METABOLISM AND NUTRITION

Modeling life-time energy partitioning in broiler breeders with differing body weight and rearing photoperiods

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ABSTRACT Understanding energy partitioning in broiler breeders is needed to provide efficiency indicators for breeding purposes. This study compared 4 nonlinear models partitioning metabolizable energy (**ME**) intake to BW, average daily gain (**ADG**), and egg mass (**EM**) and described the effect of BW and rearing photoperiod on energy partitioning. Ross 708 broiler breeders (n = 180) were kept in 6 pens, controlling individual BW of free run birds with precision feeding stations. Half of the birds in each chamber were assigned to the breeder-recommended target BW curve (Standard) or to an accelerated target BW curve reaching the 21-week BW at week 18 (High). Pairs of chambers were randomly assigned to 8L:16D, 10L:14D, or 12L:12D rearing photoschedules and photostimulated with 16L:8D at week 21. Model [I] was: $MEI_d = a \times BW^b + c \times ADG \times BW^d + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/day); BW in kg; ADG in g/day; EM in g/day. Models [II–IV] were nonlinear mixed versions of model [I] and included individual [II], age-related [III], or both individual and age-related [IV] random terms to explain these sources of variation in maintenance requirement (a). Differences were reported as significant at $P \leq 0.05$. The mean square error was 2,111, 1,532, 1,668, and 46 for models [I–IV] respectively, inferring extra random variation was explained by incorporating 1 or 2 random terms. Estimated ME partitioned to maintenance [IV] was 130.6 ± 1.15 kcal/kg$^{0.58}$, and the ME requirement for ADG and EM were 0.63 ± 0.03 kcal/g/kg$^{0.54}$ and 2.42 ± 0.04 kcal/g, respectively. During the laying period, maintenance estimates were 124.2 and 137.4 kcal/kg$^{0.58}$ for standard and high BW treatment, and 130.7, 132.2, and 129.5 kcal/kg$^{0.58}$ for the 8L:16D, 10L:14D, or 12L:12D treatments, respectively. Although hens on the standard BW treatment with a 12L:12D rearing photoschedule were most energetically conservative, their reproductive performance was the poorest. Model IV provided a new biologically sound method for estimation of life-time energy partitioning in broiler breeders including an age-related random term.

Key words: daylength, residual heat production, efficiency, maintenance requirements

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INTRODUCTION

Indirect calorimetry and the comparative slaughter technique have been often used to study energy partitioning in poultry (Birkett and de Lange, 2001). However, mathematical models have become increasingly popular to help understand energy partitioning. These energy partitioning models have focused previously on either the growing period (Sakomura et al., 2003; Pishnamazi et al., 2015; Hadinia et al., 2018) or the laying period (Pishnamazi et al., 2008; Romero et al., 2009b; Darmani Kuhi et al., 2011, 2019). Although energy partitioning estimates for each period separately are important, models could be improved including both phases such that the effect of age on energy partitioning and the efficiency of growth and egg production over their life-time can be studied. This would benefit nutritionist and breeding companies as understanding of energy partitioning would provide tools to minimize energy loss to heat. The metabolizable energy (**ME**) intake lost as heat or total heat production (**HP**) is equivalent to the ME for maintenance (**ME_m**; Zuidhof, 2019). The ME_m requirements reported in the literature have been confounded by 1) individual variation and 2) different degrees of (age-related) feed restriction during rearing and laying phase.

Several indicators have been used to determine the efficiency of growth and egg production in poultry, such as the feed conversion ratio (**FCR**), residual feed intake (**RFI**), or residual heat production (**RHP**), also known as residual maintenance ME requirements (Willems

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et al., 2013). Feed conversion ratio is defined as the amount of feed consumed per unit of weight gain (**FCR_g**) or unit of egg production (**FCR_{egg}**; Skinner-Noble and Teeter, 2003). Feed conversion ratio does not account for the variability ME_m requirements; therefore, FCR_g increases with age and BW because of higher ME_m requirements. Residual feed intake is defined as the difference between actual and expected feed intake as predicted from the requirements for ME_m, BW gain, and egg production (Byerly, 1941; Luiting, 1990). Although RFI accounts for ME_m requirements, it does not account for the heat increment of feeding (Swennen et al., 2007). Therefore, RFI can penalize high producing animals, as they increase feed intake to support production, yet consequentially also have an increased heat increment of feeding. Environmental factors affecting ME_m requirements may also bias estimates of FCR and RFI. Residual heat production or residual maintenance ME is the residual of the linear relationship between ME_m requirement, also referred to as total HP and ME intake (Romero et al., 2009a; Hadinia et al., 2018). Residual heat production removes the confounding effect of ME intake or feed intake, including the heat increment of feeding and may therefore be a better indicator of biological efficiency in poultry (Romero et al., 2009a).

The above described efficiency indicators are both phenotypically and genetically correlated, and the strength of this correlation depends on the age of the bird (Willems et al., 2013) and potentially environmental factors affecting ME_m requirements, such as temperature. For example, genetic correlations between FCR and RFI were higher in broilers assessed from 28 to 35 D (0.31) compared with broilers assessed from 35 to 42 D (0.84, Aggrey et al., 2010). In addition, the level and composition of gain changes during the lifetime (Vignale et al., 2017; Salas et al., 2019); therefore, ME_m requirements might change as a result of body composition changes (Sakomura et al., 2003). It was concluded that estimated ME_m requirements for broiler breeders reduced from week 4 (~200 kcal/day) to week 16 (~100 kcal/day; Pishnamazi et al., 2008), which was related to feed intake per unit of metabolic BW ($R^2 = 0.99$, $P < 0.001$). However, to our knowledge, models including an effect of age on ME_m have not been reported.

Energy partitioning is affected by dietary and environmental factors, such as lighting and feed allowance. Lighting programs in broiler breeders aim almost exclusively at dissipating the photorefractory state to prepare pullets for photostimulation, sexual maturation, and egg production (Lewis, 2006). It was concluded that BW at week 20 decreased by about 15 g for each hour of photoperiod increase for pullets provided the same feed allocation during rearing (Lewis, 2006). It was hypothesized to be an effect of increased ME_m requirements with longer photoperiod, as broiler breeders reduced HP during the scotoperiod (Macleod et al., 1980). In addition, it was found that at the same level of production, birds allowed accelerated growth from week 10 to achieve 2.1 kg at week 17 had a higher FCR_{egg} compared with birds reared to achieve 2.1 kg at week 21 (Lewis et al., 2005). The birds achieving the 2.1 kg target at week 17 had a higher BW at sexual maturity compared with birds that achieved the 2.1 kg at week 21 (3.6 kg vs. 3.4 kg); hence, their ME_m requirements would have been higher as well.

Data used to test energy efficiency have often been collected from caged birds to measure individual feed intake and egg production. However, in practice, broiler breeders are housed free run in groups to facilitate natural mating. Novel technologies such as the precision feeding (**PF**) system (Zuidhof et al., 2017, 2019) allow for the first time collection of feed intake and BW data from individual free run birds. The aim of this study was to compare 4 different models partitioning ME intake to BW, average daily gain (**ADG**), and egg mass (**EM**) over the lifetime of group housed broiler breeders fed with the PF system. Model fit and bias were compared. The best fitting model was used to estimate RFI and RHP. It was hypothesized that FCR_g, FCR_{egg}, RFI, and RHP would be decreased in treatments with reduced photoperiod and reduced BW.

MATERIALS AND METHODS

Experimental Design

The animal protocol for the study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed principles established by the Canadian Council on Animal Care Guidelines and Policies (CCAC, 2009). The experiment was conducted as randomized block design of a 2 × 3 factorial arrangement of treatments with pullets reared either on a breeder-recommended target BW curve (Standard; Aviagen, 2016) or an accelerated target BW curve reaching the 21 wk BW at 18 wk (high) and maintained under 8L:16D, 10L:14D, or 12L:12D photoschedules during rearing. The high target BW was 22% higher than the standard target BW at 21 wk of age, and the 565 g BW difference was maintained from day 193 to the end of the study. Rooms were randomly assigned to the rearing photoschedules, and birds within rooms were randomly assigned BW treatments. Individual bird was used as experimental unit.

Animals and Housing

The experimental protocol was previously described in full detail by van der Klein et al. (2018). Ross 708 broiler breeder chicks (n = 180; provided by Aviagen, Huntsville, AL) were randomly allocated in 6 environmentally controlled rooms. Each room was equipped with a PF system (Zuidhof et al., 2017, 2019), which controlled individual feed intake to achieve and adhere to the assigned target BW curves. The PF system recorded individual BW and individual feed intake for every feeding bout. Water was provided *ad libitum* during the entire experiment. From day 0 to 16, birds were fed *ad libitum* and were trained to use the PF system after which birds were tagged with a radio frequency identification (**RFID**) wing band. Birds were randomly assigned to either the standard or high BW treatment, such that approximately half of the birds per room were assigned to either target BW curve. From day 16 onwards, birds were fed individually and were allowed access to 10 g feed for a duration of 45 s when their BW was lower than their treatment target BW. At week 28, feed allowance was increased from 10 g to 20 g. The duration of the feed bout was maintained at 45 s throughout the study. Birds were ejected from the PF system when their measured BW was equal to or higher than their treatment target. At the start of the experiment, pairs of rooms were randomly assigned to either an 8L:16D, 10L:14D, or 12L:12D rearing photoschedule. All treatments were photostimulated at week 21 with a single abrupt increase to 16L:8D. In each room, environmental temperature was set at 32.0°C at placement, which gradually decreased every day to 20.7°C at day 26. Environmental set temperature remained at 20.7°C throughout the remainder of the experiment. For the first 3 wk, birds received a standard wheat based starter diet (2,900 AME, 19% CP, 1.1% Ca); from week 4 to week 23, pullets received a wheat and barley-based grower diet (2,589 AME, 14.2% CP, and 0.9% Ca); from week 23 to week 34, hens received a wheat-based peak layer diet (2,689 AME, 15.0% CP, and 3.3% Ca); and from week 35 to week 55, hens received a wheat-based post-peak layer diet (2,682 AME, 14.6% CP, and 3.3% Ca). AME, CP, and Ca values of the diets were not analyzed. At week 18, a nest box with 8 nesting sites equipped with RFID readers was installed in each room, which identified eggs of individual hens.

Data Collection

Birds were weighed manually on a daily basis for the first 2 wk to confirm growth and adoption of the PF system. After individual feeding started, the PF system recorded individual BW and feed intake on a per visit basis. Feed intake and visit frequency was checked on a daily basis to ensure all birds were accessing the PF system. Because it would not be possible for floor eggs to be linked with individual hens because hens on different BW treatments were housed in the same room, cloacae of all hens were palpated daily to detect hard-shelled eggs in the shell gland to measure age at first egg and individual egg production from 20 wk to 36 wk. As the majority of the birds on the 8L:16D photoschedule treatment had entered lay by week 36, from 36 wk onward, daily palpation was performed every second week. Eggs were associated with individual hens using the RFID equipped nest box and were weighed daily. Because not all eggs could be associated with individual hens, average egg weight per BW by rearing photoperiod treatment interaction was calculated and used for EM calculations. Eggs between 40 g and 90 g were included in the calculation for average egg weight and egg mass. Average weekly BW [(BW at start of the week + BW at the start of next week)/2] was used for metabolic BW calculations. Average daily gain was defined as the difference between BW at start of the week and BW at the start of the following week, divided by 7 D. Egg production was defined as the number of eggs produced per week divided by 7 D. For week where individual egg production was not measured, egg production was estimated as the average of the egg production of the week before the missing week and the week after the missing week. Egg mass was defined as the product of individual egg production and the average egg weight for the individual's treatment interaction. Cumulative FCR_g was calculated as the cumulative feed intake divided by the cumulative BW gain. The FCR_{egg} was calculated as the average daily feed intake divided by EM. Cumulative FCR_{egg} was calculated as the cumulative feed intake divided by the cumulative EM.

Specification of Models

Four models were evaluated: 1 nonlinear model, 2 nonlinear mixed models with 1 random term, and 1 nested nonlinear mixed model with 2 random terms (Table 1; based on Romero et al., 2009b). For all models, the metabolic BW scaling coefficient was allowed to fluctuate. All models included interactions between metabolic BW and ADG because requirements for gain may differ at different BW (Romero et al., 2009b). Model I was a simple nonlinear model of ME intake as a function of metabolic BW, ADG, and EM based on Byerly et al. (1980), Schulman et al. (1994), and Romero et al. (2009b). Model II was a nonlinear mixed model based on the function of model I, but included a random term $u \sim N(0, Vu)$ associated with the coefficient of metabolic BW to separate individual variation in

Table 1. Functional specifications[1] of the evaluated models.

Model	Function specification
I	$MEI_d = a \times BW^b + c \times ADG \times BW^d + e \times EM + \varepsilon$
II[2,4]	$MEI_d = (a + u) \times BW^b + c \times ADG \times BW^d + e \times EM + \varepsilon$
III[3,4]	$MEI_d = (a + uu) \times BW^b + c \times ADG \times BW^d + e \times EM + \varepsilon$
IV[2–4]	$MEI_d = (a + u + uu) \times BW^b + c \times ADG \times BW^d + e \times EM + \varepsilon$

Abbreviation: ME, metabolizable energy.
[1]Estimated parameters are lowercase letters. MEI_d = daily ME intake (kcal/day); BW = BW (kg); ADG = ADG (g/day); EM = egg mass (g/day); u = bird related random term; uu = age related random term; ε = residual error.
[2]The error term u was associated with each bird.
[3]The error term uu was associated with each age.
[4]Variances V, Vu, and Vuu were estimated in the regressions.

maintenance ME from other sources of random variation. Model III was a nonlinear mixed model based on the function of model I but included a random term $uu \sim N(0,Vuu)$ associated with the coefficient of metabolic BW by week to separate age variation in maintenance ME from other sources of random variation. Model IV was a nonlinear mixed model and a combination of model II and model III, including both random terms $u \sim N(0,Vu)$ and $uu \sim N(0,Vuu)$ where the age term was nested within the term of individual bird.

Statistical Analysis

All statistical analyses were performed with SAS (Version 9.4. SAS Institute Inc., Cary, NC, 2012). The 4 models were fitted with the NLMIXED procedure, for complete code see Supplementary Information. Mean square errors and R^2 were manually calculated from the estimated values using the following equations:

$$MSE = \frac{1}{n}\sum_{i=1}^{n}(Y_i - \hat{Y}_i)^2$$

$$R^2 = 1 - \frac{\sum_i \varepsilon_i^2}{\sum_i (y_i - \overline{y}_i)^2}$$

The linear regression between observed and estimated values of daily ME intake was conducted in the regression procedure. The analysis of BW, ADG, EM, FCR_{egg}, and cumulative FCR_{egg} was conducted in the HPMIXED and MIXED procedures. The ANOVA for treatment differences in RFI, RHP, total HP, visit frequency, and meal size were conducted using the MIXED procedure. Tukey's range test was used to compare treatment means. Differences were reported where $P \leq 0.05$. The statistical ANOVA model for RHP included BW treatment and rearing photoschedule as fixed effects and their interaction. The statistical ANOVA model for BW, ADG, EM, FCR_g, FCR_{egg}, RFI, HP, visit frequency, and meal size included BW treatment, rearing photoschedule, and age as fixed effects and all 2- and 3-way interactions. Random variation attributable to individual hens was estimated in all analyses that included serial measurements.

RESULTS AND DISCUSSION

Animal Performance

Animal performance, including BW, BW variation, and feed intake was previously described by van der Klein et al. (2018). A summary overview with treatment differences BW, ADG, and EM for both the rearing and the laying phase is provided in Table 2, as these were used to fit the models. The effects of the treatments on sexual maturation (van der Klein et al., 2019) and reproductive performance (van der Klein et al., 2018) have been discussed elsewhere. From these earlier publications, it is important to highlight that treatments significantly differed in age at first egg and egg production. Of the Standard BW hens on the 8L:16D, 10L:14D, and 12L:12D photoschedules, 3.3, 18.1, and 37.6%, respectively, never commenced egg production throughout the experiment (van der Klein et al., 2018). Nonlaying birds were included in the data set used for fitting the models. For the subset of birds that were laying,

Table 2. BW, average daily gain (ADG), and egg mass (EM) of broiler breeder hens for the rearing (< 21 wk) and laying (> 20 wk) phase fed to achieve a high or standard BW[1] curve and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D rearing photoschedule (RPS).

			BW (kg).				ADG (g).				EM (g/day).	
Effect	BW	RPS	Rearing	SEM	Laying	SEM	Rearing	SEM	Laying	SEM	EM	SEM
BW	High		1.365[a]	0.001	3.763[a]	0.002	17.3[a]	0.15	7.3	0.14	42.3[a]	0.42
	Standard		1.127[b]	0.001	3.294[b]	0.002	14.1[b]	0.15	7.2	0.14	27.8[b]	0.41
RPS		8L:16D	1.250[a]	0.001	3.489[c]	0.003	15.7	0.18	7.2	0.17	42.6[a]	0.48
		10L:14D	1.246[b]	0.001	3.520[b]	0.003	15.7	0.19	7.1	0.18	35.3[b]	0.54
		12L:12D	1.241[c]	0.001	3.577[a]	0.003	15.8	0.18	7.5	0.17	27.2[c]	0.50
BW × RPS	High	8L:16D	1.370[a]	0.001	3.709[c]	0.004	17.3[a]	0.25	7.2	0.23	45.7[a]	0.68
		10L:14D	1.367[a]	0.001	3.743[b]	0.004	17.3[a]	0.28	7.2	0.27	43.9[a]	0.80
		12L:12D	1.357[b]	0.001	3.837[a]	0.004	17.4[a]	0.25	7.6	0.24	37.3[b]	0.70
	Standard	8L:16D	1.131[c]	0.001	3.269[f]	0.004	14.1[b]	0.25	7.2	0.23	39.6[b]	0.69
		10L:14D	1.125[d]	0.001	3.297[e]	0.004	14.1[b]	0.27	6.9	0.25	26.8[c]	0.73
		12L:12D	1.124[d]	0.001	3.317[d]	0.004	14.1[b]	0.27	7.3	0.25	17.0[d]	0.73
Source of variation			*P*-value									
BW			<0.001		<0.001		<0.001		0.42		<0.001	
RPS			<0.001		<0.001		0.93		0.26		<0.001	
BW × RPS			<0.001		<0.001		0.98		0.68		<0.001	
Age			<0.001		<0.001		<0.001		<0.001		<0.001	
Age × BW			<0.001		0.97		<0.001		<0.001		0.95	
Age × RPS			<0.001		0.033		<0.001		<0.001		<0.001	
Age × BW × RPS			0.96		1.00		0.8377		<0.001		1.00	

[a-f]LSMeans within a column and treatment group lacking a common superscript differ ($P \leq 0.05$).
[1]Hens followed either the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high).

Table 3. Regression coefficients of nonlinear model I, describing ME partitioning to maintenance, gain, and egg production.

Coefficient	Estimate	SE	t	P > t
A	129.25	1.47	88.15	<0.001
B	0.51	0.01	55.5	<0.001
C	0.92	0.08	12.08	<0.001
D	0.44	0.06	6.89	<0.001
E	3.14	0.03	103.11	<0.001
V	2,111.44	33.83	62.42	<0.001
Estimated equation[1]	$MEI_d = 129.25 \times BW^{0.51} + 0.92 \times ADG \times BW^{0.44} + 3.14 \times EM + \varepsilon$			

Abbreviation: ME, metabolizable energy.
[1]MEI_d = daily ME intake (kcal/day); BW = BW (kg); ADG = average daily gain (g/day); EM = egg mass (g/day); ε = residual error; Converged in 5 iteration calls and cpu time 0.28 s.

productivity did not differ between treatments; hence, the difference in egg production originated from the rate (%) of hens reaching sexual maturity within each treatment. Even though age at first egg did not differ between hens under the 8L:16D and 10L:14D photoschedules (173 vs. 172 D, respectively), in the standard BW treatment, the 12L:12D rearing photoschedule delayed age at first egg compared with the 8L:16D rearing photoperiod (266 vs. 180 D, respectively). These differences resulted in challenges comparing EM, FCR_{egg}, and cumulative FCR_{egg}; therefore, data were analyzed from week 26 onward.

Model Bias and Fit Evaluation

Coefficients of model I, II, III, and IV are reported in Tables 3–6, respectively. All models converged. A variation on model IV was initially attempted, where the random term associated with the individual bird was nested within the random term of age. However, this model would not converge or was unstable, depending on the starting parameters. It is hypothesized that the model would not converge because of the large variability in age at first egg between birds. As energy partitioning in birds changes from growth to egg production once birds reach sexual maturity (Leeson and Summers, 2001), birds in our population were in different physiological states at the same age. Therefore, individual bird rather than age would explain a large proportion of the differences in ME_m requirements over age.

Table 7 reports the results of a linear regression of the observed vs. predicted daily ME intake for the 4 energy partitioning models. All regressions had a slope close to 1, which means that there was no change in overestimation or underestimation of estimates at low to high daily ME intake. For all models except model IV, the intercept was not different from 0; a systematic overestimation of 3.131 kcal/day ME intake is inferred for model IV. Figure 1 shows the individual residuals (RFI) of all 4 models over age. In Figure 1I, model I, a pattern can be observed where around 5 wk and around 15 to 25 wk residuals are larger than 0, which indicates underestimation of MEI. Adding the random term associated with individual bird did not change this pattern (Figure 1II) but adding the random term associated with age reduced the issue (Figure 1III). Adding a random term both for each individual bird and for the age of the bird significantly reduced the overall residuals (Figure 1IV) and seemed to reduce the issue with bias around 15 to 25 wk. However, the same pattern of underestimation could be seen at week 5 as in model I and II. Standard deviation was 20.1 $kcal/kg^{0.58}$ for the random age term ($\sqrt{Vu}$, Table 6) and 10.9 $kcal/kg^{0.58}$ for the random individual term ($\sqrt{Vuu}$, Table 6), indicating twice as much variation was explained by age compared with the individual bird.

In the literature, estimates for ME_m requirements ranged from 147.6 kcal/day to 245.2 kcal/day for a 2 kg pullet or mature broiler breeder (Spratt et al., 1990; Sakomura et al., 2003; Rabello et al., 2006; Romero et al., 2009a, 2011; Hadinia et al., 2018). Estimates for the energy partitioning to maintenance for a 2 kg bird were similar for model I, II, III, and IV fell all within that range (184.1 kcal/day, 196.6 kcal/day, 179.4 kcal/day, and 195.2 kcal/day, respectively). All models also showed coefficients for the ME

Table 4. Regression coefficients of nonlinear mixed model II describing ME partitioning to maintenance, gain, and egg production and including 1 random term associated with individual bird.

Coefficient	Estimate	SE	t	P > t
a	130.64	1.84	70.91	<0.001
b	0.59	0.01	64.08	<0.001
c	0.71	0.07	9.80	<0.001
d	0.34	0.08	4.31	<0.001
e	2.28	0.04	59.10	<0.001
b	1,561.64	25.28	61.77	<0.001
V*u*	232.71	28.10	8.28	<0.001
Estimated equation[1]	$MEI_d = (130.64 + u) \times BW^{0.59} + 0.71 \times ADG \times BW^{0.34} + 2.28 \times EM + \varepsilon$			

Abbreviation: ME, metabolizable energy.
[1]MEI_d = daily ME intake (kcal/day); BW = BW (kg); ADG = average daily gain (g/day); EM = egg mass (g/day); *u* = bird related random term; ε = residual error. Converged in 3 iteration calls and CPU time 1.12 s.

Table 5. Regression coefficients of nonlinear mixed model III describing ME partitioning to maintenance, gain, and egg production and including 1 random term associated with age.

Coefficient	Estimate	SE	t	P > t
a	95.45	3.30	28.94	<0.001
b	0.91	0.03	32.88	<0.001
c	0.56	0.11	4.99	<0.001
d	−1.21	0.23	−5.16	<0.001
e	3.43	0.03	116.74	<0.001
V	1,692.61	27.55	61.44	<0.001
V*uu*	314.75	41.24	7.63	<0.001
Estimated equation[1]	$MEI_d = (95.45 + uu) \times BW^{0.91} + 0.56 \times ADG \times BW^{-1.21} + 3.43 \times EM + \varepsilon$			

Abbreviation: ME, metabolizable energy.
[1]MEI_d = daily ME intake (kcal/day); BW = BW (kg); ADG = average daily gain (g/day); EM = egg mass (g/day); *uu* = age related random term; ε = residual error. Converged in 58 iteration calls and CPU time 7.06 s.

requirement for EM production close to values from the literature. The coefficient associated with EM were 3.14 kcal/g, 2.28 kcal/g, 3.43 kcal/g, and 2.42 kcal/g for model I, II, III, and IV, respectively. Literature reported values ranged between 1.8 kcal/g and 3.1 kcal/g (Combs, 1968; Sakomura, 2004; Romero et al., 2009b, 2011; Reyes et al., 2012; Pishnamazi et al., 2015). Model I and III estimated slightly higher values, potentially because these models did not appropriately account for sources of variation. Individuals varied substantially in egg production and unaccounted individual variation in ME_m requirements related to an increased feed intake for egg production was likely accounted for in the EM coefficient. Model III showed very different values for ME requirements for gain compared with the literature and compared with the other models. For a 2 kg bird, ME requirement per gram of gain was 1.25 kcal/g, 0.90 kcal/g, and 0.92 kcal/g for model I, II, and IV, but only 0.24 kcal/g for model III. As the exponent of BW for the requirement for gain was negative (−1.21), model III predicted a decrease in ME requirement for gain with increasing BW (Figure 2). This is in contrast to all other models, which predicted an increase in the ME requirement for gain with increasing BW. It was hypothesized that at higher BW (hence closer to maturity or within mature birds), more fat tissue was deposited, whereas lean mass deposition stayed relatively constant (Vignale et al., 2017). Fat tissue has a higher energy content (9.1 kcal/g) compared with lean tissue (5.5 kcal/g; Atwater, 1900). Therefore, as BW increased, the ME requirement for gain should also have increased. Model I, II, and IV coefficients are in line with this hypothesis and also approach the range of values reported in the literature: 0.71 kcal/g through 5.80 kcal/g (Pishnamazi et al., 2008, 2015; Romero et al., 2009b, 2011; Reyes et al., 2012; Hadinia et al., 2018). The literature mostly reported values associated with the mature phase only, except for Hadinia et al. (2018) at 1.52 kcal/g and Pishnamazi et al. (2008) at 0.71 kcal/g. The fact that the current models were fitted using data from both the rearing and the laying phase may have caused lower values for the ME requirement for gain. The energy requirement for gain for *ad libitum* fed broilers was previously reported at 1.15 kcal/g for females and 1.41 kcal/g for males (Romero et al., 2011), although the authors concluded that this could have been an underestimation as their model may have overestimated ME_m requirements.

All models including random terms had a better fit than model I (Table 8), as they showed a reduced Bayesian information criterion, reduced mean squared error, and a R^2 closer to 1. Model IV showed a significant drop in mean squared error and had a R^2 very close to 1; therefore, model IV was selected for further discussion of ME_m requirements and energy efficiency evaluation.

Table 6. Regression coefficients of nonlinear nested mixed model IV describing ME partitioning to maintenance, gain, and egg production and including 2 random terms associated with individual bird and age, where the age term was nested within the individual term.

Coefficient	Estimate	SE	t	P > t
a	130.57	1.15	113.80	<0.001
b	0.58	0.01	108.23	<0.001
c	0.63	0.03	18.05	<0.001
d	0.54	0.06	9.76	<0.001
e	2.42	0.04	67.10	<0.001
V	117.79	13.58	8.68	<0.001
V*u*	404.23	11.53	35.05	<0.001
V*uu*	232.73	20.66	11.26	<0.001
Estimated equation[1]	$MEI_d = (130.57 + u + uu) \times BW^{0.58} + 0.63 \times ADG \times BW^{0.54} + 2.42 \times EM + \varepsilon$			

Abbreviation: ME, metabolizable energy.
[1]MEI_d = daily ME intake (kcal/day); BW = BW (kg); ADG = average daily gain (g/day); EM = egg mass (g/day); *u* = bird related random term; *uu* = age related random term; ε = residual error. Converged in 26 iteration calls and CPU time 10 min and 47.84 s.

Table 7. Linear regression of observed (y-variable) vs. estimated (x-variable) average daily ME intake for the evaluated models[1].

Model	Coefficient	Estimate[2]	SE	P > t[3]
I	Intercept	−1.171	1.363	0.39
	Slope	1.003	0.004	<0.001
II	Intercept	0.455	1.135	0.69
	Slope	0.999	0.004	<0.001
III	Intercept	0.105	1.190	0.93
	Slope	1.000	0.004	<0.001
IV	Intercept	−3.131	0.186	<0.001
	Slope	1.011	0.001	<0.001

Abbreviation: ME, metabolizable energy.
[1]Predicted values were calculated with 1 nonlinear model (I), 2 nonlinear mixed models with 1 random term linked with metabolic BW (associated with each individual bird (II) or age (III)), and 1 nested nonlinear mixed model with 2 random terms (IV) to describe ME partitioning to maintenance, gain, and egg production in broiler breeders.
[2]Estimated intercepts and slopes measure systematic bias of the models. Intercepts different from 0 and slopes different from 1 indicate bias.
[3]Probability indicates if the estimate differs from 0.

Maintenance Energy Requirements and Energy Efficiency

Residual heat production and HP were evaluated using model IV and are presented separately for the rearing (< 21 wk, Table 9) and laying (> 20 wk, Table 10) phase. During the scotoperiod, HP is reduced in broiler breeders (Macleod et al., 1980) and broilers (Kim et al., 2014). Therefore, it was hypothesized that during rearing, the treatment with the shortest scotoperiod, that is the 12L:12D treatment, would be the least efficient and show the highest cumulative FCR_g, highest RFI, and RHP and highest HP. The 12 L:12D photoschedule treatment had indeed the highest cumulative FCR_g (2.86 g/g) and highest RFI (1.51 kcal) during rearing. However, the 12L:12D treatment also had the lowest RHP (−1.62 kcal/$kg^{0.58}$) and lowest HP (129.5 kcal/$kg^{0.58}$) during rearing. Potentially, the increased photoperiod increased the level of activity in the 12L:12D treatment. The increased ME_m expenditure because of activity may have provided stimulus for a metabolic shift to become more energetically conservative with ME partitioning to HP overall in the 12L:12D treatment during rearing. During the scotoperiod melatonin secreted from the pineal gland is increased (Pang et al., 1996). Increased melatonin levels have been linked directly to improvement in feed efficiency, as they reduced energy partitioning to physical activity and therefore reduced HP in broiler chickens (Apeldoorn et al., 1999). In addition, decreased heart rate, increased blood pressure, and increased body temperature in the scotoperiod compared with the photoperiod were closely associated with energy expenditure in adult broiler breeders (Savory et al., 2006). Heart rate, blood pressure, and body temperature were also lower in restricted vs. *ad libitum* fed birds, except within 1 h of consuming the daily feed allotment for restricted fed birds (Savory et al., 2006), indicating that feed restriction results in a metabolic shift toward energy conservation.

Figure 3 shows the regression between average daily ME intake and HP summarized over the total experimental period, Figures 4 and 5 show separate regression analysis of average daily ME intake and HP for the rearing and laying phases, respectively. The slope coefficient represents the proportion of increased ME intake that was lost as heat, within the reported range, that is the heat increment of feeding. The model predicted that 79% of the increase in ME intake was lost as heat during the rearing phase, whereas 44% of the increase in ME intake is lost as heat during the laying phase. Hadinia et al. (2018) estimated that 87% of the increase in ME intake was lost as heat during rearing (week 10–23) in broiler breeders, and Romero et al. (2011) estimated that at 65% for *ad libitum* fed broilers (week 1–6). Although ME intake was not corrected for metabolic BW, Romero et al. (2009b) estimated the slope of ME intake on estimated HP between 19 and 34% during the laying phase (week 20–60; depending on the model used). Both the literature and the current results indicated that a lower proportion of an increase in ME intake was lost as heat in mature birds compared with immature birds. When estimated HP in the current study was summarized based on maturity (reaching age at first egg), instead of age, 87% and 47% of the increase in ME intake was lost as heat for immature and mature birds, respectively. This suggested that the heat increment of feeding depended on the age and/or reproductive state of the bird. The results could have been confounded by dietary factors, as the diet was switched at week 23 (from a grower to peak layer diet). However, it was previously concluded that diet composition did not affect the heat increment feeding in broilers (van der Klein et al., 2020). In immature feed restricted birds, it is possible that part of the increase in ME intake will directly partition to gain, predominantly toward lean tissues. Lean tissues are estimated to have a 10-fold higher energy requirement for maintenance compared with fat (Scott and Evans, 1992). In mature birds, an increase in ME intake partitioned to gain would mostly result in fat deposition in broiler breeders (Leeson and Summers, 2001). Therefore, the increase in HP with increased ME intake could be lower for mature birds compared with immature birds because of a decrease in deposition of metabolically costly tissues and a relative increase in deposition of metabolically inexpensive tissues. Both BW treatment and photoschedule treatment significantly affected age at first egg (van der Klein et al., 2018); therefore, an analysis was performed without accounting for treatment differences to study the differences in HP for birds in lay (mature) compared with those that had not commenced egg production (immature). Mature birds had a higher HP compared with immature birds (135.09 ± 0.35 kcal/$kg^{0.58}$ vs. 126.91 ± 0.32 kcal/$kg^{0.58}$, respectively, $P < 0.001$). The increased HP in mature birds was likely because of an increase in feed intake to support egg production and an obligatory increase in the heat increment of feeding.

The RHP measures energy efficiency without being confounded by feed intake, including the heat increment of feeding, BW gain, and egg production

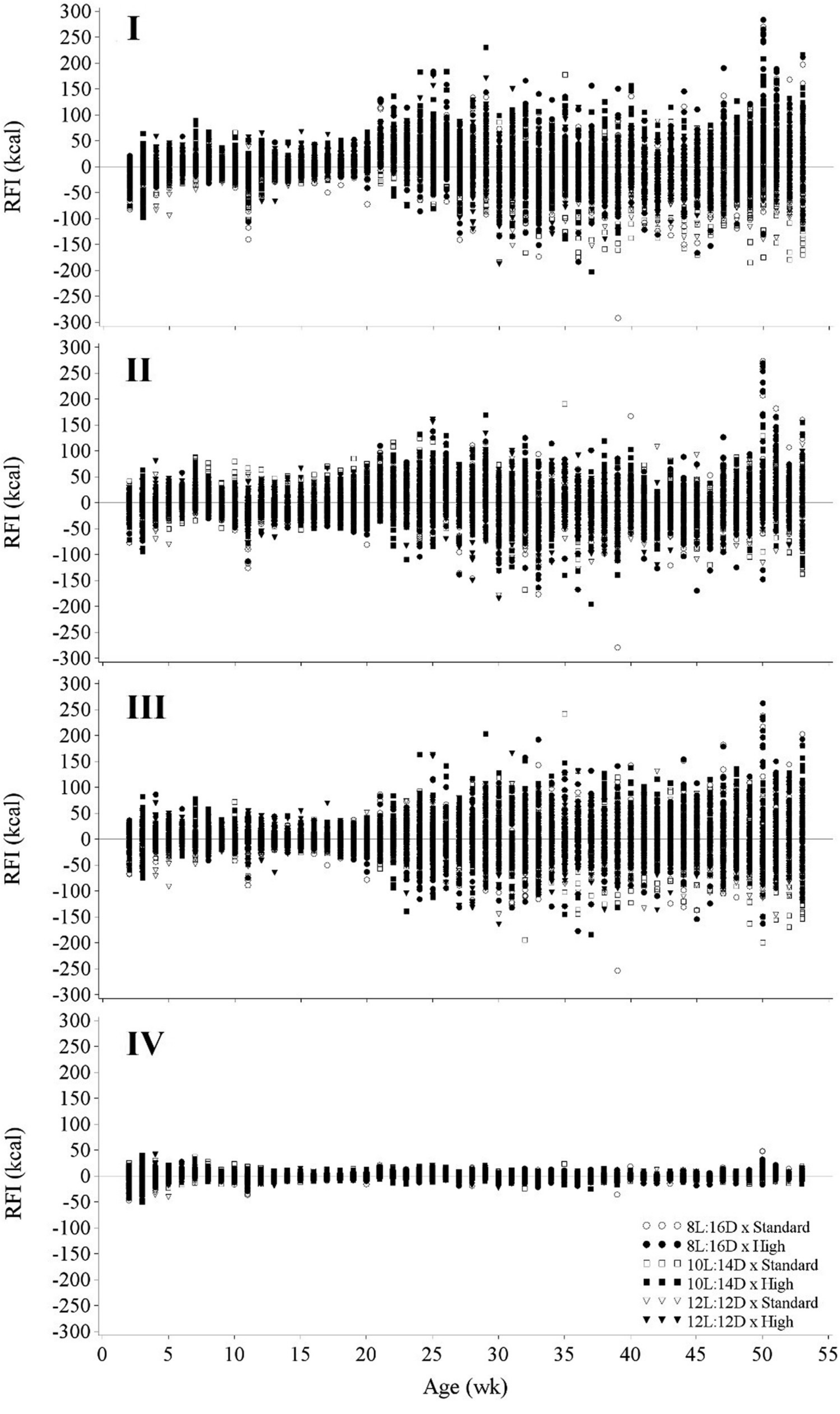

Figure 1. Residual feed intake (RFI) estimated from 2 to 54 wk of age for individual birds with a nonlinear model (I), 2 nonlinear mixed models with 1 random term linked with metabolic BW (associated with each individual [II] or age [III]), and a nonlinear mixed model with 2 nested random term (IV) to describe ME partitioning to maintenance, gain, and egg production. Abbreviation: ME, metabolizable energy.

(Romero et al., 2009a). Therefore, RHP can be used as a good estimator for energy efficiency for maintenance requirements. Standard BW birds had a lower RHP compared to High BW birds during the laying phase (1.47 ± 0.643 kcal/kg$^{0.58}$ vs. -1.30 ± 0.645 kcal/kg$^{0.58}$, $P = 0.003$), but this difference was less clear during rearing (0.54 ± 0.434 kcal/kg$^{0.58}$ vs. -0.61 ± 0.435 kcal/kg$^{0.58}$, $P = 0.062$). During rearing, birds might already be extremely conservative with ME utilization, because of the severe level of

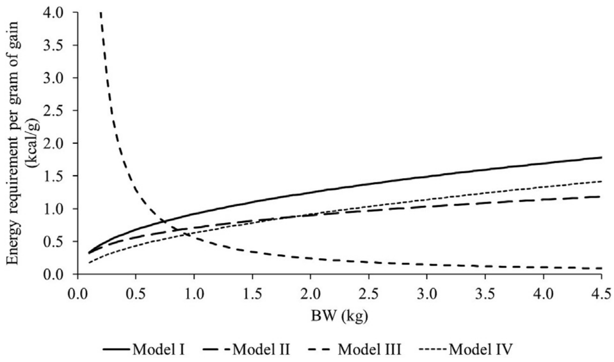

Figure 2. Energy requirement per gram of average daily gain as a function of BW estimated by 4 models explaining average daily ME intake as a function of metabolic BW, gain, and egg mass. Abbreviation: ME, metabolizable energy.

feed restriction. Therefore, there was little variation in RHP, that is they showed a RHP close to zero. Residual heat production did not differ between hens reared under different photoschedules. It was previously concluded that adult broiler breeder hens with low RHP and low RFI produced more efficient broilers compared with broiler breeders with a low RHP and a high RFI (Romero et al., 2011). Therefore, it is suggested that future research evaluates the relationship between offspring performance for birds with differing lifetime HP, RHP, and RFI.

The FCR_{egg} was higher for standard BW compared with high BW birds (3.83 ± 0.07 g/g egg vs. 3.65 ± 0.05 g/g egg, $P < 0.001$; Table 10). Standard BW birds had a much lower EM compared with high BW birds (27.8 ± 0.41 g vs. 42.3 ± 0.42 g, respectively; $P < 0.001$; Table 2). The lower feed intake and lower ME_m requirements in standard BW birds did not balance out the loss in EM. The FCR_{egg} and cumulative FCR_{egg} were heavily influenced by the age at first egg. BW was higher at first egg when age at first egg was delayed; therefore, ME_m requirements were higher as well, requiring a higher feed intake for the same EM. In addition, cumulative feed intake increased without an increase in EM with delayed age at first egg. This highlights that FCR_{egg} is an incomplete indicator of production efficiency for broiler breeder reproductive performance. Our results are partially congruent with results from Lewis et al. (2005). They observed that for birds reared under differing rearing photoschedules and on different BW curves, the amount of feed needed to produce 1 g of egg reduced by 0.025 g for each extra egg produced, independent from BW treatment. They also concluded that birds allowed accelerated growth were less efficient than conventionally reared birds for a given number of eggs, because of increased ME_m requirements. Similarly, the relationship between average individual FCR_{egg} and total egg production till week 55 in the current study inferred that the decrease in FCR_{egg} with increased total egg production depended on BW treatment (−0.021 g/g for the high BW treatment and −0.040 g/g for the standard BW treatment). The FCR_{egg} of birds on the high BW treatment was higher compared with birds on the standard BW treatment, when corrected for total egg production (analysis not shown).

Feeding Station Visit Frequencies and Meal Size

The total weekly average of daily number of visits is reported in Figure 6. Visiting a feeding station is a foraging-type behavior (Girard et al., 2017); therefore, an increase in feeding station visits could indicate increased feed seeking motivation, which was previously linked to level of feed restriction and hunger (Dixon et al., 2014). Therefore, treatment differences in visit frequencies could be an indicator of hunger. However, no direct comparison has yet been made between visit frequency and foraging or hunger indicators currently used in the literature (behavioral or physiological). Increased visit frequency is also a measure of locomotive activity, and increased locomotive activity increased ME_m requirements (van Kampen, 1976; MacLeod et al., 1982, 1988). Therefore, increased visit frequency could also be linked to increased HP (Johnson and Farrell, 1984). A linear regression between HP and daily visit frequency up to week 21 showed that 1 extra visit per day corresponded to a 0.076 kcal increase in HP, after correcting for the fixed effects and interactions between BW treatment, photoschedule, and age ($P < 0.001$; $R^2 = 0.96$; results not shown).

During the rearing phase, daily visits to the feeding stations ranged between 50 and 85 times, peaking at week 8 (Figure 6). Surprisingly, the 10L:14D treatment had a higher visit frequency compared with the 8L:16D and 12L:12D treatment, which aligned with a higher

Table 8. Bayesian information criterion (BIC[1]), mean squared error (MSE), and R square[2] (R2) values of the evaluated models describing ME partitioning to maintenance, gain, and egg production.

Model	Random terms associated with metabolic BW (ME_m)	BIC[1]	MSE	R[2]
I	None	81,826	2,111.44	0.844
II	Associated with individual bird	79,957	1,531.85	0.893
III	Associated with age	80,315	1,667.63	0.882
IV	Both individual bird and age	78,810	45.84	0.997

Abbreviation: ME, metabolizable energy.
[1]Smaller values indicate a better fit of the model.
[2]Values closer to 1 indicate a better fit of the model.

Table 9. Cumulative feed conversion ratio for gain ($cFCR_g$), residual feed intake (RFI[1]), residual heat production (RHP[2]), and total heat production (HP[3]) of broiler breeder pullets up to 21 wk of age fed to achieve a high or standard BW[4] curve and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D rearing photoschedule (RPS).

Effect	BW	RPS	$cFCR_g$ (g/g)	SEM	RFI (kcal)	SEM	RHP (kcal/$kg^{0.58}$)	SEM	HP	SEM
BW	High		2.76	0.018	0.09	0.193	0.54	0.434	137.4[a]	0.29
	Standard		2.79	0.018	−0.16	0.196	−0.61	0.435	124.2[b]	0.29
RPS		8L:16D	2.71[b]	0.021	−2.03[c]	0.228	1.85[a]	0.509	130.7[b]	0.34
		10L:14D	2.76[b]	0.024	0.41[b]	0.250	−0.34[b]	0.562	132.2[a]	0.38
		12L:12D	2.86[a]	0.022	1.51[a]	0.237	−1.62[b]	0.524	129.5[c]	0.34
BW x RPS	High	8L:16D	2.77[a,b]	0.030	−1.31[c]	0.322	1.42[a]	0.720	135.4[b]	0.49
		10L:14D	2.66[b,c]	0.034	−0.25[b,c]	0.359	1.44[a]	0.812	139.8[a]	0.55
		12L:12D	2.85[a]	0.030	1.4[a]	0.323	−1.22[b]	0.720	136.9[b]	0.49
	Standard	8L:16D	2.64[c]	0.030	−2.75[d]	0.323	2.28[a]	0.720	126.1[c]	0.49
		10L:14D	2.86[a]	0.033	1.08[a,b]	0.348	−2.11[b]	0.778	124.6[c]	0.53
		12L:12D	2.87[a]	0.032	1.18[a]	0.346	−2.01[b]	0.762	122.1[d]	0.52
Source of variation			*P*-value							
Age			<0.001		<0.001		–		<0.001	
BW			0.24		0.36		0.062		<0.001	
RPS			<0.001		<0.001		<0.001		<0.001	
Age × BW			0.99		<0.001		–		<0.001	
Age × RPS			0.59		<0.001		–		<0.001	
BW × RPS			<0.001		<0.001		0.015		<0.001	
Age × BW × RPS			0.936		0.43		–		0.96	

[a-d]LSMeans within a column and treatment group lacking a common superscript differ ($P \leq 0.05$).

[1]Calculated using residuals of the nonlinear mixed model describing daily ME intake (MEI_d) as a function of metabolic BW, average daily gain (ADG), and egg mass (EM): $MEI_d = (130.57 + u + uu) \times BW^{0.58} + 0.63 \times ADG \times BW^{0.54} + 2.42 \times EM + \varepsilon$, where u is associated with each individual bird, and uu is associated with age of the individual bird, and RFI = observed MEI_d - predicted MEI_d.

[2]Calculated as the residual of the regression between a + u + uu and MEI for each bird: $a + u + uu = 19.83 + 0.79 \times MEI + \varepsilon$, where $a + u + uu$ = predicted total HP; ε = RHP.

[3]Calculated as $130.57 + u + uu$ from the nonlinear model described under footnote 1.

[4]Hens followed either the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high).

Table 10. Cumulative feed conversion ratio for egg mass (FCR_{egg}), residual feed intake (RFI[1]), residual heat production (RHP[2]), and total heat production (HP[3]) of broiler breeder hens from week 21 to week 55 fed to achieve a High or Standard BW[4] curve and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D rearing photoschedule (RPS).

Effect	BW	RPS	FCR_{egg} (g/g egg)	SEM	$cFCR_{egg}$ (g/g egg)	SEM	RFI (kcal)	SEM	RHP (kcal/$kg^{0.58}$)	SEM	HP	SEM
BW	High		3.65[b]	0.051	20.6[b]	1.38	0.23[a]	0.100	1.47[a]	0.643	138.0[a]	0.42
	Standard		3.83[a]	0.071	40.6[a]	1.72	−0.14[b]	0.099	−1.30[b]	0.645	123.0[b]	0.42
RPS		8L:16D	3.63	0.058	14.6[b]	1.54	0.69[a]	0.116	−0.92	0.754	136.4[a]	0.49
		10L:14D	3.79	0.070	13.2[b]	1.91	0.05[b]	0.129	0.89	0.833	132.1[b]	0.55
		12L:12D	3.80	0.094	63.9[a]	2.22	−0.63[c]	0.120	0.29	0.777	122.9[c]	0.51
BW × RPS	High	8L:16D	3.73[a,b]	0.078	9.3[d,e]	2.15	0.66[a]	0.162	0.23	1.067	140.2[a]	0.69
		10L:14D	3.76[a,b]	0.092	7.2[e]	2.55	0.52[a]	0.190	3.70	1.204	143.2[a]	0.81
		12L:12D	3.46[b]	0.093	45.3[b]	2.45	−0.52[b]	0.166	0.49	1.067	130.7[b]	0.70
	Standard	8L:16D	3.53[b]	0.085	20.0[c]	2.20	0.73[a]	0.164	−2.06	1.067	132.6[b]	0.70
		10L:14D	3.82[a,b]	0.106	19.2[c,d]	2.86	−0.41[b]	0.175	−1.91	1.152	121.1[c]	0.74
		12L:12D	4.14[a]	0.164	82.5[a]	3.71	−0.74[b]	0.174	0.09	1.129	115.2[d]	0.74
Source of variation							*P*-value					
Age			<0.001		<0.001		<0.001		–		<0.001	
BW			0.040		<0.001		0.011		0.003		<0.001	
RPS			0.111		<0.001		<0.001		0.25		<0.001	
Age × BW			0.014		0.86		<0.001		–		0.077	
Age × RPS			<0.001		0.73		<0.001		–		<0.001	
BW × RPS			<0.001		<0.001		0.013		0.073		<0.001	
Age × BW × RPS			0.41		0.98		0.022		–		0.68	

[a-e] LSMeans within a column and treatment group lacking a common superscript differ ($P \leq 0.05$).

Abbreviation: ME, metabolizable energy.

[1]Calculated using residuals of the nonlinear mixed model describing daily ME intake (MEI_d) as a function of metabolic BW, average daily gain (ADG), and egg mass (EM): $MEI_d = (130.57 + u + uu) \times BW^{0.58} + 0.63 \times ADG \times BW^{0.54} + 2.42 \times EM + \varepsilon$ and RFI = observed MEI_d - predicted MEI_d.

[2]Calculated as the residual of the regression between a + u + uu and MEI for each bird: $a + u + uu = 55.30 + 0.44 \times MEI + \varepsilon$, where $a + u + uu$ = predicted total HP; ε = RHP.

[3]Calculated as $130.57 + u + uu$ from the nonlinear model described under footnote 1.

[4]Hens followed either the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high).

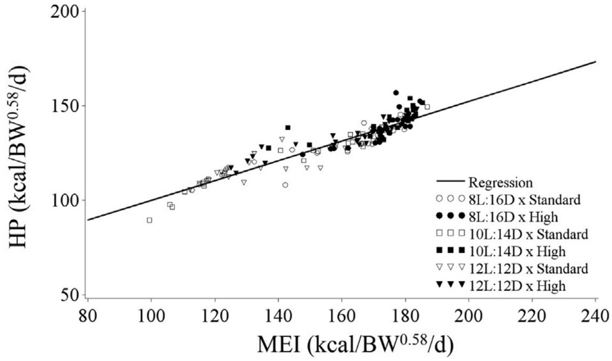

Figure 3. Total heat production (HP) relative to average daily ME intake (MEI) for the duration of the experiment (wk 2–55) as estimated by a model describing ME partitioning to maintenance, gain, and egg production and including 2 random terms associated with individual bird and age (IV). Broiler breeders were fed to achieve the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. Regression equation was HP = 47.74 + 0.52 × MEI + ε ($P < 0.001$; $R^2 = 0.86$). Abbreviation: ME, metabolizable energy.

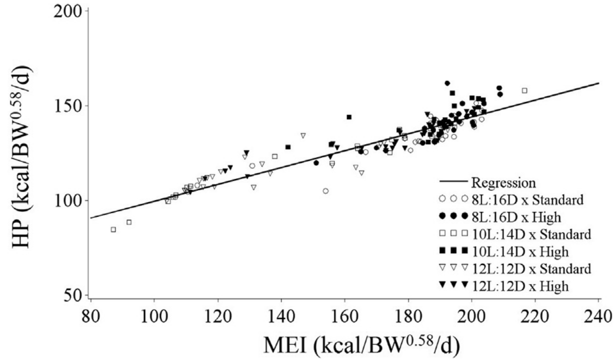

Figure 5. Total heat production (HP) relative to average daily ME intake (MEI) during the laying phase (week 21–week 55) as estimated by a model describing ME partitioning to maintenance, gain, and egg production and including 2 random terms associated with individual bird and age (IV). Broiler breeders were fed to achieve the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. Regression equation was HP = 55.30 + 0.44 × MEI + ε ($P < 0.001$; $R^2 = 0.86$). Abbreviation: ME, metabolizable energy.

cumulative feed intake during the rearing period (8,260 g for the 10L:14D photoschedule vs. 8,091 g for the 8L:16D photoschedule; van der Klein et al., 2018) and a higher HP (Table 9). It is unclear why the 10L:14D treatments differed from the 8L:16D and 12L:12D treatment.

The meal:visit ratio was defined as the number of meals per day (Figure 7) divided by the total number of visits to the feeding station per day (Figure 6). The meal:visit ratio was hypothesized to be an indicator of feeding motivation. Meal:visit ratio was much lower (around 20% for all treatments) in the rearing phase compared with the laying phase (around 80%) for those treatments that commenced egg production earlier (8L:16D and high BW treatment; Figure 8). The meal:visit ratio was in line with results from Zuidhof (2018) who looked at Cobb grandparent pullets and found an average meal:visit ratio of 17% between week 2 and 22. However, the meal:visit ratio of the 12L:12D standard BW treatment stayed around 30% in the laying phase, indicating these birds were hungrier compared with those treatments that had commenced egg production. It is hypothesized that birds that commenced egg production were less hungry as 1) treatments with high egg production had a lower overall visit frequency (Figure 6), 2) treatments with high egg production had a higher meal:visit ratio (i.e., they were allowed to eat around 80% of the time they visited the feeding station; Figure 8). In addition, every day a hen produced an egg, BW of the hen was reduced by the weight of the egg. With this BW reduction, hens qualified for additional feed allocation through the PF system, as the PF feed allocation decision was based on BW.

Birds did not restrict their visits to the PF system to the photoperiod; Standard BW birds visited the PF stations more often during the scotoperiod than the High BW birds (1.14 ± 0.01 vs. 0.84 ± 0.01 times per hour). It was hypothesized that birds with shorter photoperiods, that is longer scotoperiods, would visit the feeding stations more often during the scotoperiod. Contrary to this hypothesis, birds with shorter photoperiod visited the stations less often during the scotoperiod (0.85 ± 0.01, 1.03 ± 0.01, and 1.10 ± 0.01 times per hour for the 8L:16D, 10L:14D, and 12L:12D photoschedules respectively, over the complete experimental period; $P < 0.001$). During the rearing phase, this might have been the result of the higher energy expenditure for birds with an increased photoperiod length, which may have resulted in a higher ME_m requirement and overall energy requirement, hence a higher motivation to visit the feeding stations.

In addition to visit frequency, meal size might also be an indicator of feeding motivation. A larger meal size was related to a faster feed intake rate, as birds were limited to 45 s to finish their meal before being ejected

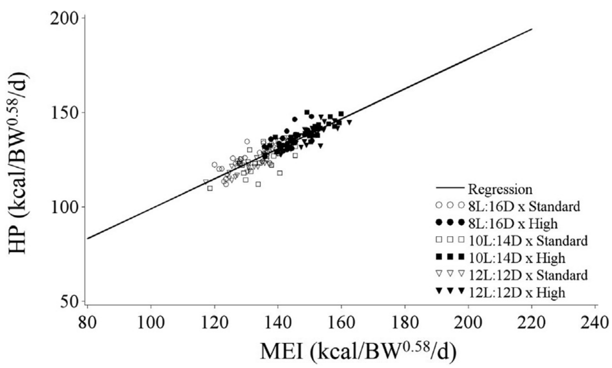

Figure 4. Total heat production (HP) relative to average daily ME intake (MEI) during the rearing phase (week 2–week 21) as estimated by a model describing ME partitioning to maintenance, gain, and egg production and including 2 random terms associated with individual bird and age (IV). Broiler breeders were fed to achieve the breeder-recommended BW curve (Standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (High) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. Regression equation was HP = 19.83 + 0.79 × MEI + ε ($P < 0.001$; $R^2 = 0.78$). Abbreviation: ME, metabolizable energy.

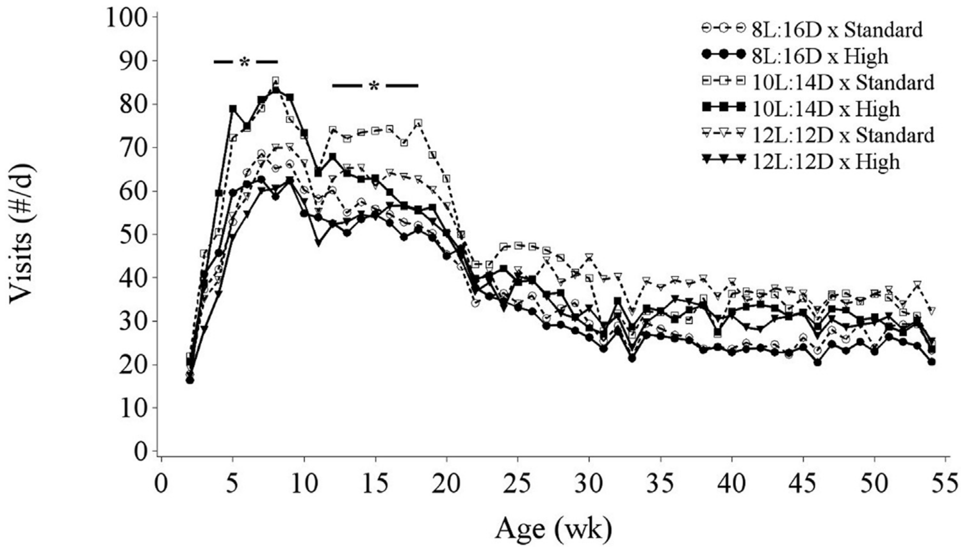

Figure 6. Number of daily visits to the feeding station for broiler breeders fed to achieve the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. The asterisks indicate ages where treatment means differed ($P < 0.05$); all fixed effects and interactions were significant ($P < 0.001$), except the interaction between age and BW treatment ($P = 0.08$) and the 3-way interaction between age, BW treatment, and photoschedule ($P = 0.99$).

from the feeding station. In line with the result from the visit frequency data, in week 10, meal size was greater in the 10L:14D photoschedule treatment compared with the 8L:16D and 12L:12D photoschedule treatments (8.4 ± 0.21 g vs. 6.6 ± 0.19 g and 6.0 ± 0.19 g, respectively; $P < 0.001$). At week 28, feed allowance was increased from 10 g to 20 g, and this caused an increase in meal size (Figure 9). The larger feed allowance elucidated treatment differences in meal size from week 28 to the end of the study. Meal size was largest for the 12L:12D photoschedule treatment, indicating the 12L:12D photoschedule treatment had the highest feeding motivation. This is in line with the meal:visit ratio results, as birds on the 12L:12D photoschedule treatment had the lowest meal:visit ratio (Figure 8). However, there may have been trade-off between meal size and number of daily meals, where birds with smaller meals size could have been allowed more meals per day to fulfill their daily feed intake requirement for the associated weight gain. Still, at week 25, meal:visit ratio for the 12L:12D photoschedule treatment was lower compared with the 8L:16D and 10L:14D photoschedule (43 ± 2.4% vs 66 ± 2.3% and 56 ± 2.6% respectively, $P < 0.001$; Figure 8), even though meal size was the same (6.4 ± 0.11 g; $P > 0.05$). Overall, meal size was smaller for the high BW treatment compared with the standard BW treatment (7.38 g ± 0.02 g vs. 8.14 ± 0.02 g, respectively).

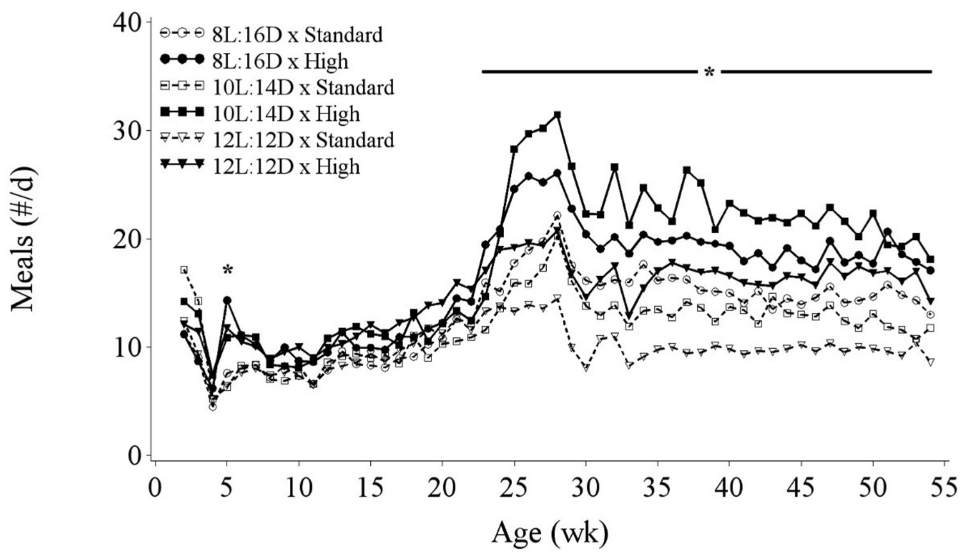

Figure 7. Number of daily meals of broiler breeders fed with a precision feeding system to achieve the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. The asterisks indicate ages where treatment means differed ($P < 0.05$); all fixed effects and interactions were significant ($P < 0.001$).

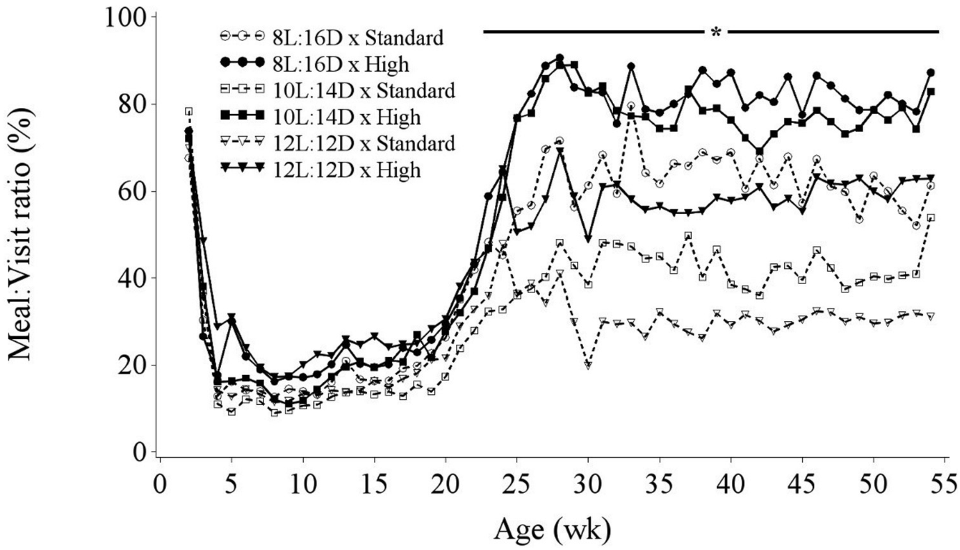

Figure 8. Meal:visit ratio of broiler breeders fed with a precision feeding system to achieve the breeder-recommended BW curve (Standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (High) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. The asterisks indicate ages where treatment means differed ($P < 0.05$); all fixed effects and interactions were significant ($P < 0.001$), except the 3-way interaction between age, BW treatment, and photoschedule ($P = 0.07$).

CONCLUSIONS

This is the first time an energy partitioning model was developed using individual data from both the rearing and the laying phase of broiler breeders housed in a free-run setting. Including random terms for both individual and age-related variation in ME_m requirements resulted in a biologically sound estimation of ME partitioning to maintenance, gain, and egg production for both the rearing and the laying phase and reduced residuals substantially. It allowed for efficiency indicators to be estimated for the rearing and the laying phase separately and overall. In the rearing phase, HP was related to level of egg production and therefore level of feed intake, and FCR_{egg} was confounded by age at first egg. Residual heat production of hens on the standard BW treatment was lower compared with hens on the high BW treatment. Age and/or reproductive status significantly affected the proportion of ME intake partitioned to HP; the slope of the regression between individual HP and ME intake was 79% during the rearing phase and decreased to 44% during the laying phase. Station visit frequency, meal:visit ratio, and meal size gave further insight into feed seeking behavior and hunger, where birds on the 10L:14D treatment seemed to be hungriest during the rearing phase, and birds on the 12L:12D

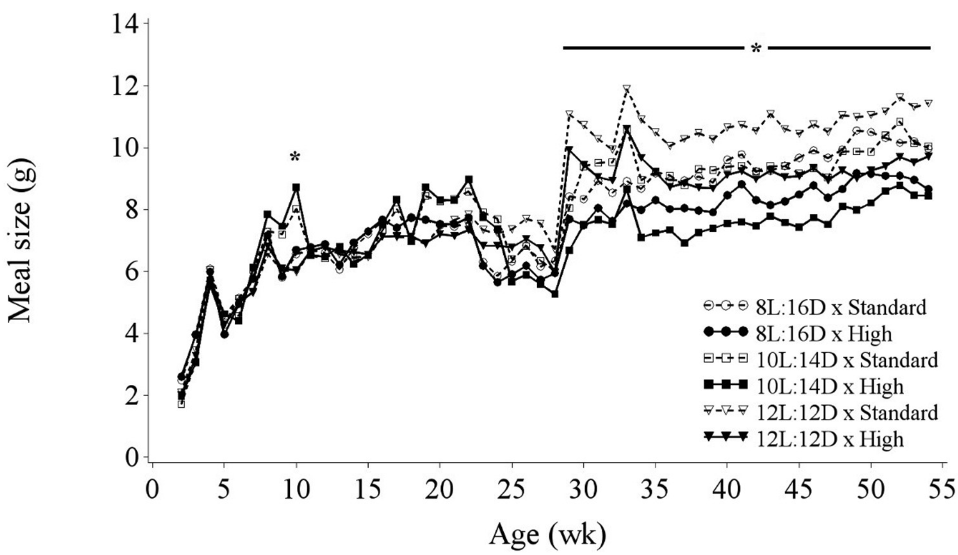

Figure 9. Meal size of broiler breeders fed with a precision feeding system to achieve the breeder-recommended BW curve (standard) or an accelerated BW curve reaching the 21 wk BW at 18 wk (high) and reared to week 21 on an 8L:16D, 10L:14D, or 12L:12D photoschedule. The asterisks indicate ages where treatment means differed ($P < 0.05$); all fixed effects and interactions were significant ($P < 0.001$), except the 3-way interaction between age, BW treatment, and photoschedule ($P = 1.00$).

standard treatment, with the largest proportion of non-laying birds, seemed to be hungriest during the laying phase.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found in the online version at https://doi.org/10.1016/j.psj.2020.05.016.

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