Animal Nutrition 24 (2026) 192–199

Contents lists available at ScienceDirect

Animal Nutrition

journal homepage: http://www.keaipublishing.com/en/journals/aninu/

Original Research Article

Exploring the net energy for maintenance and the allometric exponent of the metabolic body weight in different categories of poultry: A Meta-analysis approach

Rony Riveros Lizana [a,*], Marie-Pierre Létourneau Montminy [b], Amélia K. Almeida [c], Raully L. Silva [a], Audasley T.S. Fialho [a], Marcos Macari [a], Nilva K. Sakomura [a,*]

[a] Department of Animal Science, College of Agrarian and Veterinary Science, São Paulo State University, Jaboticabal 14884-900, Brazil
[b] Department of Animal Science, Laval University Faculty of Agricultural and Food Sciences, Laval G1V 0A6, Canada
[c] School of Agriculture and Environment, Massey University, Palmerston North 4442, New Zealand

ARTICLE INFO

Article history:
Received 19 November 2024
Received in revised form
21 April 2025
Accepted 22 April 2025
Available online 19 September 2025

Keywords:
Basal metabolism
Fasting heat production
Growth broiler chick
Laying hen
Rooster
Allometric coefficient

ABSTRACT

The basal metabolic rate in poultry, expressed as net energy requirements for maintenance (NEm), is often characterized by measuring fasting heat production (FHP) under standardized conditions. This study applies Meta-analysis techniques to 206 individual observations from 23 peer-reviewed papers to evaluated the allometric relationship between FHP and body weight (BW), described by the model: FHP (kJ/d) $= a \times$ BW (kg)^b, where FHP is the fasting heat production, BW is the body weight, a is the NEm requirement per unit of metabolic body weight (MBW), and b is the allometric exponent. The objective of this study was to estimate b and determine the appropriate NEm for growing broiler chickens, laying hens, and roosters. We evaluated three non-linear models: Model 1, category-specific exponents; Model 2, common exponent across categories; and Model 3, exponent fixed at the theoretically value of 0.75. Model 1 showed distinct b of 0.73, 0.65, and 0.58 for growing broilers, laying hens, and roosters, respectively, with corresponding NEm values of 450, 352, and 385 kJ per kg of MBW. Model 2, which estimated a common exponent ($b = 0.64$), improved model fit (root mean square prediction error (RMSPE) = 173 kJ/d, $R^2 = 0.76$). Model 3, using the standardized $b = 0.75$, yielded NEm of 478 kJ/kg BW$^{0.75}$ for growing chickens and 320 kJ/kg BW$^{0.75}$ for adult birds (RMSPE = 184 kJ/d, $R^2 = 0.78$), with a model performance comparable to Model 1 (RMSPE = 187 kJ/d, $R^2 = 0.72$). Error decomposition further indicated that Model 3 presented a lower error due to regression (0.66%), a lower intercept (80 kJ/d) and a higher slope (0.68) in the observed-predicted regression, demonstrating its robust predictive ability. In conclusion, while category-specific exponents offer a precise FHP characterization, adopting a wide-know exponent of 0.75 is a practical alternative, provided the NEm is adjusted for each category. These findings provided a framework for estimating NEm recommending values of 480 kJ/kg BW$^{0.75}$ for growing chickens and 320 kJ/kg BW$^{0.75}$ for adult birds, to support accurate energy requirements models and cross-study comparison in poultry nutrition.

1. Introduction

The metabolic rate is a fundamental indicator of animal metabolic activity, quantified by measuring energy expenditure as heat production from nutrient oxidation (McLean and Tobin, 1987). In endothermic animals, fasting heat production (FHP) represents the minimal energy requirement for maintaining homeostatic equilibrium during rest under normothermic, post-absorptive condition before any tissue syntheses (Mitchell,

* Corresponding author.
E-mail addresses: ronriveros@gmail.com (R.R. Lizana), nilva.sakomura@unesp.br (N.K. Sakomura).

Production and Hosting by Elsevier on behalf of KeAi

https://doi.org/10.1016/j.aninu.2025.04.016

1964). This parameter directly reflects the net energy requirement for maintenance (NEm) (Noblet et al., 2015; Zuidhof, 2019).

Multiple factors influenced FHP measurements, including the previous feeding level (Labussière et al., 2011; Teofilo et al., 2023), fasting duration (Lopez and Leeson, 2005), physical activity (Riveros et al., 2023a), and environmental temperature. These variables necessitated strict methodological standardization when determining NEm (Riveros et al., 2023a). Animal-specific characteristics, particularly physiological differences between mature and growing birds (Johnson and Farrell, 1985), significantly affect FHP through body composition changes during growth (Martinez et al., 2022).

The allometric equation describes a power-law relationship between FHP and body weight (BW), expressed as:

$$\text{FHP (kJ/d)} = a \times \text{BW (kg)}^{b},$$

where FHP is fasting heat production, BW is the body weight, a is the maintenance requirement per unit of metabolic body weight (MBW), and the exponent b determines how the metabolic rate scales with body size (e.g., $b = 0.75$ represents the classical interspecies scaling law).

The theoretical value for b is the subject of longstanding discussion. Kleiber's work (1932, 1947) establishes 0.75 as the interspecies exponent for adult animals, Rubner's surface area law (Rubner, 1883) proposed an exponent of 0.667. However, these values face scrutiny for intraspecies applications, particularly in growing poultry. Reported exponents for poultry range from 0.60 to 0.77 without consensus (Noblet et al., 2015).

In this context, we propose a Meta-analytic approach considering various studies that evaluated the FHP in different poultry categories. The objective is to assess the allometric exponent and maintenance requirement per unit of MBW as a function of physiological stage in comparison with the widely accepted allometric exponent of 0.75.

2. Materials and methods

2.1. Literature screening

Quantitative meta-analysis incorporated peer-reviewed literature from 1971 to 2022. Publications were exhaustively searched across different databases, including Google Scholar, Web of Science, and Scopus. The search employed the following keyword combinations: ("heat production" OR "energy metabolism" OR "energy expenditure" OR "gas exchange" OR "fasting heat production" OR "metabolic rate") AND ("poultry" OR "*Gallus gallus*" OR "avian" OR "birds" OR "chickens" OR "laying hens" OR "roosters"). Additional relevant studies were identified through cross-referencing.

Inclusion criteria required that studies: 1) measured FHP or equivalent terms (basal metabolic rate, resting metabolic rate, or NEm) using indirect calorimetry; 2) conducted measurements under thermoneutral conditions; and 3) excluded data collected before 1970 to avoid potential methodological inconsistencies from older equipment. After screening (Supplementary Material S1), we selected 23 studies categorized by physiological stage: growing chickens (0 – 140 d), laying hens, and roosters.

Essential information was extracted from the materials and methods section of each study: sample size (n), birds age (days), calorimetry setup (open/closed-circuit), documented environmental temperature (T), fasting duration (hours), year of publication, and number of birds per chamber. In the results section, we also collected a quantitative data set of individual BW (kg), measured FHP (kJ/bird per day), daily gas exchange parameters of oxygen consumption (VO_2, L/bird per day), carbon dioxide production (VCO_2, L/bird per day), and the respiratory quotient (RQ). For studies reporting FHP in kcal, we converted values to kJ using 1 kcal = 4.18 kJ. When studies reported gas exchange parameters without FHP values, we calculated FHP using Brouwer's equation (Brouwer, 1965):

$$\text{FHP (kJ/d)} = 16.18 \times VO_2\text{(L/d)} + 5.06 \times VCO_2\text{(L/d)}.$$

The complete dataset is in Supplementary Material S2.

2.2. Data selection and inclusion criteria

Each observation from the manuscript main text was subjected to meticulous individual scrutiny, whereby its quality and relevance to the core objective of the meta-analysis were evaluated, following the framework set forth by Sauvant et al. (2008). The exclusion criteria eliminated studies involving metabolic disturbances, including health complications, temperature stress, and induced physiological responses, while preserving control group data. A critical inclusion requirement was the proper characterization of FHP, verified by RQ values between 0.67 and 0.85. These RQ values confirm the fasting state, with values approaching 0.7 indicating predominant endogenous fat catabolism (Chwalibog et al., 1998; Riveros et al., 2023a). We considered FHP measurements taken during 12 to 24 h fasting periods as valid, as metabolic rate typically stabilizes within this timeframe, ensuring data reliability.

2.3. Statistical analysis and model validation

To examine the relationship between BW on the FHP, a weighted multi-series scatter and bubble plot was generated (Fig. 1). The plot visualizes the inter-study-specific effect on the response variable (Fig. 1A), with the size effect of each study data point encoded by its respective sample size (n_j) to represent the weight of each study (Fig. 1B). The weighting assigned to each study (w_j; $j = 1, 2, \ldots, j$ for the j-th study) was determined using the following formula:

$$w_j = n_j^2 \Big/ \left(\overline{n^2}\right),$$

where n_j represents the sample size of the j-th study, and $\overline{n^2}$ denotes the overall average of squared sample sizes across all studies. This preliminary visualization revealed fundamental patterns in the BW–FHP relationship.

Subsequently, we assessed diagnostic data analysis among variables (correlation and mixed-effect analysis). The Pearson correlation analysis identified pairwise associations among FHP,

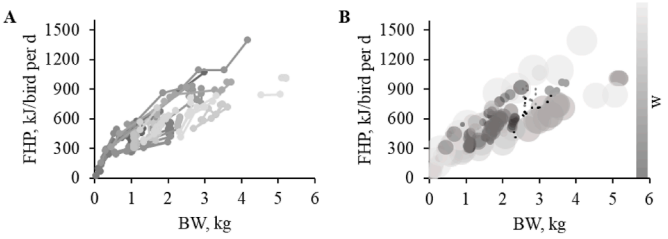

Fig. 1. Scatter plot of fasting heat production against body weight. (A) Data points with connecting lines grouped by study. (B) Weighted scatter plot (weight $w_j = n_j^2/(\overline{n^2})$, where n_j represents the sample size of the j-th study, and $(\overline{n^2})$ denotes the overall average of squared sample sizes n across all studies. FHP = fasting heat production; BW = body weight.

BW, bird age, publication year, and T, with coefficient of correlation (R) reported.

A linear mixed-effects model was conducted to evaluate the fixed factor (bird category) and its interaction with BW, while accounting for the random effects (study):

$$Y_{ijk} = \beta_0 + \beta_1 X_{ijk} + c_i + u_j + \beta_2 X_{ijk} \times c_i + \beta_3 X_{ijk} \times u_j + \varepsilon_{ijk},$$

where Y_{ijk} is the dependent variable (FHP) of the k-th observation from the i-th bird category and j-th study; X_{ijk} is the value of continuous predictor (BW) for the corresponding observation; c_i is the fixed effect of the i-th bird category ($i = 1$: growing chickens, 2: laying hens, 3: adult roosters); u_j is the random effect associated with the j-th study, assumed to be normally distributed $u_j \sim N(0, {\sigma_u}^2)$; β_0 is the intercept value of the dependent variable; β_1 is the coefficient for BW effect; β_2 and β_3 are coefficients for the interaction term between BW and category, and between BW and study, respectively; and ε_{ij} is the residual error, assumed to be normally distributed $\varepsilon_{ij} \sim N(0, {\sigma_\varepsilon}^2)$.

Based on inherently non-linear nature of metabolic scaling, non-linear mixed models were performed to describe the relationship between FHP and BW. This approach allows for the direct estimation of the allometric exponent and the unit of NEm for each category (dummy variable), considering the inter-study effect as a random effect. The following models were tested:

$$\text{FHP} = \left(a + \Delta a_i + u_j\right) \times \text{BW}^{(b+\Delta b_i)} + \varepsilon_{ij}, \quad \text{(Model 1)}$$

$$\text{FHP} = \left(a + \Delta a_i + u_j\right) \times \text{BW}^{(b)} + \varepsilon_{ij}, \quad \text{(Model 2)}$$

$$\text{FHP} = \left(a + \Delta a_i + u_j\right) \times \text{BW}^{(0.75)} + \varepsilon_{ij}, \quad \text{(Model 3)}$$

where a is the overall unit of maintenance (intercept) for all bird categories, b is the allometric exponent for all bird categories, u_j is the subject-specific random effect for the j-th study, assumed to be $u_j \sim N(0, {\sigma_u}^2)$. The dummy variables Δa_i and Δb_i are fixed deviation from the overall coefficients a and b for the i-th bird category ($i = 1$ for growing chickens, $i = 2$ for adult laying hens, and $i = 3$ for roosters), and ε_{ij} is the residual error, assumed to be $\varepsilon_{ij} \sim N(0, {\sigma_\varepsilon}^2)$. The category-specific deviations (Δa_i and Δb_i) was tested using likelihood ratio test to compare nested models.

All statistical analyses were conducted using SAS software (version 9.4, SAS Institute Inc., Cary, NC, USA), with statistical significance defined as $P < 0.05$.

Graphical analyses of the dataset were carried out by generating scatter plots categorized by each study and accounting for the weight of each study, employing the PROC GPLOT procedure. Pearson correlation analysis was performed using the PROC CORR procedure. The mixed-effect model was applied, treating the study as a random effect through the PROC MIXED procedure. Lastly, the estimation of the allometric exponent and the maintenance constant to test the hypotheses of difference between bird's category was accomplished using a non-linear mixed model, implemented with the PROC NLIN procedure. We used dummy variables to assess the category effect on parameter estimated (a and b). All the SAS code detailing each procedure is detailed in the Supplementary Material S3.

Model validation was performed using an independent dataset (19 studies, 57 observations; Supplementary Material S4) that met the same selection criteria. Unlike the original dataset, this validation dataset exhibited substantial intra-study variation in BW and FHP. The validation included only studies reporting both FHP (Y_{ij}) and corresponding BW values. For each model, we predicted FHP ($\widehat{Y}_{ij}$) and calculated the individual prediction error:

$$\varepsilon = \widehat{Y}_{ij} - Y_{ij},$$

and defined the root mean square prediction error (RMSPE):

$$\text{RMSPE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\sum_{j=1}^{m}\left(\widehat{Y}_{ij} - Y_{ij}\right)^2},$$

where n = total number of observations; m = number of studies; Y_{ij} = observed FHP for observation i in study j; and $\widehat{Y}_{ij}$ = predicted FHP. To facilitate interpretation, a relative RMSPE was calculated by expressing the RMSPE as a fraction of the overall mean observed FHP, $\overline{Y_{ij}}$:

$$\text{Relative RMSPE} = \frac{RMSPE}{\overline{Y_{ij}}}.$$

These metrics quantified the accuracy of the models across the validation dataset.

Other statistical indicators used were the coefficient of determination (R^2), regression parameters (slope and intercept) between Y_{ij} and $\widehat{Y}_{ij}$ values were used to evaluate the predictiveness of each model. The MSPE was decomposed into error in central tendency (ECT), error due to regression (ER), and error due to disturbance (ED) (Pomar and Marcoux, 2005):

$$\text{ECT} = \left(\overline{\widehat{Y}_j} - \overline{Y_i}\right)^2,$$

$$\text{ER} = \left(S_{\hat{Y}_{ij}} - R \times S_{Y_{ij}}\right)^2,$$

$$\text{ED} = \left(1 - R^2\right) \times {S_{Y_{ij}}}^2,$$

where $S_{\hat{Y}_{ij}}$ and $S_{Y_{ij}}$ are the standard deviations of the predicted and observed values, respectively; R is the correlation coefficient of Pearson. The error components are expressed as percentages of the total MSPE, where the ECT is interpreted as the bias proportion, the ER as the slope deviation proportion, and the ED as the random or unexplained proportion.

Finally, we compiled literature-reported allometric exponents for avian species, presenting them in a summary table and boxplot with 95% confidence intervals.

3. Results

3.1. Dataset selection

The systematic literature search identified 53 studies measuring energy metabolism and gas exchange in poultry. After rigorous quality assessment and statistical evaluation for outliers (Supplementary Material S1), we retained 24 studies comprising 83 observations for growing birds, 100 for laying hens, and 23 for cockerels. Table 1 presents descriptive statistics (mean ± SD, range) for all collected variables.

The dataset revealed significant metabolic differences among poultry categories. Adult roosters exhibited the highest FHP (808 ± 183 kJ/bird per day), surpassing both growing broiler chickens (461 ± 268 kJ/bird per day) and laying hens (534 ± 170 kJ/

Table 1
Descriptive observations of the principal variables collected ($n = 329$).

Variable	Category[1]	Mean	SD	Minimum	Maximum
FHP, kJ/bird per day	1	461	268	20	1394
	2	534	170	300	971
	3	808	183	415	1013
BW, kg/bird	1	1.17	0.86	0.04	4.16
	2	1.89	0.81	1.06	3.72
	3	3.76	1.22	2.31	5.21
Year	1	2001	14	1977	2022
	2	1996	14	1974	2014
	3	1990	22	1971	2017
Age, d	1	36	30	0	140
	2	260	93	137	504
	3	448	111	210	540
T, °C	1	24.8	3.3	21.0	33.0
	2	21.9	1.8	20.0	26.8
	3	23.0	0.7	22.0	25.0

FHP = fasting heat production; BW = body weight; T = environmental temperature; SD = standard deviation.
[1] 1, broiler chicken; 2, laying hens; 3, adult roosters.

bird per day). The substantial FHP range (20 – 1394 kJ/bird per day) reflected considerable metabolic variation, likely attributable to body size differences. Mean BW increased progressively across categories: roosters (3.76 ± 1.22 kg) > laying hens (1.89 ± 0.81 kg) > growing chickens (1.17 ± 0.86 kg). Additional variables including study year, environmental temperature, and bird age also showed wide variability.

The plotted dataset considering the FHP in function of the BW (Fig. 1) showed that when each observation was weighted based on sample size expressed as w_j, the weight factor did not visibly affect data trends, and all studies consistently demonstrated increasing FHP with greater BW.

3.2. Correlation, weighting, and mixed model effect

Pearson correlation analyses revealed significant relationships among key variables (Table 2). FHP showed strong positive correlations with BW ($R = 0.857$, $P < 0.05$) and bird age ($R = 0.411$, $P < 0.05$), while demonstrating a negative correlation with environmental temperature (T; $R = -0.267$, $P < 0.05$). Publication year showed no significant association with FHP. Body weight correlated positively with age ($R = 0.532$, $P < 0.05$) and negatively with environmental temperature ($R = -0.255$, $P < 0.05$). Similarly, age exhibited a negative correlation with environmental temperature ($R = -0.399$, $P < 0.05$).

The mixed-effects model analysis (Table 3) identified BW as a highly significant predictor of FHP ($P < 0.01$), with a significant BW × study interaction ($P < 0.05$). However, neither bird category nor the category × BW interaction reached statistical significance.

Table 2
Pearson correlation between the collected variables.

Item	FHP	BW	Year	Age	T
FHP	1.000				
BW	0.857	1.000			
	<0.001				
Year	0.059	0.015	1.000		
	0.434	0.841			
Age	0.411	0.531	−0.367	1.000	
	<0.001	<0.001	<0.001		
T	−0.267	−0.255	−0.296	−0.399	1.000
	<0.001	0.001	<0.001	<0.001	

FHP = fasting heat production; BW = body weight; T = environmental temperature.

Table 3
Mixed model to determine the fixed and random factor effect on the fasting heat production response.

Fixed and random effects	*P*-value
Intercept	0.623
BW	<0.001
Study effect	0.109
Category[1]	0.364
BW × study effect[2]	0.015
BW × category[3]	0.298

BW = body weight.
[1] 1, growing broiler chickens; 2, laying hens; and 3, roosters.
[2] Interaction between body weight and study effect.
[3] Interaction between body weight and each category.

This initial model served as a preliminary screening for linear relationships and interactions characterization. The absence of a significant category × BW interaction suggests that a single, overarching linear term does not adequately describe the data across all categories. Consequently, a subsequent non-linear allometric model was employed to quantitatively evaluate category-specific scaling relationships.

3.3. Non-linear mixed analysis and allometric exponent

The non-linear mixed effects analysis revealed distinct NEm and allometric exponent coefficients across poultry categories (Table 4). Study random effect of each study did not reach significance in any model. On the other hand, all models presented a significant fit ($P < 0.05$) and the random effect of each study (u_j)

Table 4
A non-linear mixed model to determine the maintenance and allometric exponent coefficient.[1]

Parameter	Estimate	Standard error	*P*-value	95% Confidence limits	
Model 1: FHP = $(a + u_j + \Delta a_i) \times BW^{(b + \Delta bi)}$, $u_j \sim$ Normal $(0, \sigma^2)$					
a	394	0.29	<0.001	393.7	394.9
Δa_1	55.5	0.51	<0.001	54.5	56.6
Δa_2	−42.5	0.51	<0.001	−43.6	−41.5
Δa_3	−9.7	1.51	<0.001	−12.9	−6.6
b	0.594	0.001	<0.001	0.593	0.596
Δb_1	0.132	0.001	<0.001	0.129	0.135
Δb_2	0.058	0.002	<0.001	0.055	0.061
Δb_3	−0.011	0.003	0.001	−0.017	−0.005
u_j	−1.11E-12	0.0009	0.998	−0.002	0.002
ε	7.93	0.01	<0.001	7.90	7.96
Model 2: FHP = $(a + u_j + \Delta a_i) \times BW^{b}$, $u_j \sim$ Normal $(0, \sigma^2)$					
a	378	0.22	<0.001	378	379
Δa_1	113	0.32	<0.001	112	113
Δa_2	−22	0.24	<0.001	−23	−22
Δa_3	−72	0.28	<0.001	−72	−71
b	0.645	0.001	<0.001	0.642	0.648
u_j	0.0001	0.001	0.998	−0.001	0.001
ε	7.14	0.01	<0.001	7.12	7.17
Model 3: FHP = $(a + u_j + \Delta a_i) \times BW^{0.75}$, $u_j \sim$ Normal $(0, \sigma^2)$					
a	329	0.13	<0.001	329	329
Δa_1	148	0.35	<0.001	148	149
Δa_2	−6	0.23	0.051	−6	−5
Δa_3	−10	0.28	0.064	−11	−10
u_j	-1E-12	0.00058	0.999	−0.001	0.001
ε	9.74	0.02	<0.001	9.71	9.78

FHP = fasting heat production; BW = body weight; a = maintenance parameter; b = fitted allometric exponent.
[1] Dummy variables are denoted by the differential symbol Δ followed by a letter (e.g., $\Delta a, \Delta b$) to assess the category-specific effects on parameters, a and b. Subscript numbers indicate bird categories: 1, broiler chicken; 2, laying hens; 3, adult roosters. u_j: random effect of each study with normal distribution; ε: overall residual variability.

was not significative in all models ($P > 0.05$), in agreement with the mixed-effect model analysis.

In Model 1, the estimated overall NEm was $a = 394$ kJ per MBW with an allometric exponent of $b = 0.594$. Category-specific analysis showed growing chickens required the highest NEm ($a = 450$ kJ/MBW; $b = 0.73$), followed by roosters ($a = 385$ kJ/MBW; $b = 0.58$) and laying hens ($a = 352$ kJ/MBW; $b = 0.65$).

Model 2, which constrained the allometric exponent to $b = 0.64$ across categories, revealed difference in NEm response. This model showed a numerical increase in NEm for growing birds to 491 kJ per MBW (41 kJ when decreasing b from 0.73 to 0.64). The estimated allometric exponent for laying hens ($b = 0.65$) was closer than estimated for all categories, resulting in the same NEm estimated of 356 kJ per MBW. On the other hand, the NEm estimated for roosters decreased from 385 kJ/kg $BW^{0.58}$ to 307 kJ/kg $BW^{0.64}$ when adopting an overall $b = 0.64$.

Model 3, which imposed the conventional allometric exponent ($b = 0.75$), produced divergent results. Growing chickens exhibited moderately higher NEm (478 kJ/kg $BW^{0.75}$) due to their native exponent's ($b = 0.73$) proximity to 0.75. In contrast, both adult categories converged at 320 kJ/kg $BW^{0.75}$, reflecting the greater disparity between their native exponents and the imposed value.

3.4. Model evaluation with external dataset

The external evaluation of the model revealed consistent relationships between observed and predicted FHP values across broiler chickens, laying hens, and roosters (Fig. 2). All models demonstrated similar predictive trends, with regression slopes less than 1 (0.66, 0.65, and 0.68 for Model 1, 2, and 3, respectively), indicating a systematic tendency to underestimate NEm, particularly in older birds.

Model 3 exhibited superior predictive performance in terms of systematic bias, demonstrating the lowest intercept (80 kJ/d). Although their RMSPE was intermediate (184 kJ/d) which corresponds to a relative RMSPE of 37%.) but Model 1 showed an intermediate level of systematic bias (intercept = 85 kJ/d) but yielded the highest prediction error (RMSPE = 187 kJ/d, 38% relative RMSPE). In contrast, Model 2 achieved the lowest RMSPE (173 kJ/d, 35% relative RMSPE); however, this was coupled with the highest systematic bias (intercept = 102 kJ/d).

The coefficient of determination further elucidated model performance. Model 1, which incorporating category-specific NEm and allometric exponents, demonstrated considerable predictive power ($R^2 = 0.72$). Model 3 achieved a similar R^2 of 0.72, indicating an equivalent predictive ability. Model 2, which employed a unified exponent ($b = 0.64$), attained a marginally higher $R^2 = 0.76$. Despite this, Model 2 displayed greater variability in its predictions, particularly for laying hens.

Error decomposition analysis provided deeper elucidation into the sources of prediction inaccuracy and confirmed the patterns observed in the regression parameters. Model 3 demonstrated the most favorable performance, with lowest slope derivation proportion (ER = 0.66%), indicating near-optimal slope. It also exhibited an intermediate error in bias proportion (ECT = 18.4%), while the main sources of error were random (ED = 80.9%). Conversely, Model 2 showed the poorest performance in slope-related error (ER = 5.11%), confirming their suboptimal regression slope, coupled with a relatively high bias component (ECT = 16.6%). Model 1 presented high bias proportion (ECT = 19.2%), with intermediated slope deviation proportion (ER = 1.15%) and random disturbance (ED = 79.6%). Across all models, random error remained the predominant error source, as is often expected in biological models, accounting for approximately 79% to 81% of total error.

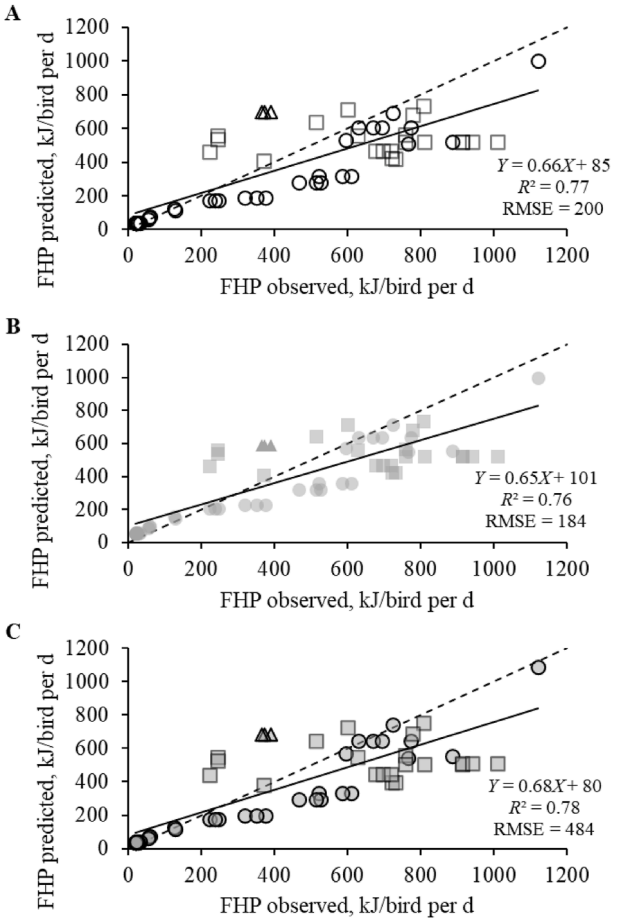

Fig. 2. Relationship between observed and predicted fasting heat production values for three models evaluated on an independent validation dataset. The model are: (A) Model 1, FHP = $(a + \Delta a_i + u_j) \times BW^{(b + \Delta bi)}$; (B) Model 2, FHP = $(a + \Delta a_i + u_j) \times BW^{b}$ and (C) Model 3, FHP = $(a + \Delta a_i + u_j) \times BW^{0.75}$, where a is the overall maintenance requirement, b is the overall allometric exponent, Δa_i and Δb_i are fixed deviation for the i-th bird category, and u_j is a study-specific random effect. The root mean square prediction error decomposition for each model are as follows: Model 1, Error in central tendency (ECT) = 19.2%, Error due to regression (ER) = 1.15%, and Error due to disturbances (ED) = 79.6%; Model 2, ECT = 16.6%, ER = 5.11%, and ED = 78.2%; Model 3, ECT = 18.4%, ER = 0.66%, and ED = 80.9%. Symbols: broiler chickens (○), laying hens (□), and roosters (△). Lines: the dashed line represents the line of equality (1:1); the solid line represents the regression line. FHP = fasting heat production; RMSE = root mean square error.

Comparative analysis of allometric exponents from literature (Table 5, Fig. 3) revealed substantial variation (0.60 – 0.77) across avian species and categories, underscoring the biological and methodological diversity in energy metabolism studies. These results collectively validate the models' robustness for NEm estimation while highlighting opportunities for refinement to address residual prediction variability stemming from study-specific, genetic, and physiological factors.

4. Discussion

The dataset obtained from the meta-analyses demonstrated consistent data collection across diverse poultry categories. By weighting study effect according to sample size, we accounted for methodological variation in FHP determination protocols. The random distribution of study effect confirmed no individual study bias, validating the analytical approach. This analysis considered multiple factors influencing FHP, including publication year

Table 5
The allometric exponent *b* reported on the literature between different avian species.

Author	Body weight range, kg	Category	*b*
Brody and Procter (1932)	0.020 – 100.000	Different mature bird species	0.64
King and Farner (1961)	0.001 – 10.000	Different avian species	0.74
Berman and Snapir (1965)	1.670 – 2.020	Laying hens	0.61
Lasiewski and Dawson (1967)	0.001 – 0.866	Passarine	0.72
Lasiewski and Dawson (1967)	0.003 – 100.000	Non-passarine	0.72
Johnson and Farrell (1985)	0.810 – 3.930	All bird categories	0.61
Johnson and Farrell (1985)	1.550 – 3.930	Mature	0.60
Johnson and Farrell (1985)	0.810 – 2.190	Immature	0.65
Lopez and Leeson (2005)	0.095 – 2.100	Broiler chicks	0.60
McNab (2009)	0.004 – 156.000	Non-passarine	0.72
McNab (2009)	0.002 – 1.259	Passarine	0.71
McNab (2009)	0.002 – 159.000	All avian species	0.65
Rivera-Torres et al. (2010)	0.540 – 13.770	Fast growth turkey	0.77
Hudson et al. (2013)	0.003 – 156.000	All avian species	0.71
Noblet et al. (2015)	0.620 – 2.820	Broiler chicks	0.69
Ballesteros et al. (2018)	0.005 – 9.900	Flaying birds (small birds)	0.66
Ballesteros et al. (2018)	0.250 – 420.000	Flightless birds (including big bids)	0.74

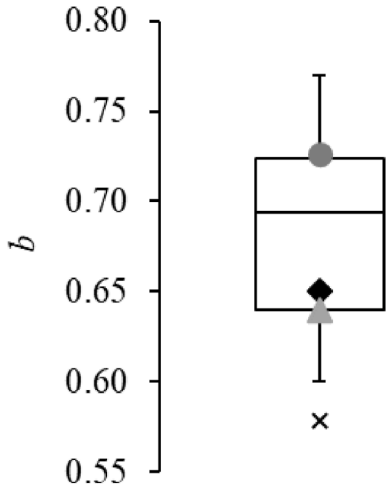

Fig. 3. Distribution of allometric exponents from literature (based on Table 5) for avian species, estimated using Model 1. Box plot shows values for: broiler chickens (●), laying hens (◆), roosters (×), and combined categories (▲).

(reflecting genetic improvements) and environmental temperature. We exclusively included indirect calorimetry studies conducted under thermoneutral conditions (Noblet et al., 2015) to minimize environmental temperature effect on FHP measurements. The observed negative correlation between environmental temperatures and FHP aligns with established age-dependent temperature recommendations for poultry, representing an indirect physiological relationship rather than direct metabolic impact. These findings reinforce the critical importance of conducting FHP measurements under normothermic conditions to prevent thermoregulatory energy expenditure from confounding results (McLean and Tobin, 1987). Additionally, the linear mixed effects model initially identified BW as a significant predictor of FHP, with no significant interaction between bird category and BW. This result suggests that, from a general linear perspective, a simple, additive effect of BW describes the data across all categories. However, this apparent consistency should not be misinterpreted. The linear model tests for a uniform difference in the slope of the relationship but is inherently limited for capturing the fundamentally non-linear nature of metabolic scaling. Consequently, a non-linear allometric model was employed, as it is more biologically appropriate for modeling allometric relationships. This approach is better suited to quantify the category-specific scaling parameters that a linear mixed-model may fail to capture, thereby revealing the underlying differences in how FHP scales with BW across bird categories.

Interestingly, while genetic improvements in broiler chickens have significantly altered body composition and growth patterns (Martinez et al., 2022), these changes did not substantially affect FHP when expressed per MBW, when collecting studies from different years. This apparent discrepancy may stem from the post-absorptive measurement protocol, which isolates fasting metabolism from dietary thermogenesis. Supporting this interpretation, Teofilo et al. (2022) demonstrated that previous feeding levels minimally affect FHP in poultry, unlike in swine and calves (de Lange et al., 2006; Labussière et al., 2011). Despite incorporating studies with varying methodologies (including both open and closed-circuit calorimetry systems), BW emerged as the predominant factor explaining FHP variation across all analyses.

This study's category-specific allometric exponents revealed fundamental metabolic differences: growing chickens (0.73), laying hens (0.65), and roosters (0.58). These values diverge from the conventional 0.75 exponent, highlighting the importance of life stage considerations in metabolic scaling. The allometric exponent for growing chicken aligns closely with McNab's (2009) reported value of 0.72 for non-passerine species but is higher than the 0.69 estimate by Noblet et al. (2015). The substantially lower exponent (0.60) reported by Lopez and Leeson (2005) likely reflects their use of metabolizable energy rather than net energy measurements.

The allometric exponent of 0.64 observed in the present study for laying hens is consistent with previous reports. This estimated aligns with the exponent of 0.65 reported for mature birds (Johnson and Farrell, 1985) and the value of 0.66 found in small bird species (Ballesteros et al., 2018). Furthermore, it corroborates early work in laying hens, which reported an exponent of 0.61 (Berman and Snapir, 1965). Various reports suggest that the allometric exponent is higher in growing birds and decreases in adult birds (Meltzer, 1983; Johnson and Farrell, 1985). Although the allometric exponents reported in the literature are similar, intra-species comparisons can enhance the accuracy of MBW representation. Physiologically, the value of allometric exponent 0.64 represents an optimal compromise between surface-area-to-volume ratios governing heat dissipation and the mass-specific metabolic demands that dominate in smaller birds. However, the validation result showed a higher bias, which does not support the use of this exponent for poultry, a group characterized by a high body mass in relation to surface area (Nascimento et al., 2017).

The practical challenge of implementing category-specific exponents led us to propose a conventional 0.75 exponent, balancing accuracy with usability. This adjustment increased NEm estimates for growing chickens (from 450 to 478 kJ/kg $BW^{0.75}$) while decreasing values for roosters (from 385 to 319 kJ/kg $BW^{0.75}$). This explains why growing birds demonstrate elevated NEm requirements consistent with their accelerated tissue deposition, while mature birds show reduced metabolic turnover. Physiologically, allometric exponent 0.75 reflects the compromise between surface-area constraints (favoring lower exponents) and mass-specific metabolic demands (favoring higher exponents). The 0.75 value finds support in both theoretical (McNab, 2009) and empirical (Brody and Procter, 1932; Kleiber, 1932) metabolic scaling studies. When testing the unified 0.64 exponent, we observed expected increases in NEm for growing birds (491 kJ/kg $BW^{0.75}$) and convergence in adult categories (356 kJ/kg $BW^{0.75}$). Despite widespread adoption of the 0.75 coefficient in nutritional studies, the analysis reveals its application increases NEm estimates for broilers while lowering values for adults, consistent with reports on larger species like turkeys (0.77; Rivera-Torres et al., 2010a).

This study's meta-analytical approach effectively addresses BW variation effects on FHP determination by revealing how allometric coefficients reflect fundamental differences in fasting metabolism between growing and mature birds (Johnson and Farrell, 1985). The strong correlation between coefficients *a* and *b* enables predictive adjustments when fixing either parameter, as implemented in Model 3. The obtained NEm values for growing chickens (approximately 450 kJ/kg $BW^{0.75}$) show excellent agreement with existing literature (Liu et al., 2017; Noblet et al., 2015), while the estimates for laying hens match those reported by Sakomura (2004). The lower NEm values for roosters may reflect methodological differences from Riveros et al. (2023a), who employed linear regression—an approach which introduces biological controversial by extrapolating to zero intake. Compared to alternative approaches, the fasting calorimetry method provides more physiologically realistic estimates of FHP. However, this method requires careful control of physical activity during prolonged measurements to ensure accurate FHP plateau determination (Riveros et al., 2023a, 2023b).

5. Conclusion

Fasting heat production is an essential metric for estimating the NEm of poultry. This study highlights the importance of adopting a robust allometric exponent to ensure practical utility. These findings suggest that while precise FHP estimation may require category-specific allometric exponents, adopting a universally accepted exponent of 0.75 can also be effective, provided the maintenance constant is adjusted for each category. Model evaluation supports this approach, demonstrating that a standardized exponent, when paired with adjusted constants, yields reliable estimating net energy requirements for maintenance tailored to a specific category of poultry which are 478 kJ/kg $BW^{0.75}$ per day for growing chickens, and 320 kJ/kg $BW^{0.75}$ for laying hens and roosters, adopting a wide known single allometric exponent. This methodology offers a standardized framework that facilitates cross-study comparison and can be implemented on net energy requirement estimation for poultry.

Credit Author Statement

Rony Riveros Lizana: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marie-Pierre Létourneau Montminy:** Writing – review & editing, Validation, Supervision, Data curation. **Amélia K. Almeida:** Writing – review & editing, Visualization, Validation, Formal analysis, Data curation. **Raully L. Silva:** Writing – review & editing, Validation, Investigation. **Audasley T.S. Fialho:** Writing – review & editing, Visualization, Validation. **Marcos Macari:** Writing – review & editing, Visualization, Validation, Supervision, Resources. **Nilva K. Sakomura:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interests

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

Acknowledgments

The authors acknowledge the São Paulo Research Foundation—FAPESP (Brazil) for financial support grant number 2019/26575-6 and fellowship of first author grant number 2024/04197-8. This study was financed in part by PROPG/UNESP through call number 01/2025.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aninu.2025.04.016.

References

Ballesteros FJ, Martinez VJ, Luque B, Lacasa L, Valor E, Moya A. On the thermodynamic origin of metabolic scaling. Sci Rep 2018;8. https://doi.org/10.1038/s41598-018-19853-6.

Berman A, Snapir N. The relation of fasting and resting metabolic rates to heat tolerance in the domestic fowl. Br Poult Sci 1965;6:207–16. https://doi.org/10.1080/00071666508415576.

Brody S, Procter TC. Relations between basal metabolism and mature body weight in different species of mammals and birds. Res Bull Missou Agricult Res Stat 1932;166:89–101.

Brouwer E. Report of sub-committee on constants and factors. In: Symposium of energy metabolism held at European association for animal production. London: EAAP Academic; 1965. p. 441–3. 1965.

Chwalibog A, Jakobsen K, Tauson AH, Thorbek G. Heat production and substrate oxidation in rats fed at maintenance level and during fasting. Comp Biochem Physiol Mol Integr Physiol 1998;121:423–9. https://doi.org/10.1016/s1095-6433(98)10153-8.

de Lange K, van Milgen J, Noblet J, Dubois S, Birkett S. Previous feeding level influences Plateau heat production following a 24 h fast in growing pigs. Br J Nutr 2006;95:1082–7. https://doi.org/10.1079/bjn20061748.

Hudson LN, Isaac NJB, Reuman DC. The relationship between body mass and field metabolic rate among individual birds and mammals. J Anim Ecol 2013;82:1009–20. https://doi.org/10.1111/1365-2656.12086.

Johnson RJ, Farrell DJ. Relationship between starvation heat production and body size in the domestic fowl. Br Poult Sci 1985;26:513–7. https://doi.org/10.1080/00071668508416842.

King JR, Farner DS. Energy metabolism, thermoregulation and body temperature. In: Biology and comparative physiology of birds. Elsevier; 1961. p. 215–88. https://doi.org/10.1016/B978-1-4832-3143-3.50014-9.

Kleiber M. Body size and metabolic rate. Physiol Rev 1947;27:511–41. https://doi.org/10.1152/physrev.1947.27.4.511.

Kleiber M. Body size and metabolism. Hilgardia 1932;6:315–53. https://doi.org/10.3733/hilg.v06n11p315.

Lasiewski RC, Dawson WR. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 1967;69:13–23. https://doi.org/10.2307/1366368.

Labussière E, van Milgen J, de Lange CFM, Noblet J. Maintenance energy requirements of growing pigs and calves are influenced by feeding level. J Nutr 2011;141:1855–61. https://doi.org/10.3945/jn.111.141291.

Liu W, Lin CH, Wu ZK, Liu GH, Yan HJ, Yang HM, et al. Estimation of the net energy requirement for maintenance in broilers. Asian-Australas J Anim Sci 2017;30:849–56. https://doi.org/10.5713/ajas.16.0484.
Lopez G, Leeson S. Utilization of metabolizable energy by young broilers and birds of intermediate growth rate. Poult Sci 2005;84:1069–76. https://doi.org/10.1093/ps/84.7.1069.
Martinez DA, Suesuttajit N, Hilton K, Weil JT, Umberson C, Scott A, et al. The fasting heat production of broilers is a function of their body composition. Anim Open Space 2022;1:100029. https://doi.org/10.1016/j.anopes.2022.100029.
McLean JA, Tobin G. Animal and human calorimetry. Cambridge, England: Cambridge University Press; 1987.
McNab BK. Ecological factors affect the level and scaling of avian BMR. Comp Biochem Physiol Mol Integr Physiol 2009;152:22–45. https://doi.org/10.1016/j.cbpa.2008.08.021.
Meltzer A. Thermoneutral zone and resting metabolic rate of broilers. Br Poult Sci 1983;24:471–6. https://doi.org/10.1080/00071668308416763.
Mitchell HH. Comparative nutrition of man and domestic animals: v2. San Diego, CA: Academic Press; 1964.
Nascimento ST, Maia ASC, Gebremedhin KG, Nascimento CCN. Metabolic heat production and evaporation of poultry. Poult Sci 2017;96:2691–8. https://doi.org/10.3382/ps/pex094.
Noblet J, Dubois S, Lasnier J, Warpechowski M, Dimon P, Carré B, et al. Fasting heat production and metabolic BW in group-housed broilers. Animal 2015;9:1138–44. https://doi.org/10.1017/S1751731115000403.
Pomar C, Marcoux M. The accuracy of measuring backfat and loin muscle thicknesses on pork carcasses by the Hennessy HGP2, Destron PG-100, CGM and ultrasound CVT grading probes. Can J Anim Sci 2005;85:481–92. https://doi.org/10.4141/a05-041.
Rivera-Torres V, Noblet J, Dubois S, van Milgen J. Energy partitioning in male growing turkeys. Poult Sci 2010;89:530–8. https://doi.org/10.3382/ps.2009-00353.
Riveros RL, de Sousa Camargos R, Macari M, de Paula Reis M, Balbino Leme B, Kazue Sakomura N. Dynamic of heat production partitioning in rooster by indirect calorimetry. Anim Biosci 2023a;36:75–83. https://doi.org/10.5713/ab.22.0026.
Riveros RL, Camargos R de S, Silva RL, Leme BB, Sakomura NK. Description and validation of flow-through chambers of respirometry for measuring gas exchange in animal trials. Animals (Basel) 2023b;13. https://doi.org/10.3390/ani13162675.
Rubner M. Über den Einfluß der Körpergröße auf Stoff- und Kraftwechsel. Z Biol 1883;19:535–62.
Sakomura NK. Modeling energy utilization in broiler breeders, laying hens and broilers. Rev Bras Cienc Avic 2004;6:1–11. https://doi.org/10.1590/s1516-635x2004000100001.
Sauvant D, Schmidely P, Daudin JJ, St-Pierre NR. Meta-analyses of experimental data in animal nutrition. Animal 2008;2:1203–14. https://doi.org/10.1017/S1751731108002280.
Teofilo GF da S, Lizana RR, Camargos R de S, Leme BB, Morillo FAH, Silva RL, et al. Effect of feed restriction on the maintenance energy requirement of broiler breeders. Anim Biosci 2022;35:690–7. https://doi.org/10.5713/ab.21.0183.
Teofilo GFS, Riveros RL, Leme BB, Camargos RS, Macari M, Fernandes JBK, et al. Energy utilization and requirement of broiler breeders during the production phase. Poult Sci 2023;102:102980. https://doi.org/10.1016/j.psj.2023.102980.
Zuidhof M. A review of dietary metabolizable and net energy: uncoupling heat production and retained energy. J Appl Poultry Res 2019;28:231–41. https://doi.org/10.3382/japr/pfx062.