ME to meet their maintenance requirements, and ADG also increased with age, for which ME was also required. The ME requirement for broiler breeders has been defined as that required for maintenance, gain, and egg production (Sakomura, 2004). However, there is no egg production in rearing period of broiler breeders. Thus, pullets partition ME to maintenance and BW gain. Since ME_m is equal to total HP (Zuidhof, 2018), MEI is partitioned to total HP and growth during rearing period of broiler breeder pullets.

Metabolizable energy intake was reported as 155 and 316 kcal/d for broiler breeder pullets at 10 and 23 wk of age, respectively (Sakomura, 2004). At 20 wk of age, MEI was estimated 270 kcal/d for broiler breeder pullets (Pinchasov and Galili, 1990). In the present study, the average MEI of broiler breeder pullets from 10 to 12 wk of age was 147 and from 20 to 23 wk of age was 241 kcal/d. This suggests that MEI of pullets in

Table 3. Body weight of breeder pullets on precision feeding (PF) and conventional skip-a-day (CON) feeding treatments from 10 to 23 wk of age.

	Treatment × age effect		Age effect
	PF	CON	Overall
Age (wk)		g	
10	1,033[a]	977[b]	1,005[p]
11	1,169[a]	1,061[b]	1,115[o]
12	1,255[a]	1,149[b]	1,202[n]
13	1,308[a]	1,221[b]	1,265[m]
14	1,354[a]	1,300[b]	1,327[l]
15	1,415[a]	1,365[b]	1,390[k]
16	1,482[a]	1,433[b]	1,458[j]
17	1,584[a]	1,538[b]	1,561[i]
18	1,715[a]	1,645[b]	1,680[h]
19	1,870[a]	1,751[b]	1,811[g]
20	2,048[a]	1,885[b]	1,966[f]
21	2,200[a]	2,039[b]	2,120[e]
22	2,391[a]	2,226[b]	2,308[d]
23	2,610[a]	2,424[b]	2,517[c]
Treatment effect	1,674[r]	1,572[s]	-
Source of variation	DF	SEM	*P*-value
Treatment	1	5.3	<0.001
Age	12	10.1	<0.001
Treatment × age	12	14.8	<0.001

[a,b]Means within row within treatment × age effect with no common superscript differ ($P < 0.05$).
[c–o]Means within age effect with no common superscript differ ($P < 0.05$).
[r,s]Means within treatment effect with no common superscript differ ($P < 0.05$).

Table 4. Average daily gain of breeder pullets on precision feeding (PF) and conventional skip-a-day (CON) feeding treatments from 10 to 23 wk of age.

	Treatment × age effect		Age effect
	PF	CON	
Age (wk)		g/d	
10 to 11	11.8	9.7	10.7[d-f]
11 to 12	11.6	15.1	13.4[b-d]
12 to 13	2.5	6.8	4.6[f]
13 to 14	9.9	16.2	13.0[c-e]
14 to 15	8.8	3.6	6.2[e,f]
15 to 16	9.9	15.7	12.8[c-e]
16 to 17	18.3	15.2	16.7[a-d]
17 to 18	18.5	15.2	16.8[a-d]
18 to 19	21.8	15.1	18.5[a-c]
19 to 20	21.3	18.8	20.0[a,b]
20 to 21	20.6	21.7	21.2[a]
21 to 22	21.6	22.5	22.0[a]
22 to 23	23.3	23.0	23.1[a]
Treatment effect	15.4	15.3	–
Source of variation	DF	SEM	*P*-value
Treatment	1	0.96	0.94
Age	12	2.45	<0.001
Treatment × age	12	3.47	0.72

[a–f]Means within age effect with no common superscript differ ($P < 0.05$).

2017 has reduced gradually since 1990. There are 2 main reasons for this. The first relates to changes in broiler breeder body composition. Broilers in 2005 had greater breast muscle weight and yield compared to birds in 1957, whereas abdominal fat pad decreased from 1957 to 2005 due to commercial selection pressure (Zuidhof et al., 2014). The selection pressure has also affected the body composition of broiler chickens parents stocks. Broiler breeders in 1980 had lower breast muscle percentage compared to the broiler breeders in 2000 (14.9% vs. 21.2%) and higher fat pad percentage (5.4% vs. 2.7%) due to genetic selection for broiler productivity traits (Eitan et al., 2014).

Increasing breast muscle in modern broiler breeders indicates that protein deposition is increased. Lean tissue is composed of protein (4.1 kcal/g) and water (0 kcal/g) and deposition in the body is less energetically expensive compared to fat deposition, which requires approximately 9.2 kcal/g (Zuidhof et al., 2014). A reduction in MEI over time is consistent with highly feed restricted modern broiler breeder pullets depositing relatively more lean tissue and less adipose tissue. The second reason that MEI was reduced may be related to increased efficiency. Although the growth potential of broilers increased more than 450% from 1957 to 2005, FCR to 56 d of age has decreased to 1.918 in 2005 from 2.854 in 1957 (Zuidhof et al., 2014). Moreover, modern broilers have greater gut mass compared to unselected birds which increase digestion and absorption in modern broilers relative to unselected ones (Jackson and Diamond, 1996). It follows that body composition changes and increased efficiency in modern broiler breeder pullets resulted in their lower MEI compared to the pullets in the 2000s and in the 1990s.

From 10 to 12 wk of age, while PF pullets were being familiarized with the feeding station, the target BW was set to the weight of the heaviest bird. During this time, most of the PF birds were allowed to eat more than the CON treatment birds. Much of this occurred during the first week of the study—during week 10, PF pullets consumed 42% more ME compared to CON pullets ($P < 0.05$, Table 2). The overall average daily MEI for PF treatment (174 kcal/d) was 90% of the CON treatment (194 kcal/d; $P < 0.001$, Table 2). Similarly, but to a lesser degree, MEI of daily fed pullets (15,204 kcal/bird; 159 kcal/d) from 15 to 22 wk of age was 97% of MEI in skip-a-day broiler breeder pullets (15,729 kcal/bird; 164.5 kcal/d; Zuidhof et al., 2015). Skip-a-day broiler breeder hens had around 70 kcal/d higher feed intake (246 g/bird/d) compared to hens in daily restricted method to reach the same BW (de Beer and Coon, 2007). Skip-a-day feeding can reduce metabolic efficiency because broiler breeders need to store and mobilize greater amounts of nutrients constantly compared to daily fed (Richards et al., 2010). Deposition and mobilization of nutrients are not completely efficient processes (McCue 2006; de Beer and Coon, 2007) and lower efficiency of skip-a-day broiler breeders compared to daily fed broiler breeders can be attributed to repeated storage and mobilization of nutrients (de Beer and Coon, 2007). Increased feeding frequency in PF pullets could have increased their efficiency, thereby requiring a lower MEI to photostimulation age compared with the CON treatment.

Table 5. Daily total heat production (HP), residual feed intake (RFI), residual daily total heat production (RHP), and proportion of expected ME intake (MEI) partitioned to HP and growth by breeder pullets on precision feeding (PF) and conventional skip-a-day (CON) feeding treatments from 10 to 23 wk of age.

	PF	CON	SEM	*P*-value
Total HP[1] (kcal/kg$^{0.68}$)	111	129	0.54	<0.001
RFI[2] (kcal/d)	–3.8	3.7	2.84	0.064
RHP[3] (kcal/kg^{b})	–0.12	0.12	0.47	0.73
Total HP (% of MEI)	86.9	89.0	0.61	0.020
Growth (% of MEI)	13.1	11.0	0.62	0.020

[1]Calculated using a nonlinear mixed model: MEI = (120 + u) × BW$^{0.68}$ + 1.52 × ADG + ε, where u ∼ N(0, $\sigma^2{}_u$); ADG = average daily gain

[2]Calculated using residuals of the nonlinear mixed model: RFI = observed MEI - predicted MEI MEI = 120 + u)× BW $^{.68}$ + 1 .52 × ADG + ε

[3]Calculated as the residual of the regression between $a + u$ and *MEI* for each pen: a + u = 1.56 + 0 .87 MEI + ε

where $a + u$ = predicted total HP; ε = RHP

The first priority of animals is to satisfy maintenance energy requirement after which energy is partitioned to growth and egg production (Pishnamazi et al., 2015). Although PF hens had lower MEI compared to CON hens during the entire experimental period, they had greater BW relative to CON birds (Table 3). The CON and PF pullets in the present study partitioned 89.0 vs. 86.9% of the MEI into total HP, respectively, during the entire experimental period ($P = 0.020$, Table 5). Conversely, birds in the CON and PF treatments partitioned 11.0 and 13.1% of MEI into BW gain (growth), respectively ($P = 0.02$, Table 5). The results of the present study suggest that CON and PF hens partitioned MEI in different proportions, which may infer differences in their underlying metabolism.

Growth

Both treatments were grown using the same target BW until 23 wk of age, with the exception that from 10 to 12 wk of age the target BW for PF pullets was higher in the PF treatment to ensure the heaviest birds had access to feed. There was no treatment difference in mortality (4.1% in both treatments; data not shown). Weekly and overall ADG did not differ between PF and CON pullets from 10 to 23 wk of age (Table 4). It was reported that ADG was 13 and 16 g/d for broiler breeder pullets from 9 to 14 and 15 to 20 wk of age, respectively (Sakomura et al., 2003). Moreover, ADG was 14 g/d from 3 to 20 wk of age (Pinchasov and Galili, 1990). These values were similar to the 15 g/d reported in the current study. The target BW of broiler breeders have undergone little changes during the past 30 yr

Table 6. Proportional breast muscle and abdominal fat pad weights of breeder pullets on precision feeding (PF) and conventional skip-a-day (CON) feeding treatments from 10 to 23 wk of age.

	Breast muscle						Fat pad					
	Treatment × age effect				Age effect		Treatment × age effect				Age effect	
Age (wk)	PF	SEM	CON	SEM	Overall	SEM	PF	SEM	CON	SEM	Overall	SEM
						% of live BW						
16	16.3	0.60	16.1	0.45	16.2[y]	0.44	0.2	0.10	0.2	0.10	0.2[y]	0.10
23	19.7	0.48	19.9	0.41	19.8[z]	0.41	1.2[b]	0.17	1.7[a]	0.14	1.4[z]	0.13
Treatment effect	18.0	0.46	18.0	0.39	–		0.7[s]	0.12	0.9[r]	0.11	–	
Source of variation	DF	*P*-value					DF		*P*-value			
Treatment	1	0.92					1		0.002			
Age	1	<0.001					1		<0.001			
Treatment × age	1	0.49					1		0.015			

[a,b]Means within variable within row for treatment × age effect with no common superscript differ ($P < 0.05$).
[y,z]Means within variable within age effect with no common superscript differ ($P < 0.05$).
[r,s]Means within variable within treatment effect with no common superscript differ ($P < 0.05$).

relative to large increases in growth potential (Renema et al., 2007).

Carcass Traits

There was no treatment effect on breast muscle as a percentage of BW at 16 or 23 wk (Table 6). There was no significant treatment difference in fat pad percentage at 16 wk of age; however, in spite of having lower BW at 23 wk, pullets in the CON treatment had a 1.4-fold increase in relative fat pad weight compared with the PF treatment (Table 6). Skip-a-day broiler breeder pullets had 10% greater fat pad weights compared to daily fed pullets (37.4 g vs. 33.6 g), 11% less pectoralis major weight (395.0 g vs. 444.3 g), and 10% less pectoralis minor weight (122.3 g vs. 135.5 g) at 22 wk of age ($P < 0.05$; Zuidhof et al., 2015). It was suggested that repeated long durations of negative energy balance in skip-a-day pullets conditioned them to partition more energy into storage in the abdominal fat pad (Zuidhof et al., 2015). In pullets fed skip-a-day, increased expression of genes was involved in lipogenic activity in the liver, such as acetyl–coenzyme A carboxylase, malic enzyme, fatty acid synthase compared to daily fed birds (de Beer et al., 2007). Moreover, excess dietary energy during feeding is converted to triglycerides which are stored in adipose tissues (de Beer et al., 2007). Fasting alters metabolism in broiler breeders, increasing lipid mobilization and plasma free fatty acid levels to provide required energy (Richards et al., 2010). During fasting, the body needs to mobilize fatty acids from adipose tissues and glucose from liver glycogen (de Beer et al., 2007). In skip-a-day programs, more short-term nutrient storage and subsequent mobilization is needed compared with daily feeding program (Richards et al, 2010) to maintain homeostasis. After depleting liver glycogen, catabolism of muscle proteins meets the energy requirements for the body through gluconeogenesis (Robert et al., 2003). After feeding, more glucose is available from feed source. Some is used to meet energy requirements immediately, much is stored in the liver as glycogen and some is stored in muscles, and the rest is converted via lipogenesis and stored as fat (Robert et al., 2003). Lipogenesis starts with acetyl-CoA, a molecule that is formed from the metabolism of glucose (Robert et al., 2003). Surplus glucose and intermediates such as pyruvate, lactate, and acetyl-CoA are converted to fat through lipogenesis during the anabolic phase of the feeding cycle (Robert et al., 2003).

In the current experiment, the CON treatment had a lower feeding frequency (once per 48 h) and therefore greater temporal variation in glucose availability, requiring more storage and mobilization of nutrients, which probably provided more substrate for lipogenesis in CON birds. The CON pullets had higher MEI compared to PF pullets, which indicates that they had more total energy available; however, they lost more energy as heat relative to PF pullets (discussed further in the total HP section).

ME Partitioning Model

The quantitative model (3) describing ME partitioning in both treatments was ($P < 0.001$):

$$\begin{aligned} \mathrm{MEI} = (120 + u) \times \mathrm{BW}^{0.68} + 1.52 \times \mathrm{ADG} + \varepsilon \\ u\tilde{N}\left(0, \sigma_u^2\right); \sigma_u = 12.1; \\ e\tilde{N}\left(0, \sigma_e^2\right); \sigma_e = 40.6 \end{aligned} \quad (3)$$

The coefficient $a = 120$ indicates that total HP averaged 120 kcal/BW$^{0.68}$; the coefficient $c = 1.52$ estimates that broiler breeder pullets needed 1.52 kcal of ME per g of BW gain. The SD for total HP (σ_u) was 12.1 kcal/kg$^{0.68}$ and the SD for the residual term (σ_e) was 40.6 kcal/d. The SD for total HP was 22.8 and $\sigma_e = 6.6$ kcal/kg$^{0.75}$ in broiler chickens (Zuidhof et al., 2014). The SD for total HP was 21.3 for broiler breeders whose feed was allocated on a group basis from 20 to 60 wk of age, and $\sigma_u = 58.3$ kcal/kg$^{0.54}$ when feed was allocated on an individual basis (Romero et al., 2009a). The analysis in the current study was conducted at pen level, which may explain the lower variance compared with Romero et al. (2009a).

The ME Requirement for BW Gain

The ME cost for BW gain ($\mathbf{ME_g}$) in the current study was 1.52 kcal/g. Two age-specific ME requirement models were developed for specific ages of Hubbard Hi-Yield broiler breeder pullets using a factorial method (Sakomura et al., 2003). They estimated ME_g to be 2.50 kcal/g from 9 to 14 wk, and 3.24 kcal/g from 15 to 20 wk. Moreover, these researchers used a linear model to estimate ME_g, in contrast with the nonlinear model used in the current study. 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 body composition.

Age-related changes in the chemical composition of growth can affect ME requirement for growth. Protein contains 5.5 kcal/g (Pullar and Webster, 1977; Chwalibog, 1991), and lean tissue is made up of 75% water (0 kcal/g) and 25% protein (Claus and Weiler, 1994). Thus, assuming lean tissue contains primarily water and protein and without considering any total HP as a byproduct of formation, the retained energy for each g of lean tissue is approximately 1.38 kcal/g. The coefficient $c = 1.52$ kcal/g estimated in the current experiment is very close to the value of retained energy for each gram of lean tissue and it is consistent with the observation that modern broiler breeders deposit primarily lean tissue while under conventional feed restriction. Because of continued selection for broiler traits, modern broiler breeder pullets deposit less fat and may require less energy for BW gain compared to broiler breeders in 2003 (Sakomura et al., 2003).

Total HP

The ME_m includes energy required for basal metabolism, thermal regulation, and activity (NRC, 1981; Emmans, 1994; Zuidhof, 2018) and since this energy is lost as heat, ME_m is equal to total HP (Zuidhof, 2018). Total HP of broiler breeders raised on the floor was 20% higher than those raised in cages (Sakomura, 2004). Physical activity accounted for 20% of total HP (Wenk, 1997). Temperature can also affect total HP. Total HP decreased in a quadratic manner with increasing temperature to 24.3°C, after which total HP increased (Pishnamazi et al., 2015). There was a positive relationship between feed intake and total HP in broiler breeder pullets ($R^2 = 0.95$; Pishnamazi et al., 2008).

Body composition can also influence total HP. For example, body fat has a lower maintenance cost than body protein (Close, 1990). Total HP in broiler breeder pullets was higher than in hens because mature birds have a higher proportion of fat compared to protein in their bodies (Sakomura, 2004). Moreover, higher total HP in growing animals was due to high energy demand for protein synthesis (Blaxter, 1989). In the current experiment, total HP of CON pullets was 16% higher than PF pullets (129 and 111 kcal/kg $BW^{0.68}$, respectively; $P < 0.001$; Table 5). However, CON pullets had greater fat pad percentage at 23 wk of age compared to PF pullets and CON pullets had higher total HP compared to PF pullets. Still, the CON pullets had higher total HP compared to PF pullets, and a higher MEI (194 vs. 174 kcal/d, respectively). Thus, one factor contributing to higher total HP by CON birds is diet-induced thermogenesis. The slope of a regression between total HP and MEI quantifies this (Figure 1). In the current study 75% of every additional kcal of ME consumed was lost as heat. This will be discussed further in the next section.

Behavioral observations from the current experiment showed that although PF pullets had 1.6-fold higher incidence of aggressive behaviors (12.7 vs. 8.0 per 15 min) compared with CON pullets ($P = 0.001$; Girard et al., 2017), they walked and stood 7% less than CON pullets (Gilmet, 2015). Thus, CON pullets had higher physical activity compared to PF pullets. No observations were made during CON feeding time, which was likely the time when CON birds had much higher rates of activity and aggression. Thus, physical activity may have also contributed to higher total HP of CON compared with PF treatment pullets.

Residual Total HP

Regression analysis using combined PF and CON treatment data defined the relationship between total HP and MEI ($P < 0.001$; Figure 1):

$$E\,(a + u) = 1.56 + 0.87 \text{ MEI} \tag{4}$$

This result infers that total HP increases linearly with increasing MEI. Since the units for the slope coefficient cancel, the slope can be directly interpreted as the proportion of MEI that is lost as heat. Specifically, the model predicts that 87% of ME consumption by broiler breeder pullets from 10 to 23 wk of age is lost as heat. This linear regression model (Eq. 4) was firstly defined by Romero et al. (2009b) to account for intake-related changes in total HP, which was the main shortcoming of previous mathematical models. Those authors reported an apparently lower rate of total HP (0.34 kcal/$kg^{0.54}$/kcal consumed) for broiler breeder hens from 20 to 60 wk of age. When MEI is corrected to metabolic BW, this translates to a total HP of 25% early in production to 15% later in the laying phase. Since feed restriction is less severe during the laying phase, lower total HP would be expected compared with the pullet phase. By changing the units of the independent x-axis variable to intake per unit of metabolic BW, interpretation of the result directly as efficiency of dietary energy use is simplified.

It was reported earlier that PF and CON treatments partitioned 86.9 and 89.0%, respectively, of MEI toward total HP. The estimate of 87% thus seems a reasonable estimate. It was estimated that 70 to 88% of MEI partitioned to total HP in broiler breeder pullets from 5 to 20 wk of age (Sakomura et al., 2003). This value appears to have increased with further selection for broiler traits.

Energetic Efficiency

In the current study, RFI was not affected by treatment at the $P < 0.05$ level (–3.8 and 3.7 kcal/d, respectively; $P = 0.064$; Table 5). Residual feed intake was estimated by deducting expected MEI (for total HP + ADG) from the observed MEI. Differences in the composition of BW gain affected RFI (Basarab et al., 2003). Inefficient steers with high RFI had higher MEI, higher HP ($P < 0.01$), and greater carcass fat ($P < 0.05$) compared to efficient ones (Basarab et al., 2003). The higher MEI of inefficient steers was due to an increase in the ME_m and heat increment of feeding (Basarab et al., 2003). The variation in feed efficiency of high and low RFI steers was due to differences in fat deposition of internal organs and energy requirements (Gomes et al., 2012). The increase in carcass fat of the CON treatment (0.5% of live BW) in the current experiment (Table 6) may have been insufficient to identify a significant difference in RFI.

In the current experiment, although CON pullets had higher MEI compared to PF pullets, they did not have greater BW or ADG compared with PF hens. Moreover, CON pullets had higher total HP (89% of MEI) relative to PF pullets (86.9% of MEI) due to temporal variation in ME supply, creating conditions that required storage and mobilization of nutrients. Thus, CON pullets were less efficient than PF pullets.

Decreased energetic efficiency of laying hens (estimated using RFI) was due to higher feed intake, which indicated that RFI was impacted by heat increment of feeding (Swennen et al., 2007). However, it is important to note that, in most cases, high producing animals have higher feed intake and RFI can penalize the extra feed intake. Residual maintenance ME (RHP in the current study) can estimate energetic efficiency without being confounded by feed intake (Romero et al., 2009a). Residual HP is estimated from the residual of a linear regression between total HP (a + u) and MEI, and it indicates heat loss in a way that is unbiased by MEI. It is therefore, an estimate of relative efficiency after considering not only energy requirements for maintenance and retained energy but also for feed intake.

The points below the regression line in Figure 1 indicated the more efficient pens and the points above the regression line indicated the less efficient pens. Residual HP did not differ between CON and PF treatments ($P = 0.73$; Table 5). Although the CON hens had higher MEI (194 kcal/d) compared to the pullets in PF treatment (174 kcal/d) and partitioned more energy toward total HP (89.0% of the observed MEI) relative to PF pullets (86.9% of the observed MEI), they did not lose more energy daily per unit of metabolic BW. Thus, treatment differences in body composition and feeding frequency-related differences in nutrient mobilization and storage likely contributed to differences in efficiency between treatments in the current study.

Table 7. Cumulative feed conversion ratio of breeder pullets on precision feeding (PF) and conventional skip-a-day (CON) feeding treatments from 10 to 23 wk of age.

	Treatment × age effect		Age effect
	PF	CON	
Age (wk)		g feed:g gain	
10 to 11	2.273[b]	3.510[a]	2.982[h]
10 to 12	3.063[b]	4.033[a]	3.548[g]
10 to 13	3.453	3.850	3.651[g]
10 to 14	4.192	4.494	4.343[e,f]
10 to 15	4.236	4.306	4.271[f]
10 to 16	4.512	4.901	4.707[c,d]
10 to 17	4.600	5.011	4.806[c]
10 to 18	4.538	4.842	4.690[c,d]
10 to 19	4.325[b]	5.176[a]	4.750[c,d]
10 to 20	4.096[b]	5.107[a]	4.601[c-e]
10 to 21	4.094[b]	5.087[a]	4.591[c-e]
10 to 22	4.189[b]	5.047[a]	4.618[c-e]
10 to 23	4.057[b]	4.888[a]	4.472[d-f]
Treatment effect	3.972[s]	4.635[r]	-
Source of variation	DF	SEM	*P*-value
Treatment	1	0.04	<0.001
Age	12	0.11	<0.001
Treatment × age	12	0.16	0.002

[a,b]Means within row for treatment × age effect with no common superscript differ ($P < 0.05$).
[c–h]Means within age effect with no common superscript differ ($P < 0.05$).
[r,s]Means within treatment effect with no common superscript differ ($P < 0.05$).

Feed Conversion Ratio

In the current experiment, cumulative FCR to 23 wk in the PF treatment was 83% of FCR in the CON treatment (Table 7). Feed conversion ratio was lower in 3 daily fed treatments (standard diet, scatter feeding, and BW grading) compared with skip-a-day pullets (Zuidhof et al., 2015). In addition, it was reported that FCR in daily fed pullets at 21 wk of age was 95% of the FCR of skip-a-day fed pullets (de Beer and Coon, 2009). Thus, research has consistently shown that birds with higher feeding frequency grow more efficiently compared to skip-a-day fed birds.

Although FCR is a good indicator of efficiency, it may not be the best one. Residual feed intake is a biological indicator of energetic efficiency and although it is more difficult to calculate, it is a more precise indicator of efficiency compared to FCR because it accounts for maintenance (total HP), BW gain, and egg production (where relevant) energy requirements.

On the other hand, RFI may not the best indicator of the energetic efficiency of biological processes. Residual feed intake is biased by differences in feed intake levels (Gabarrou et al., 1998). Residual HP is relatively new indicator of energetic efficiency. Although RHP is more complicated to calculate compared to RFI, it is to date the most precise indicator of efficiency at a biological level because it estimates the energy losses (as heat) without being biased by energy levels. According to the current analysis, the biological efficiency of the pullets in both treatments was similar. Thus, differences in efficiency can be attributed to energy using processes such as nutrient storage and mobilization, or fat deposition, which were likely managed similarly by birds in both treatments in the current study.

In conclusion, although CON pullets actually had lower BW, they had higher MEI and higher total HP compared to PF pullets. The PF pullets had lower cumulative FCR compared to CON pullets; thus, PF pullets used their feed more efficiently. However, residual HP analysis suggests that both treatments had similar biological efficiency. The CON treatment pullets did not appear to lose more energy as heat as a result of diet-induced thermogenesis, but because they were fed less frequently, probably used the extra energy they consumed to store and mobilize nutrients, and to deposit fat in their body.

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