




Architecture of broiler breeder energy partitioning models

Mohammad Afrouziyeh ^{*}, Nicole M. Zukiwsky,^{*} Jihao You,^{*} René P. Kwakkel,^{*,†}
Douglas R. Korver ^{*} and Martin J. Zuidhof ^{*,1}

^{*}Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB, Canada T6G 2P5;
and [†]Department of Animal Sciences, Animal Nutrition Group, Wageningen University, Wageningen,
The Netherlands (6700 AH)

ABSTRACT A robust model that estimates the ME intake over broiler breeder lifetime is essential for formulating diets with optimum nutrient levels. The experiment was conducted as a randomized controlled trial with 40 Ross 708 broiler breeder pullets reared on 1 of 10 target growth trajectories, which were designed with 2 levels of cumulative BW gain in prepubertal growth phase and 5 levels of timing of growth around puberty. This study investigated the effect of growth pattern on energy efficiency of birds and tested the effects of dividing data into daily, 4-d, weekly, 2-wk, and 3-wk periods and the inclusion of random terms associated with individual maintenance ME and ADG requirements, and age on ME partitioning model fit and predictive performance. Model [I] was: $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d was daily ME intake (kcal/d); BW in kg; ADG_p was positive ADG; ADG_n was negative ADG (g/d); EM was egg mass (g/d); ε was the model residual. Models [II to IV] were

nonlinear mixed models based on the model [I] with inclusion of a random term for individual maintenance requirement, age, and ADG, respectively. Model [II] – 3 wk was chosen as the most parsimonious based on lower autocorrelation bias, closer fit of the estimates to the actual data (lower model MSE and closer R^2 to 1), and greater predictive performance among the models. Estimated ME partitioned to maintenance in model [II] – 3 wk was 100.47 ± 7.43 kcal/kg^{0.56}, and the ME requirement for ADG_p , ADG_n , and EM were 3.49 ± 0.37 ; 3.16 ± 3.91 ; and 2.96 ± 0.13 kcal/g, respectively. Standard treatment had lower residual heat production (**RHP**; -0.68 kcal/kg BW^{0.56}) than high early growth treatment (0.79 kcal/kg BW^{0.56}), indicating greater efficiency in utilizing the ME consumed. Including random term associated with individual maintenance ME in a 3-wk chunk size provided a robust, biologically sound life-time energy partitioning model for breeders.

Key words: broiler breeder, feed restriction, energy partitioning model, prediction optimization, random term

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INTRODUCTION

Creating robust energy intake models is important to formulate poultry diets with optimum levels of nutrients and to make economic decisions in the poultry industry. Metabolizable energy requirement models have been developed (Sakomura et al., 1993, 2003; Sakomura, 2004; Rabello et al., 2006; Romero et al., 2009b; Reyes et al., 2012; Pishnamazi et al., 2015; Hadinia et al., 2018; van der Klein et al., 2020) according to coefficients estimated for maintenance ME requirement per metabolic BW (kcal/W^{0.75}), daily body weight gain (kcal/g), and

daily egg mass production (kcal/g). A valid estimation approach in these models should be able to estimate model coefficients with reasonable accuracy, the lowest possible bias, and the smallest variation. In statistics, the word “bias” refers to anything that causes the results to be incorrect in a systematic way (Neyman and Pearson, 1936; Motulsky, 2010). The most challenging aspect of statistical analysis is making valid inferences, which indicates reaching general conclusions from limited data (Žebec et al., 2015). As inference in mathematical modeling techniques is an important mechanism of information integration, inferential efficiency is the ability to incorporate additional information into the knowledge structure that can be used to focus the attention of the inference mechanisms in the most promising direction (Žebec et al., 2015). As an example, including random terms associated with different sources of unexplained variation in a modeling procedure can improve inferential efficiency. Every statistical inference is based on a

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¹Corresponding author: mzuidhof@ualberta.ca

list of assumptions (e.g., independency in a model residual), which need to be considered before interpreting the statistical results. Various statistical procedures need to be evaluated based on their efficiency, which is a measure of quality and robustness of an estimator in a model (Carroll and Pederson, 1993). Essentially, a more efficient estimator needs fewer observations than a less efficient one to achieve a given performance. Thus, a robust procedure of creating energy partitioning models containing valid estimated coefficients for maintenance, growth, and egg production adds to existing studies in 2 ways. First, it explicitly improves accuracy in modeling techniques, thereby going beyond the common mathematical perspective of modeling procedures. Second, it increases predictive performance of ME intake models, thereby matching nutrient supply with nutrient requirements of individual birds.

Although variety in data can be considered as an advantage in modeling, the variety caused by unexplained sources of variation can influence precise calculation of model coefficients leading to unreliability in using the models. To facilitate a robust and consistent calculation of parameters in a model, Dozza et al. (2013) developed a methodology, called “data chunking,” to analyze naturalistic data from car driving studies. The authors divided data into equivalent, elementary pieces before other data analysis steps. Dividing data to different chunk sizes was used to increase the robustness and sensitivity of parameter calculation by avoiding bias from data segments with heterogeneous durations.

Energy requirement predicting models have been used to establish optimized levels of dietary nutrients and more profitable feeding programs for poultry (Sakomura, 2004), yet the effect of dividing BW and production data to different length of periods (chunk size) on the fitting and predictive performance of the models remains to be elucidated. We hypothesized that increasing data chunk size could account for unexplained variation in data caused by variation in health status and voluntary activity level of birds, anomalies in real-time BW data recorded by a precision feeding (PF) system (You et al., 2021), and environmental conditions. Furthermore, the effect of including random terms associated with different model parameters (individual maintenance ME and age) on the fitting performance of the models has been investigated (van der Klein et al., 2020). It is not clear how inclusion of different random terms could affect the predictive performance of ME intake partitioning models.

ME intake lost as heat is equivalent to total heat production (THP) or ME for maintenance (ME_m) requirement of an animal (Zuidhof, 2019a). The ME_m requirement includes ingestion of feed, voluntary activity, immune response, and thermal regulation, which can be confounded by the individual variation and feed restriction level in broiler breeders (Zuidhof, 2019a). Residual feed intake (RFI) and residual heat production (RHP) are biological indicators of energetic efficiency of growth and egg production in poultry (Willems et al., 2013). Residual feed intake is defined as the difference between observed and predicted feed intake based on energy

requirements for production and maintenance (Luiting, 1990; Kennedy et al. 1993). Residual heat production or residual maintenance ME requirement (RME_m) is the residual of the linear relationship between ME_m and ME intake (Romero et al., 2009a). The effects of increasing cumulative BW gain in prepubertal growth phase and earlier timing of growth around puberty on feeding motivation and reproductive performance in broiler breeders has been discussed elsewhere (Afrouziyeh et al., 2021b). In the current paper we evaluate the effect of growth pattern on energy efficiency in breeders.

The objectives of the current study were to 1) evaluate inclusion of random terms associated with individual ME_m , ADG, and age in a ME partitioning model on residual dependency, model fitting and predictive performance; 2) evaluate how including random terms associated with individual maintenance ME, ADG, and age could bias the ME partitioning model; 3) evaluate the effect of chunking BW, ADG, and egg production data into different chunk sizes (daily, 4-d, weekly, 2-wk, or 3-wk) on fitting and predictive performance of ME partitioning model; and 4) determine the effect of an increased (10%) prepubertal BW gain and earlier pubertal phase growth on energy efficiency of broiler breeders.

MATERIALS AND METHODS

The animal protocol for the study was approved by the University of Alberta Animal Care and Use Committee for Livestock and followed the Canadian Council on Animal Care guidelines and policies (CCAC, 2009).

Experimental Design

The experiment was conducted as a randomized controlled trial with Ross 708 broiler breeder pullets ($n = 40$) reared on one of ten target growth trajectories. The growth trajectories were designed with 2 levels of the amount of cumulative BW gain in prepubertal growth phase and 5 levels of timing of growth around puberty (Afrouziyeh et al., 2021a). A 3-phase Gompertz growth model was fitted to the Ross 708 female broiler breeder recommended target BW to estimate the model coefficients. Growth phases 1, 2, and 3 corresponded roughly to prepubertal, pubertal, and postpubertal growth phases, respectively. The model included phase-specific BW gain and time of growth inflection coefficients. Body weight trajectories were designed with 2 levels of prepubertal phase gain (g_1) coefficient as a discrete variable and 5 levels of pubertal growth phase inflection point (I_2) coefficient as a continuous variable. The g_1 was estimated from the breeder-recommended standard BW gain (Standard g_1) target, or 10% higher (High g_1) in the prepubertal growth phase. The second (pubertal) growth phase inflection point (I_2) was advanced by 0, 5, 10, 15, or 20% of the coefficient estimated from the breeder-recommended target BW. The BW trajectories were implemented for each individual bird using a PF system. The PF system provided birds with multiple meals of

short duration (60 seconds/meal) throughout the day to achieve predetermined BW targets. The PF system collected BW and feed intake data for each individual bird. Therefore, each bird was an experimental unit.

Animals and Management

The experimental protocol was previously described in full detail elsewhere (Afrouziyeh et al., 2021b). Briefly, 40 Ross 708 broiler breeder pullets were housed in a single environmentally controlled room containing 2 PF stations, from hatch to 43 wk of age at a stocking density of 3.0 birds per m². The PF stations (Zuidhof et al., 2017, 2019b) were used to apply the growth trajectory treatments and to control individual feed intake to achieve and maintain the assigned target BW curves. At 14 d of age, each bird was equipped with a wing band containing a radio frequency identification (RFID) transponder to be individually recognized by the PF system. The PF system recorded individual BW and individual feed intake throughout the experiment. All birds were fed the same commercial diets in each nutritional phase: starter (crumble; ME 2,726 kcal/kg, 21.0% CP, 1.00% Ca, and 0.70% available P) from hatch to d 34; grower (mash; ME 2,799 kcal/kg, 15.0% CP, 0.79% Ca, and 0.45% available P) from d 35 to d 179; and laying diet (crumble; ME 2,798 kcal/kg, 15.3% CP, 3.30% Ca, and 0.64% available P) from d 180 onward. Water was provided ad libitum throughout the experiment. The photoschedule was 24L:0D (100 lx) from d 0 to 3 then reduced to 8L:16D (15 lx) on d 4. Pullets were photostimulated at wk 22 as the photoperiod was increased to 11L:13D (20 lx). The photoperiod increased further to 12L:12D (25 lx) at wk 23, then again at wk 24 to 13L:11D (50 lx) for the remainder of the experiment. A trap-nest with 8 nesting sites and a nest box with 8 nesting sites equipped with RFID readers which identified and weighed eggs of individual hens were installed in the room at 14 wk of age; thus, the pullets had the chance to adapt to the nesting system prior to the onset of lay.

Data Collection

Individual BW and feed consumption data were collected by the PF system database. Median BW of the multiple daily BW observations of individual birds was considered as their daily BW. Observed ME intake was calculated by multiplying the observed daily feed intake

(g) by the calculated dietary ME content (kcal/g). Eggs were collected from nest boxes, weighed, and assigned to individual birds daily.

Chunking Data

Chunking (Dozza et al., 2013) was implemented on data extracted from the PF system database to obtain means for chunks of daily, 4-d, weekly, 2-, or 3-week durations. Individual BW, BW gain, feed intake, ME intake, and egg mass (EM) were calculated for each chunk. Metabolizable energy intake models were developed for each chunk of data based on the chunk-specific calculated parameters involved in the models.

Metabolizable Energy Partitioning Models

One fixed effect model and 3 mixed effect models were evaluated in each chunk size of data (Table 1). Model [I] was the basic nonlinear model of ME intake as a function of metabolic BW, ADG, and EM production (based on Romero et al., 2009a). The metabolic BW scaling exponent was allowed to fluctuate in all models. The ADG values were divided into separate positive gain (ADG_p) and negative gain (ADG_n) variables. Models [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of random terms for individual maintenance ME, age, and ADG, respectively. Model [II] included a random term $u \sim N(0, V_u)$ associated with the coefficient of metabolic BW to separate individual variation in maintenance ME into between- and within-individual components. Model [III] included a random term $uu \sim N(0, V_{uu})$ associated with the coefficient of metabolic BW by different time periods corresponding to chunk duration (daily, 4-d, weekly, 2-, or 3-wk durations) to separate age variation in maintenance ME into between- and within-individual components. Model [IV] included a random term $v \sim N(0, V_v)$ associated with the coefficient of ADG to separate individual variation in ADG into between- and within-individual components.

Test for Dependent Residuals

Autocorrelation in a model residual indicates a violation of the assumption of independence that is relied upon by many analyses (Dormann et al., 2007). Autocorrelation analysis was used to determine the extent to which

Table 1. Functional specifications of the evaluated models.

Model ¹	Function specification
I	$MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$
II	$MEI_d = (a + u) \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$
III	$MEI_d = (a + uu) \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$
IV	$MEI_d = a \times BW^b + (c + v) \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$

¹Estimated coefficients are lowercase letters. MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); u = bird-specific random term associated with individual maintenance; uu = age-related random term; v = bird-specific random term associated with individual ADG; ε = residual error. Model [I] was a fixed effect model. Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively.

chunking affected dependent residuals in the ME partitioning models. This analysis was used to estimate dependency across chunks and to determine the extent to which traditional statistical analysis (which requires independence of observations) was still possible to apply after chunking. Autocorrelation coefficient (**ACF**), coefficient of determination (**R**²) of residuals vs. lag-residuals in the ME partitioning models, and Durbin Watson (**DW**) statistic were used to evaluate dependent residuals in the models:

$$DW = \frac{\sum_{i=1}^n (e_i - e_{i-1})^2}{\sum_{i=1}^n e_i^2}$$

where e_i was the residual for the i^{th} observation, e_{i-1} was the lagged residual for the $i-1^{\text{th}}$ observation, and n was the number of observations. In the current study, tabulated lower (d_L) and upper (d_U) critical values and were 1.285 and 1.721, respectively ($n = 40$, $\alpha = 0.05$). The DW value was compared to the lower and upper critical values, d_L and d_U . If DW was lower than d_L , there was a positive autocorrelation (DW close to 0) in the error terms. If the calculated DW was higher than d_U , there was not an autocorrelation (DW close to 2) or there was a negative autocorrelation (DW close to 4) in the error terms. If DW was between d_L and d_U , the test was inconclusive (Cetin et al., 2007).

The notation of ACF (m = number of time periods between points) is the correlation between points separated by m time periods. Autocorrelation coefficient determines how correlated points are with each other, based on how many time steps by which they are separated.

$$ACF(m) = \frac{\sum_{t=k+m}^n (y_t - \bar{y})(y_{t-k} - \bar{y})}{\sum_{t=1}^n (y_t - \bar{y})^2}$$

where y_t was the residual at time t , \bar{y} was the mean value for residual, y_{t-k} was the residual at the time before time t . Essentially, autocorrelation is a measure of the degree of correlation between past and future data points, for different degrees of time separation.

Model Comparison

In addition to the SD of the residuals, which was directly estimated in the NLMIXED procedure of SAS software (Version 9.4, SAS Institute Inc., Cary, NC), models were evaluated using model fitting and predictive performance criteria. Mean square error (**MSE**) and **R**² of the models were used to evaluate fitting performance of the models. Model fitting evaluation criteria were computed as follows:

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

$$R^2 = 1 - \frac{\sum_i e_i^2}{\sum_i (y_i - \bar{y})^2}$$

where y_i was the i^{th} ME intake observation, \hat{y}_i was the predicted value for the i^{th} ME intake observation, \bar{y}_i was the mean value of ME intake, and n was the number of observations.

A K-fold cross validation method was used to evaluate the predictive performance of the models. The dataset was randomly partitioned into 5 ($K = 5$) mutually exclusive equal subsets and this procedure was repeated 10 times. Each time, $K-1$ subsets were used as a training set and one subset was used for testing. The **R**² of the relationship between observed and predicted ME intake; the mean absolute error (**MAE**), MSE, and the root mean square error (**RMSE**) were calculated as cross validation statistics for the testing data (Yang and Huang, 2014). Cross validation statistics were computed as follows:

$$MAE = \frac{1}{n} \sum_{i=1}^n |y_i - \hat{y}_i|$$

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2}$$

where y_i was the i^{th} ME intake observation, \hat{y}_i was the predicted value for the i^{th} ME intake observation, and n was the number of observations.

Evaluation of Energy Efficiency

Total heat production, RHP, and RFI were evaluated using the model of choice (model [II] – 3 wk) and used as indicators of energy efficiency of growth and egg production. Total heat production was calculated as daily maintenance requirement $((a + u) \times BW^{0.56})$ and reported as kcal/d. The residual of the linear relationship between bird ME_m (kcal/ $BW^{0.56}$ /d) and ME intake (kcal/ $BW^{0.56}$ /d) was calculated as RHP (kcal/kg $BW^{0.56}$). The slope of the recent relationship represented the proportion of ME lost as heat per unit of ME intake. Predicted ME intake was estimated using the model [II] – 3 wk. Residual feed intake was calculated as the difference between observed and predicted ME intake.

Statistical Analysis

All statistical analyses were performed using SAS software (Version 9.4, SAS Institute Inc., Cary, NC). Metabolizable energy partitioning models were fitted using the NLMIXED procedure. Partitioning of dataset into training and testing subsets, for cross validation method, was performed using the SURVEYSELECT procedure. The linear regression between maintenance requirement coefficient and ME intake was conducted using the MIXED procedure. Analysis of covariance was conducted on ME_m , RHP, and RFI using the HPMIXED and MIXED procedures, with g_1 and time period as discrete sources of variation, and I_2 as a continuous predictor variable. Period was included in the model as a random effect with individual birds as the

subject to account for within-bird variation. Pairwise differences between means within each period were determined using Tukey's HSD test and were reported as different when $P \leq 0.05$.

RESULTS AND DISCUSSION

Estimated Coefficients in ME Intake Models

Increasing chunk size from daily to 3-wk period decreased coefficient for metabolic BW (maintenance requirement) and instead increased coefficients for daily gain and EM in all models (Tables 2-6). For instance, for a 2.00 kg bird, maintenance energy requirement (kcal/d) ranged from 147.10 to 216.33 kcal/d for the 3-wk (model [IV] – 3 wk) and daily (model [III] – daily) chunk sizes, respectively. These were similar to previously reported estimates for ME_m requirement, which ranged from 147.6 to 245.2 kcal/d for a 2.00 kg broiler breeder pullet or hen (Sakomura et al., 2003; Romero et al., 2011; Hadinia et al., 2018; van der Klein et al., 2020). An estimated ME_m for a 2.00 kg broiler breeder hen in the current study was 148.1 kcal/d ($119.73 \times 2.00^{0.49}$; based on the coefficients of model [II] – 3 wk Table 6), which is less than that reported by van der Klein et al. (2020), in which weekly chunked data were used ($130.64 \times 2.00^{0.58} = 195.1$ kcal/d; based

on the coefficients in the model of choice in their study). This wide range for ME_m requirement in the literature was due to animal behavior, bird age, strain, temperature, and dietary energy level. Furthermore, different housing systems (20% greater ME_m requirement in floor pens than cage-raised ones; Rabello et al., 2006), feed intake (10% greater heat increment in ad libitum fed birds compared to that of pullets restricted to 54% of the ad libitum feed intake; Sakomura et al., 2003), and methodology being used to estimate ME_m requirement (indirect calorimetry, Spratt et al., 1990; comparative slaughter method, Rabello et al., 2006; Reyes et al., 2012; mathematical modeling approach, van der Klein et al., 2020) could affect the estimated ME_m requirement. This study revealed that chunk size of data used in modeling of ME partitioning can also affect the estimated ME_m requirement.

The coefficient for ADG_p , which indicated ME requirement for each gram of gain, ranged from 0.46 to 3.66 kcal/g for the daily (model [III] – daily) and 3-wk (model [III] – 3wk) chunks, respectively. A wide range of ME requirements for gain has been reported from 0.71 to 5.80 kcal/g in the literature (Sakomura, 2004; Reyes et al., 2012; Hadinia et al., 2018). Variation in ME requirements for growth can be associated with differences in composition of gain as affected by stage of maturity; fat tissue contains a higher energy content

Table 2. Regression coefficients of nonlinear ME intake models analyzed based on daily data, representing ME partitioning to maintenance, gain, and egg production in Ross 708 broiler breeder females.

Model ¹	Model [I]			Model [II]			Model [III]			Model [IV]			
	Coefficient ²	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t
a (kcal/BW ^b)		152.04	1.53	<0.001	153.58	1.88	<0.001	157.27	2.19	<0.001	152.04	1.54	<0.001
b		0.46	0.01	<0.001	0.45	0.01	<0.001	0.46	0.01	<0.001	0.46	0.01	<0.001
c (kcal/g)		0.56	0.06	<0.001	0.53	0.06	<0.001	0.46	0.05	<0.001	0.58	0.11	<0.001
d (kcal/g)		0.58	0.08	<0.001	0.57	0.08	<0.001	0.63	0.08	<0.001	0.58	0.08	<0.001
e (kcal/g)		1.86	0.03	<0.001	1.87	0.03	<0.001	1.60	0.03	<0.001	1.88	0.02	<0.001
σ_u					6.56	0.89	<0.001						
σ_{uu}								21.92	1.07	<0.001			
σ_v											0.57	0.07	<0.001
ε		60.13	0.42	<0.001	59.34	0.42	<0.001	53.25	0.38	<0.001	59.26	0.42	<0.001

¹Model [I] was a fixed effect model with the form of $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d). Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively. u = bird-specific random term associated with individual maintenance; uu = age-related random term; v = bird-specific random term associated with individual ADG.

Table 3. Regression coefficients of nonlinear ME intake models analyzed based on a 4-d data, representing ME partitioning to maintenance, gain, and egg production in Ross 708 broiler breeder females.

Model ¹	Model [I]			Model [II]			Model [III]			Model [IV]			
	Coefficient ²	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t
a (kcal/BW ^b)		125.76	3.22	<0.001	128.42	3.29	<0.001	133.75	4.17	<0.001	124.1	3.25	<0.001
B		0.51	0.01	<0.001	0.49	0.01	<0.001	0.55	0.02	<0.001	0.51	0.01	<0.001
c (kcal/g)		2.03	0.15	<0.001	1.94	0.15	<0.001	1.69	0.15	<0.001	2.14	0.20	<0.001
d (kcal/g)		0.86	0.37	0.024	0.83	0.37	0.033	1.28	0.32	0.023	0.81	0.36	0.035
e (kcal/g)		2.36	0.06	<0.001	2.36	0.05	<0.001	1.81	0.07	<0.001	2.41	0.05	<0.001
σ_u					5.52	0.88	<0.001						
σ_{uu}								19.75	1.93	<0.001			
σ_v											0.74	0.10	<0.001
E		41.71	0.59	<0.001	40.82	0.58	<0.001	-34.97	0.50	<0.001	40.13	0.57	<0.001

¹Model [I] was a fixed effect model with the form of $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d). Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively. u = bird-specific random term associated with individual maintenance; uu = age-related random term; v = bird-specific random term associated with individual ADG.

Table 4. Regression coefficients of nonlinear ME intake models analyzed based on weekly data, representing ME partitioning to maintenance, gain, and egg production in Ross 708 broiler breeder females.

Model ¹ Coefficient ²	Model [I]			Model [II]			Model [III]			Model [IV]		
	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t
a (kcal/BW ^b)	116.48	4.45	<0.001	119.73	4.436	<0.001	119.76	5.79	<0.001	118.34	4.28	<0.001
B	0.52	0.02	<0.001	0.49	0.02	<0.001	0.60	0.04	<0.001	0.50	0.02	<0.001
c (kcal/g)	2.58	0.21	<0.001	2.45	0.21	<0.001	2.44	0.24	<0.001	2.50	0.24	<0.001
d (kcal/g)	0.65	0.48	0.17	0.72	0.47	0.13	0.94	0.41	0.023	0.70	0.46	0.14
e (kcal/g)	2.66	0.08	<0.001	2.66	0.07	<0.001	1.98	0.10	<0.001	2.69	0.07	<0.001
σ_u				5.13	0.95	<0.001						
σ_{uu}							19.16	2.52	<0.001			
σ_v										0.73	0.11	<0.001
E	37.57	0.70	<0.001	36.73	0.69	<0.001	-31.32	0.59	<0.001	36.03	0.68	<0.001

¹Model [I] was a fixed effect model with the form of $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d). Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively. u = bird-specific random term associated with individual maintenance; uu = age-related random term; v = bird-specific random term associated with individual ADG.

Table 5. Regression coefficients of nonlinear ME intake models analyzed based on a 2-wk data, representing ME partitioning to maintenance, gain, and egg production in Ross 708 broiler breeder females.

Model ¹ Coefficient ²	Model [I]			Model [II]			Model [III]			Model [IV]		
	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t
a (kcal/BW ^b)	106.54	5.70	<0.001	109.51	5.61	<0.001	113.14	7.58	<0.001	106.54	5.70	<0.001
B	0.53	0.03	<0.001	0.51	0.03	<0.001	0.59	0.05	<0.001	0.53	0.03	<0.001
c (kcal/g)	3.14	0.28	<0.001	3.02	0.28	<0.001	2.81	0.34	<0.001	3.14	0.28	<0.001
d (kcal/g)	3.57	2.24	0.11	3.77	2.23	0.091	3.38	2.01	0.10	3.57	2.24	0.12
e (kcal/g)	2.96	0.10	<0.001	2.97	0.10	<0.001	2.33	0.15	<0.001	2.96	0.10	<0.001
σ_u				4.63	1.05	0.001						
σ_{uu}							15.30	2.95	<0.001			
σ_v										1.05	0.05	<0.001
E	31.27	0.81	<0.001	30.41	0.81	<0.001	-27.52	0.73	<0.001	31.27	0.81	<0.001

¹Model [I] was a fixed effect model with the form of $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d). Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively. u = bird-specific random term associated with individual maintenance; uu = age-related random term; v = bird-specific random term associated with individual ADG.

(9.1 kcal/g) compared to lean tissue (5.5 kcal/g of DM basis or 3.7 kcal/g of wet tissue; [Leeson and Summers, 2001](#)). As age increases, the amount of body fat increases ([Leenstra, 1986](#)). Lean mass increases until egg peak production and then there is a loss in lean tissue toward 50 wk of age in broiler breeders; this process is a net mobilization of lean tissue to support egg production ([Salas et al., 2010](#); [van Emous et al., 2015](#); [Vignale et al.,](#)

[2016](#)). However, fat reserves increase throughout the egg production phase and reach a maximum at 50 wk of age ([van Emous et al., 2015](#); [Caldas et al., 2019](#)). Thus, the ME requirement for gain should increase as BW increases with age, with a fast accumulation rate for energetically expensive fat mass toward 50 wk of age. In the current experiment, composition of gain was not measured. One can argue that possible differences in

Table 6. Regression coefficients of nonlinear ME intake models analyzed based on a 3-wk data, representing ME partitioning to maintenance, gain, and egg production in Ross 708 broiler breeder females.

Model ¹ Coefficient ²	Model [I]			Model [II]			Model [III]			Model [IV]		
	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t	Estimate	SEM	Pr > t
a (kcal/BW ^b)	97.91	7.52	<0.001	100.47	7.43	<0.001	98.94	9.34	<0.001	97.91	7.52	<0.001
B	0.58	0.04	<0.001	0.56	0.04	<0.001	0.65	0.07	<0.001	0.58	0.04	<0.001
c (kcal/g)	3.59	0.38	<0.001	3.49	0.37	<0.001	3.66	0.46	<0.001	3.59	0.38	<0.001
d (kcal/g)	2.60	3.90	0.50	3.16	3.91	0.42	2.78	3.40	0.42	2.60	3.90	0.50
e (kcal/g)	2.96	0.13	<0.001	2.96	0.13	<0.001	2.47	0.18	<0.001	2.96	0.13	<0.001
σ_u				3.45	1.18	0.011						
σ_{uu}							12.53	2.98	<0.001			
σ_v										1.02	0.03	<0.001
E	28.85	0.92	<0.001	28.26	0.93	<0.001	24.85	0.81	<0.001	28.85	0.92	<0.001

¹Model [I] was a fixed effect model with the form of $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d). Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively. u = bird-specific random term associated with individual maintenance; uu = age-related random term; v = bird-specific random term associated with individual ADG.

composition of gain might have affected the accuracy of estimated coefficient of gain. In fact, model [IV] included a random term associated with the coefficient of average daily gain to separate individual variation in ADG into between- and within-individual components. Including age as a random term was essential a proxy to separate age variation in body composition and maintenance ME into between individual components and to capture age-associated differences in gain. Furthermore, gain requirement is less than the maintenance requirement in broiler breeders, which makes the model less vulnerable to the differences in the composition of gain. Thus, in a situation where body composition data is not known, including age as the random effect could be an acceptable approach. Models with complex sets of coefficients with gain did not converge in this experiment.

The ME requirements for each gram of EM ranged from 1.60 kcal/g with the daily chunk size (model [III] – daily) to 2.97 kcal/g with the 2 wk chunk size (model [II] – 2wk). The ME requirement for egg production ranges from 1.90 to 3.15 kcal/g (Sakomura, 2004; Romero et al., 2009b; Reyes et al., 2012; van der Klein et al., 2020). The energy content of broiler breeder eggs ranges from 1.33 kcal/g (Sibbald, 1979) to 1.79 kcal (Chwalibog, 1992) with an average value of 1.54 kcal/g (Sakomura, 2004). With an average efficiency of ME utilization for energy deposition in broiler breeder eggs (64%), an expected ME requirement for egg production would be around 2.40 kcal/g (Sakomura, 2004).

Variation of ADG_p , ADG_n , and EM decreased as the chunk size increased (data not shown). Reduced variation of an independent variable could be due to sampling choices, which subsequently could be a source of variation in estimated coefficients in a ME partitioning model. Furthermore, stability of estimated regression coefficients in a model is associated with the variance of the independent variable and sample size (O'Brien, 2007). Thus, it can be hypothesized that a reduction in the variation of the ADG and EM due to an increased chunk size was a possible reason for an increase in their estimated coefficients. This hypothesis can be accepted by comparing the pattern of ME requirement for egg production in the literature and the current study. The ME requirement for egg production has been reported as 1.78 kcal/g in a semi-weekly chunked data (Pishnamazi et al., 2015); 2.10 kcal/g in a semi-weekly chunked data until 32 wk of age and weekly chunked data thereafter (Romero et al., 2009b); 2.40 and 2.42 kcal/g in a weekly chunked data (Reyes et al., 2012; van der Klein et al., 2020); and 2.96 kcal/g in a 3-wk chunked data (current study). Therefore, it can be concluded that using a longer chunk size (3-wk vs. semiweekly or weekly) in calculating the average value of individual BW and feed intake to establish a ME intake partitioning model can highlight the contribution of ADG and EM in the model by increasing their estimated coefficient. More specifically, longer chunk might smooth out the day-to-day variation and associated costs of building up nutrients and deposition of nutrients in the egg in breeders which did not lay an egg every day.

Model Comparison

Effect of chunk size. Increasing chunk size of data decreased SD of residuals in each model (Table 2-6). The SD of residuals decreased for 4-d, weekly, 2-wk, and 3-wk period chunk sizes compared to that of daily chunk size by 30.6, 37.5, 47.9, and 52% in model [I], 31.2, 38.1, 48.7, and 52.3% in model [II], 34.32, 41.1, 48.3, and 53.3% in model [III], and 32.2, 39.2, 47.2, and 51.3% in model [IV], respectively, which indicated that more variation was accounted for in 3-wk chunk size. The smaller the residual SD, the closer is the fit of the estimate to the actual data. Therefore, chunking data to 3-wk periods provided closest fit of the ME intake estimates to the actual ME intake, demonstrating more precise and more accurate (close to being correct) estimation of coefficients in the ME partitioning model. An analytical method is precise when repeated measurements give very similar results. van der Klein et al. (2020) raised a concern about an instability issue in estimated coefficients of a ME partitioning model containing a random term associated with the individual bird nested within a random term of age. The authors hypothesized that the model did not converge because of the large variability in age at first egg between birds as the birds were in different physiological states at the same age. They concluded that individual bird rather than age would explain a large proportion of the differences in ME_m requirements over age in their study. However, the results of the current study showed that other factors such as chunk size of data would affect stability and precision of estimated coefficients in a model.

Within each model, increasing chunk size of data increased fitting performance of ME partitioning models by reducing MSE and increasing R^2 of the fitted models (Table 7). It also increased predictive performance of the models by reducing RMSE and R^2 of the linear relationship between observed and predicted ME intake in the testing subsets of a 5-fold cross validation. It is possible that increasing chunk size from daily to 3-wk reduced the influence of outliers caused by unaccounted sources of error such as environmental condition, voluntary activity level, and health status of the birds on the model parameters (Zuidhof, 2019a).

Increasing chunk size affected autocorrelation bias differently across the models (Figures 1 to 3). Chunking data to 3-wk periods resulted in the lowest autocorrelation bias in all models except for model [III] where the lowest ACF was calculated in daily chunk size (Figure 1). Lower autocorrelation bias was detected by lower ACF, lower R^2 of the relationship between residuals and lag-residuals (Figure 2), and a DW value closer to 2 (Figure 3). Investigation of alternative random-effect models and variance-covariance structures of the residuals would be valuable in future research.

Effect of random terms. The residual SD decreased for models [II], [III] and [IV] as compared to model [I] by 1.31, 11.44, and 1.44% in daily chunked, 2.13, 16.15, and 3.78% in 4-d chunked, 2.23, 16.63, and 4.09% in weekly chunked, 2.75, 11.99, and 0% in 2-wk chunked, and 2.04,

Table 7. Model fitting and performance statistics of nonlinear ME intake models analyzed based on daily, 4-d, weekly, 2-wk, and 3-wk chunked data, representing ME partitioning to maintenance, gain, and egg production in Ross 708 broiler breeder females.

Model ¹	Model fitting statistics ²		Cross validation statistics ³			
	MSE	R ²	MAE	MSE	RMSE	R ²
[I] – daily	3,616	0.730	42.8	3,689	60.7	0.725
[II] – daily	3,510	0.738	42.0	3,573	59.7	0.734
[III] – daily	2,762	0.794	37.8	2,774	52.8	0.791
[IV] – daily	3,501	0.739	42.2	3,563	59.6	0.734
[I] – 4 d	1,739	0.845	28.4	1,726	41.5	0.847
[II] – 4 d	1,649	0.853	27.7	1,635	40.3	0.855
[III] – 4 d	1,190	0.894	23.0	1,161	34.2	0.895
[IV] – 4 d	1,592	0.859	27.7	1,566	39.4	0.862
[I] – weekly	1,412	0.872	25.2	1,382	37.1	0.875
[II] – weekly	1,327	0.880	24.6	1,305	36.1	0.882
[III] – weekly	954	0.914	20.4	937	30.7	0.915
[IV] – weekly	1,273	0.885	24.6	1,259	35.5	0.886
[I] – 2 wk	978	0.908	21.5	1,047	32.3	0.903
[II] – 2 wk	900	0.915	20.7	974	31.0	0.911
[III] – 2 wk	737	0.931	18.4	776	27.8	0.928
[IV] – 2 wk	978	0.908	20.7	919	30.1	0.916
[I] – 3 wk	832	0.918	20.4	875	29.6	0.914
[II] – 3 wk	778	0.923	19.0	797	27.9	0.923
[III] – 3 wk	601	0.941	16.6	612	24.7	0.939
[IV] – 3 wk	832	0.918	19.8	786	27.8	0.924

¹Model [I] was a fixed effect model with the form of $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d). Model [II], [III], and [IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for individual maintenance ME, age, and ADG, respectively. The data were chunked to daily, 4-d, weekly, 2-wk, and 3-wk sizes.

²MSE: Mean squared error; R²: Coefficient of determination of observed ME intake with predicted ME intake by the models.

³MAE: Mean absolute error; RMSE: Root mean square error; R²: Coefficient of determination of observed ME intake with predicted ME intake by the testing model in a K-fold cross validation.

13.86, and 0% in 3-wk chunked data (Tables 2-6). Incorporating a random term associated with individual ME_m requirement or age partitioned part of the residual SD (σ_e) into bird-specific (σ_u) and age-specific (σ_{mu}) variation in maintenance. Linear fixed-effect models have a constant slope, which precludes estimation of age-related changes in energy requirements and assumes constant maintenance ME requirements (Romero et al., 2009b; Rabello et al., 2006). However, maintenance ME requirements are influenced by energy intake and subsequent heat increment of feeding and changes in metabolic rate (Richards and Proszkowiec-Weglarz, 2007; Romero et al., 2009a). Mixed-effect models compensate at least partially for inflexible linear fixed-effect model coefficients. As discussed, the random term associated with individual maintenance (u) reduced estimation bias in the model. Age-related differences in body composition and individual bird factors affecting maintenance requirements might be expected in a linear fixed-effect energy partitioning model. In fact, including random effect in the model allowed dynamic estimation of energy requirements for ADG and EM with respect to age and individual birds. It also accounted for variability in maintenance ME requirements of individual birds.

Including random term associated with individual ADG reduced residual SD in all chunk sizes except for the 2-wk and 3-wk periods. In fact, model [IV] was identical to model [I] in the 2-wk and 3-wk periods. This might be because increasing chunk size beyond weekly period had already reduced variation in ADG in a way that including the random term for ADG did not further reduce the residual SD. This can be confirmed by

reduction in ADG variation with increasing chunk size which was discussed earlier in this paper.

Selection of the model of choice. Across all chunk sizes, including a random term associated with age (model [III]) resulted in the lowest MSE (Table 7). Among the models, model [III] – 3 wk showed the lowest MSE and closet R² to 1 (best fitting performance) followed by the models [III] – 2 wk and [II] – 3 wk (Table 7). However, models [III] – 3 wk and [III] – 2 wk showed autocorrelation bias (Figures 1 to 3), which is a considerable disadvantage. As already discussed, a DW lower than the lower critical value ($d_L = 1.285$ in this study) indicated positive autocorrelation in the model residual. DW values of the models [III] – 3 wk and [III] – 2 wk were 0.910 and 0.977, respectively indicating positive autocorrelation in their residuals (Figure 2). Autocorrelation in the residual of a model indicates a violation of the assumption of independence that is relied upon by many analyses. Therefore, predictions of a model with high autocorrelation may be inefficient. This indicates that there was likely unexplained variation which, if accounted for, would improve inferential efficiency. Thus, residuals independency assumption was prioritized over the model fitting performance by selecting a model with a lower autocorrelation bias in the first place and greater fitting performance in the second place. Model [III] – daily with a DW value of 1.634 showed the lowest autocorrelation bias in the residual followed by model [II] – 3 wk with a DW value of 1.561, which both fell between the lower and upper critical DW ($d_L = 1.285$ and $d_U = 1.721$). However, model [III] – daily was not a reliable model from either fitting or

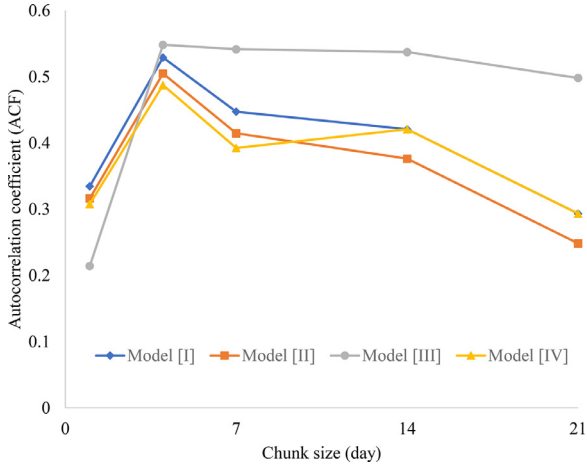


Figure 1. Autocorrelation coefficient (ACF) of ME partitioning models in different chunk sizes of data (daily, 4-d, weekly, 2-wk, and 3-wk periods). Model [I]: $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$; where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); ε = the model residual. Model [II to IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for maintenance requirement, age, and ADG, respectively.

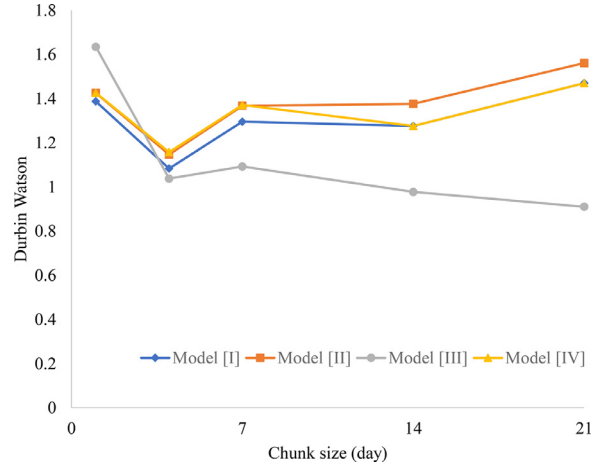


Figure 3. Durbin Watson statistic of ME partitioning models in different chunk sizes of data (daily, 4-d, weekly, 2-wk, and 3-wk periods). Model [I]: $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$; where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); ε = the model residual. Model [II to IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for maintenance requirement, age, and ADG, respectively.

predictive perspectives (Table 7). Model [III] – daily did not meet the requirements of the best fitting (i.e., lower MSE and an R^2 closer to 1) nor the predictive performance criteria (i.e., lower MSE, RMSE, and MAE and an R^2 closer to 1 in the testing models in a K-fold cross validation). Based on the above-mentioned information, model [II] – 3 wk, with a reliable fitting and predictive performance, was selected as the model of choice for further discussion of ME_m requirements and energy efficiency evaluation in this study.

Including bird-specific random terms associated with individual maintenance ME or ADG requirements reduced autocorrelation bias compared to the fixed effect

models in all chunk sizes. However, including the random term associated with age increased autocorrelation bias compared to the fixed effect model except in the daily chunk size. Thus, it can be hypothesized that including a random term associated with age can bias the model residual independency assumption except if the data is used in the daily chunk size. This was because by increasing chunk size (duration of periods) the number of periods as a proxy of “age” decreased, and as discussed earlier the variation of data decreased; as a result, dependency in the model residual would increase. Model [III] – daily showed the lowest dependent residual as including a random term associated with age in the model where it had maximum number of time periods (daily) accounted for the variation due to the age effect. For all chunk sizes, including a random term associated with individual maintenance ME requirement biased the predictive performance of the models compared to the scenario where the random term was associated with age.

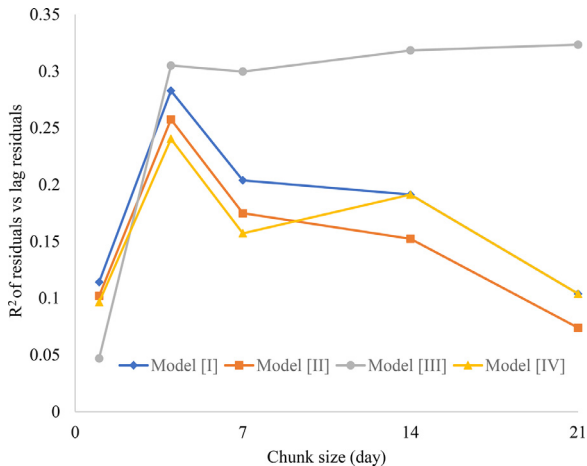


Figure 2. R^2 of residuals vs. lag residuals in ME partitioning models in different chunk sizes of data (daily, 4-d, weekly, 2-wk, and 3-wk periods). Model [I]: $MEI_d = a \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$; where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); ε = the model residual. Model [II to IV] were nonlinear mixed models based on the function of model [I] with inclusion of a random term for maintenance requirement, age, and ADG, respectively.

Energy Efficiency

Earlier pubertal growth increased ME_m in birds, which was greater in High g_1 birds (2.12 kcal/d/wk of earlier pubertal growth) than in Standard g_1 birds (1.50 kcal/d/wk of earlier pubertal growth; $P < 0.001$, Table 8). Factors contribute to energy loss as heat production have been categorized into dietary factors such as nutrient composition and feed form (Lopez and Leeson, 2008), environmental factors such as temperature (Rabello et al., 2006; Pishnamazi et al., 2015), and animal factors including age, sex, genetic potential, feed intake (Swennen et al., 2004), reproductive status (van der Klein et al., 2020), health status (van Erden et al., 2006), and activity level (van Milgen et al., 2001).

Table 8. Effects of prepubertal BW gain (g_1) and pubertal growth inflection (I_2) on maintenance energy requirement (ME_m), residual heat production¹ (RHP), and residual feed intake² (RFI) in Ross-708 broiler breeders.

Effect ³	Model [II] – 3 wk ⁴							
	g_1	I_2	ME_m	SEM	RHP	SEM	RFI	SEM
			kcal/d		kcal/kg BW ^{0.56}		kcal/d	
g_1	Standard		157.2 ^b	0.25	-0.68 ^b	0.10	-1.22 ^b	1.22
	High		165.1 ^a	0.28	0.79 ^a	0.11	2.12 ^a	1.30
I_2		17.83	166.2 ^a	0.36	1.23 ^a	0.16	4.72 ^a	1.58
		18.95	161.9 ^b	0.42	-0.26 ^{bc}	0.18	0.13 ^{ab}	1.76
		20.06	161.3 ^b	0.39	0.16 ^b	0.17	-0.19 ^{ab}	1.67
		21.18	158.5 ^c	0.44	-0.30 ^{bc}	0.19	-0.20 ^{ab}	1.84
		22.29	157.8 ^c	0.36	-0.55 ^c	0.16	-2.20 ^b	1.58
$I_2 \times g_1$	Standard	17.83	160.9 ^d	0.50	-0.07 ^{cd}	0.22	3.69 ^{ab}	2.06
		18.95	159.3 ^d	0.58	-0.18 ^{cde}	0.26	-0.19 ^{ab}	2.33
		20.06	156.1 ^e	0.50	-1.16 ^e	0.22	-2.32 ^{ab}	2.06
		21.18	155.0 ^e	0.50	-1.22 ^e	0.22	-3.22 ^b	2.06
		22.29	154.7 ^e	0.50	-0.75 ^{de}	0.22	-4.06 ^b	2.06
	High	17.83	171.4 ^a	0.50	2.54 ^a	0.22	5.74 ^a	2.06
		18.95	164.6 ^{bc}	0.58	-0.34 ^{cde}	0.26	0.45 ^{ab}	2.33
		20.06	166.5 ^b	0.58	1.47 ^{ab}	0.26	1.93 ^{ab}	2.33
		21.18	162.0 ^{cd}	0.70	0.62 ^{bc}	0.31	2.82 ^{ab}	2.79
		22.29	161.0 ^d	0.50	-0.36 ^{cde}	0.22	-0.34 ^{ab}	2.06
I_2		-1.50	0.15	-0.20	0.06	-1.72	0.53	
$I_2 \times g_1$	Standard		-1.50	0.15	-0.20	0.06	-1.72	0.53
	High		-2.12	0.36	-0.48	0.16	-1.04	1.30
Source of variation	----- P-value -----							
g_1			<0.001		<0.001		0.011	
I_2			<0.001		0.002		0.006	
$I_2 \times g_1$			<0.001		0.005		0.38	
period			<0.001		0.061		<0.001	

^{a–e}Means within columns with no common superscript differ ($P < 0.05$).

¹Residual heat production (RHP) was the residual of the linear relationship between ME_m and ME intake.

²Residual feed intake (RFI) was defined as the difference between observed and predicted feed intake based on energy requirements for production and maintenance.

³ g_1 was either the gain coefficient for the prepubertal phase, estimated from the breeder-recommended standard BW gain (Standard g_1) target, or 10% higher (High g_1). Second growth phase (pubertal) inflection point (I_2) was advanced such that I_2 -0% = 22.29 wk; I_2 -5% = 21.16 wk; I_2 -10% = 20.05 wk; I_2 -15% = 18.94 wk; I_2 -20% = 17.82 wk.

⁴Model [II] – 3 wk was a mixed effect model with inclusion of a random term for individual maintenance ME. The model was $MEI_d = (a + u) \times BW^{0.56} + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); u = bird-specific random term associated with individual maintenance.

In the current study, some animal factors such as feed intake and activity level could have contributed to the increase in ME_m requirement of birds with earlier pubertal growth. Earlier pubertal growth increased BW, frequency of daily station visits (as an indicator of activity level), feed intake, and subsequently feed intake-associated (diet-induced) thermogenesis in broiler breeders, which consequently required more energy for maintenance (Afrouziyeh et al., 2021b).

The linear relationship between average daily ME intake and ME_m for the total experimental period (Figure 4) has 2 main applications: first, it measures bias in the random term, which may be explained by changes in ME_m expenditure at various levels of ME intake. Second, the slope coefficient represents the proportion of increased ME intake that is used for ME_m requirement (lost as heat), which is the heat increment of feeding. In the current study, the model [II] – 3wk predicted that ME_m (kcal/BW^{0.56}) increased by 0.013 kcal/kcal of ME intake; in other words, 1.3% of the increase in ME intake was used for ME_m requirement and lost as heat from 2 to 43 wk of age. In the literature estimated heat increment of feeding has been reported as 52% during the life-time of broiler breeders from 2 to 55 wk of age, 79% during the rearing phase from 2 to 20 wk of age, 44% during the laying phase from 22 to 55 wk

of age (van der Klein et al., 2020), 19 and 34% during the laying phase from 20 to 60 wk of age (Romero et al., 2009a,b), and 87% from 10 to 23 wk of age (Hadinia et al., 2018). Animal factors such as bird age, composition of gain, and reproductive status (van der Klein et al., 2020) and dietary factors such as diet composition (Romero et al., 2009a) can affect heat increment of feeding. The lower coefficient for the slope of ME_m and ME intake relationship in the current study (1.3%) compared to that of in the literature (19–87%) indicated a lower bias in the model [II] – 3 wk, which has accounted for unexplained feed intake-associated heat production. The vertical distance between each individual point and the regression line (Figure 4) corresponded to the RHP value. The Standard g_1 treatment birds had a lower RHP than that of their counterparts in the High g_1 treatment. Figure 4 shows that most of the individuals in the Standard g_1 treatment had a RHP lower than the regression line representing a negative value for the RHP. Thus, Standard g_1 birds were more efficient in utilizing dietary energy compared to the High g_1 birds.

For every week of earlier pubertal growth, RHP increased by 0.20 and 0.48 kcal/kg BW^{0.56} for the Standard and High g_1 birds ($P = 0.005$, Table 8). Standard g_1 birds had lower RHP than that of the High g_1 birds

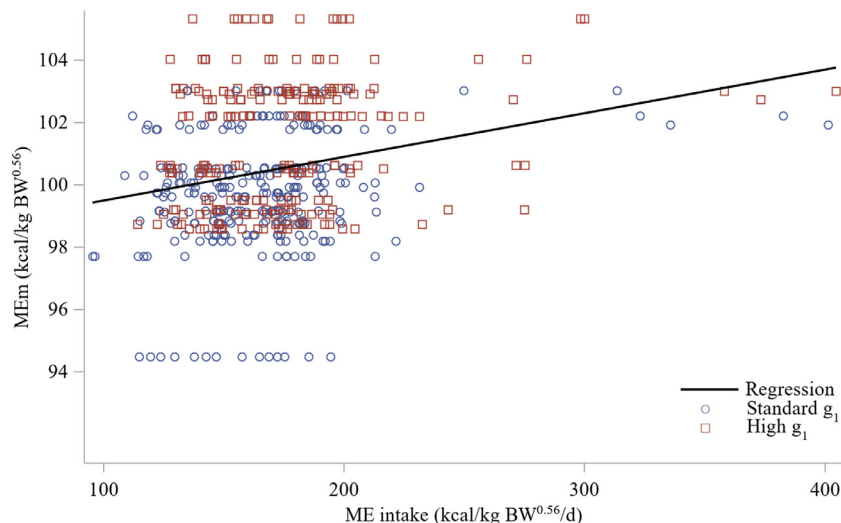


Figure 4. Estimates of the individual maintenance requirement (ME_m) relative to average daily ME intake for the duration of the experiment (from 2 to 43 wk of age) as estimated by a mixed-effect model describing ME partitioning to maintenance, gain, and egg production in a 3-wk chunked data. The model was $MEI_d = (a + u) \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \varepsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); u = bird-specific random term associated with individual maintenance. g_1 was either the gain coefficient for the prepubertal phase, estimated from the breeder-recommended standard BW gain (Standard g_1) target, or 10% higher (High g_1). Regression equation was $ME_m = 98.09 + 0.013 \times MEI + \varepsilon$ ($P < 0.001$, $R^2 = 0.073$).

(-0.68 ± 0.1 vs. 0.79 ± 0.11 kcal/kg $BW^{0.56}$, $P < 0.001$). It could be hypothesized that a higher degree of feed restriction in the Standard g_1 birds compared with that of the High g_1 birds provided stimulus for a metabolic shift in the Standard g_1 birds to become more energetically conservative with ME partitioning to HP. This means that the Standard g_1 birds were more energetically efficient in utilizing the ME intake compared to their counterparts in the High g_1 treatment. This was expected as feed restriction may increase efficiency by reducing heart rate, blood pressure, and body temperature in restricted fed birds (Savory et al., 2006). Furthermore, both caloric restriction and low RFI induced a shift to an energetically conservative mode in rodents (Selman et al., 2006) and pigs (Lkhagvadorj et al., 2010) by downregulating steroidogenesis and lipogenesis in both liver and adipose tissue.

Increasing prepubertal phase BW gain increased RFI (-1.22 ± 1.22 kcal/d in the Standard g_1 vs. 2.12 ± 1.30 kcal/d in the High g_1 treatment, $P = 0.011$, Table 8), which was in line with the RHP results. For each week of earlier pubertal growth RFI increased by 1.72 kcal/d ($P = 0.006$, Table 8). It has been previously shown that RFI values can be confounded by heat increment of feeding (Swennen et al., 2007). However, RHP is an indicator of energy efficiency which is not confounded by feed intake, heat increment of feeding, BW gain, and egg production (Romero et al., 2009a). Thus, RHP can be used as a better estimator for energy efficiency for maintenance requirements compared to RFI.

Comparison of Current Study Model With Other ME Intake Models

Model [II] – 3 wk overestimated ME requirement from 2 to 30 wk, 2 to 18 wk, and 2 to 6 wk of age and

underestimated it from 31 to 43 wk, 19 to 43 wk, and 3 to 43 wk of age compared to the models developed by van der Klein et al. (2020), Pishnamazi et al. (2015), and Reyes et al. (2012), respectively (Figure 5). The difference between the estimated ME requirement values in the current study and those of Reyes et al. (2012) could be at least partially explained by the different genetic strain used in these studies. Reyes et al. (2012) used Cobb 500, which have heavier BW compared to Ross 708 at the same age (2,600 g vs. 2,245 g at 22 wk of age; Aviagen, 2016; Cobb 500, 2019). Although Pishnamazi et al. (2015) and van der Klein et al. (2020) used the same strain as the current study (Ross 708), different chunk size of the data (weekly) was used in their studies to build the ME intake models compared to the model of choice in the current study (3-wk chunk size). The energy requirement estimated by model [II] – 3 wk was higher than the Ross 708 guideline (Aviagen, 2016) from 2 to 12 wk of age but lower than that from 13 to 43 wk of age; possibly the overestimation from 2 to 12 wk of age was due to using a higher BW profile (on average) compared to the guideline. If that is the case, that might have increased our prediction for the ME_m requirement. Overall, the previously published models with Ross 708 strain (Pishnamazi et al., 2015; van der Klein et al., 2020) along with the model developed by the current study estimated a lower energy requirement during the lifetime or after 12 wk of age compared to the recommended age-specific ME intake data by Ross 708 guideline (Figure 5). Comparison of estimated energy requirement by 3 studies revealed that the breeder recommended ME intake does not likely match the guideline-recommended target BW . It means that by applying guideline ME intake recommendation a higher achieved BW would be expected (Figure 6).

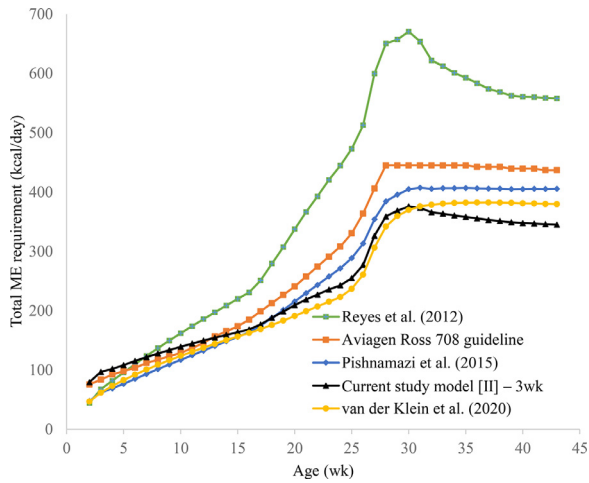


Figure 5. Simulation of broiler breeder ME requirements by applying the Aviagen guide BW, ADG and egg mass (EM) data in the Reyes et al. (2012; ■), Pishnamazi et al. (2015; ◆), van der Klein et al. (2020; ●), and the current study (model [II] – 3wk; ▲) models from 2 to 43 wk of age at 20°C environmental temperature. Ross 708 breeder guideline ME intake (■) was calculated by multiplying the guideline feed intake data by dietary energy (2,800 kcal/kg). Model [II] – 3 wk was a mixed effect model with inclusion of a random term for individual maintenance ME in a 3-wk chunked data. The model was $MEI_d = (a + u) \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \epsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); u = bird-specific random term associated with individual maintenance.

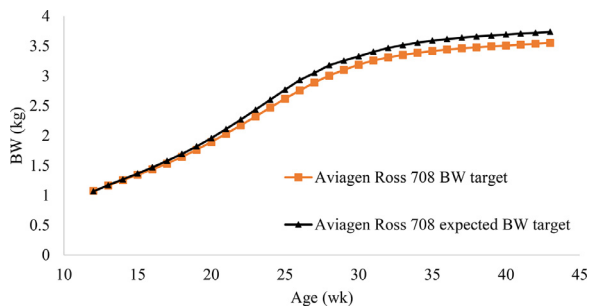


Figure 6. Ross 708 broiler breeder recommended BW target (■) and expected BW target (▲) predicted by applying the guideline performance data in the current study ME partitioning model. The current study model was a mixed effect model describing ME partitioning to maintenance, gain, and egg production with inclusion of a random term for individual maintenance ME in a 3-wk chunked data. The model was $MEI_d = (a + u) \times BW^b + c \times ADG_p + d \times ADG_n + e \times EM + \epsilon$, where MEI_d = daily ME intake (kcal/d); BW = BW (kg); ADG_p = positive ADG (g/d); ADG_n = negative ADG (g/d); EM = egg mass (g/d); u = bird-specific random term associated with individual maintenance.

CONCLUSIONS

To increase robustness of broiler breeder energy partitioning models, a novel chunking procedure was applied on precision feeding system data. To our knowledge, this is the first investigation of the effects of chunking approach on the ME partitioning models bias, fitting, and predictive performance. Increasing chunk size of data provided closer fit of the models estimated coefficients to the actual data by accounting for more variation in the residuals. Using a 3-wk chunk size provided a model with lower bias, smallest variation, and greater accuracy and precision in estimated coefficients. A

mixed effect ME partitioning model containing a random term associated with individual maintenance requirement in a 3-wk chunked data (model [II] – 3wk) increased inferential efficiency. The model can be used as a tool to estimate ME requirements and to facilitate choosing a precise energy level in feed formulation practices. Furthermore, applying Ross 708 guideline data in the model suggested a revision on the breeder-recommended target BW. The current study results indicated that an earlier pubertal growth strategy could reduce energy efficiency in broiler breeders.

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DISCLOSURES

The authors declare that there is no conflict of interest.

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