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Development of a dynamic energy-partitioning model for enteric methane emissions and milk production in goats using energy balance data from indirect calorimetry studies

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*The main objective of this study was to develop a dynamic energy balance model for dairy goats to describe and quantify energy partitioning between energy used for work (milk) and that lost to the environment. Increasing worldwide concerns regarding livestock contribution to global warming underscore the importance of improving energy efficiency utilization in dairy goats by reducing energy losses in feces, urine and methane (**CH_4**). A dynamic model of CH_4 emissions from experimental energy balance data in goats is proposed and parameterized (n = 48 individual animal observations). The model includes DM intake, NDF and lipid content of the diet as explanatory variables for CH_4 emissions. An additional data set (n = 122 individual animals) from eight energy balance experiments was used to evaluate the model. The model adequately (root MS prediction error, **RMSPE**) represented energy in milk (**E-milk**; RMSPE = 5.6%), heat production (**HP**; RMSPE = 4.3%) and CH_4 emissions (**E-CH_4**; RMSPE = 11.9%). Residual analysis indicated that most of the prediction errors were due to unexplained variations with small mean and slope bias. Some mean bias was detected for HP (1.12%) and E-CH_4 (1.27%) but was around zero for E-milk (0.14%). The slope bias was zero for HP (0.01%) and close to zero for E-milk (0.10%) and E-CH_4 (0.22%). Random bias was >98% for E-CH_4, HP and E-milk, indicating non-systematic errors and that mechanisms in the model are properly represented. As predicted energy increased, the model tended to underpredict E-CH_4 and E-milk. The model is a first step toward a mechanistic description of nutrient use by goats and is useful as a research tool for investigating energy partitioning during lactation. The model described in this study could be used as a tool for making enteric CH_4 emission inventories for goats.*

Keywords: energy transfer, environment, mixed diets, lactation, goats

Implications

The model has provided a dynamic description of energy transfer in goats, evaluating nutritional mitigation strategies to reduce methane emission. The model showed that when dry matter intake, energy and dietary fiber were elevated, the increase in energy transfer to milk and methane emissions was no linear. The increase in methane emission when the fiber content was high was reduced by introducing lipid into the diet. The model emphasized on a more efficient dietary energy partitioning into milk, reducing the methane emissions and quantifying the heat cost of the process.

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Introduction

Large-scale measurement of enteric methane (**CH_4**) is complex, expensive and impractical; therefore, models offer a useful means to predict CH_4 emissions. The United Nation Climate Change Conference celebrated in Paris agreed that there should be effort to keep global warming 'well below 2 degrees' (United Nations Framework Convention on Climate Change, 2015). Current emissions are expected to increase global temperatures by 1.5°C within 15 years and by 2°C within 35 years (Howarth, 2015). Substantial reductions in CO_2 and CO_2 equivalent (including CH_4) emissions will be needed to achieve the target.

The contribution of enteric CH_4 by livestock was estimated at approximately 38.6% of total agricultural emissions (Food and Agricultural Organization (**FAO**), 2010). Although most

CH_4 emissions come from cattle (73.8%) and buffalo (11.3%) in 2010, the remaining 10% comes from goat. The world goat population is approximately 1.01 billion (FAOSTAT, 2018) and produces around 4.61 million tons of enteric CH_4 (around 4.9% of the total CH_4 emissions from livestock). Likewise, future CH_4 emissions from goats are expected to increase due to enhanced growth of goat populations and demands of milk and meat. Thus, prediction models of CH_4 emission in goats should be useful to better estimate those contributions.

Some empirical mathematical models for predicting CH_4 emissions based on dietary composition and nutrient intake in goats have been developed (Patra and Lalhriatpuii, 2016). Intake and dietary composition are strongly related to CH_4 emissions (Niu *et al.*, 2018); and most published studies in cattle included feed intake, fiber (Moorby *et al.*, 2015) and dietary lipid (Knapp *et al.*, 2014) as external factors. However, to our knowledge, there is no model to predict CH_4 emissions in goats developed from energy transfers, including processes such as activity, consumption of food, maintenance, growth and/or milk production. Although Fernández (2018) developed a dynamic model for energy transfer, the input for feed intake was constant and the dietary fiber content was not included in the model. Jørgensen (2015) stressed the importance of distinguishing the energy transfer between animal and environment, because some energy is useful and can do work and some is lost to the environment as heat. The main objective of this study was to develop a dynamic mechanistic energy-partitioning model for dairy goats to describe and quantify energy transfer between that used for work (milk) and that lost to the environment (CH_4, urine and feces).

Material and methods

Experimental data

For modeling purposes, 48 individual animal observations from 24 animals fed two different diets (diet 1 : 33% and 2% of NDF and ether extract (**EE**), respectively, and diet 2 : 46% and 4% of NDF and EE, respectively) were used (Supplementary Table S1). A two-period crossover design (total of 30 days, 25 adaptation and 5 data collection) was used. Murciano-Granadina dairy goats at mid-lactation (16 weeks), with initial BW (48 ± 4.2 kg), were selected to determine energy balance and gas exchanges. Goats were fed twice a day with a diet containing 1.0 kg/day of forage and 1.5 kg/day of concentrate (2.5 kg/day of feed, as-fed basis). Half the daily ration was offered at 0800 h and half at 1600 h. The nutrient recommendations of Agricultural and Food Research Council (**AFRC**) (1997) were used to formulate diets; alfalfa hay as forage mixed with two commercial compound feeds. The mean gross energy (**GE**) of the two diets on DM basis was 18 MJ/kg and CP was 17.1% (Table 1). Goats had free access to water.

Goats were fed the experimental diets during a 15-day adaptation period in pens that was followed by additional 10 days in individual metabolism cages. During both periods,

Table 1 *Descriptive statistics of variables in the database used to develop the partitoning energy model in methane, heat production and milk for dairy goats (observed in n = 48 goats)*

	Lactating dairy goat fed mixed diet			
	(n = 48)			
Variable[1]	Mean	Min.	Max.	SD
Diet composition				
Forage to concentrate ratio 40/60				
DM percentage	92.7	91.9	93.5	0.55
CP (% DM)	17.1	16.2	17.5	0.63
EE (% DM)	3.0	2.0	4.0	0.72
NDF (% DM)	39.5	33.0	46.0	6.54
GE (MJ/kgDM)	17.7	17.6	17.8	0.09
Energy balance (kJ/kg $BW^{0.75}$ per day)				
Intake				
GEI	1976	1501	2447	238.4
Energy loss				
Methane	85	57	113	16.5
Fecal	633	365	936	125.4
Urinary	69	25	117	24.2
Energy not for work				
Heat production	715	534	946	57.54
Energy for work				
MEI	1190	1001	1387	166.8
Reserves	17	−159	193	79.39
Energy in milk	457	390	551	107.7
Goat characteristics				
DMI (g/day)	2034	1663	2408	192.6
BW (kg)	48	40	55	4.2
Milk yield (kg/day)	2.4	2.0	2.7	0.5

EE = ether extract; GE = gross energy; GEI = gross energy intake; MEI = metabolizable energy intake; DMI = DM intake.
[1]Breed: Murciano-Granadina goat, mid-lactation, milk production in the previous lactation = 650 kg of milk per 210 days of lactation.

animals were at thermoneutrality (20°C to 23°C determined by a Hobo probe; ONSET Data Loggers, Cape Cod, MA, USA). Feed offered and refused and total fecal, urinary and milk output were recorded daily for each goat during the 5-day period for calculation of energy balance. Each goat was milked once daily at 0700 h with a portable milking machine (Flaco, model DL-170; J. Delgado S.A., Ciudad Real, Spain). Representative samples of diet, feces, urine and milk were collected daily, stored at −20°C and pooled for energy analysis.

Gas exchange from two goats at a time was measured for a period of 24 h while housed in individual metabolism cages fitted with two ventilated head–hood units. Fernández *et al.* (2015 and 2019) described the mobile open-circuit respiration system based on indirect calorimetry for measuring real-time gaseous exchanges in small ruminants. The metabolizable energy intake (**MEI**) was calculated as the difference between GE intake (**GEI**) and energy losses in feces, urine and CH_4 (with an energy equivalent (**E-CH$_4$**)

value of 39.54 kJ/l; Brouwer 1965). The heat production (**HP**) was determined from measurements of O_2 consumption, CO_2 and CH_4 production, and urinary nitrogen (N_{urine}), using the equation of Brouwer (1965):

$$HP(kJ/day) = 16.18 \times O_2 + 5.02 \times CO_2 - 2.17 \times CH_4 - 5.99 \times N_{urine}$$

where gases were expressed in l/day and N_{urine} in g/day. The retained energy in reserves (kJ/day) was determined as the difference between MEI (kJ/day) and the energy retained in milk (kJ/day) plus the loss of energy as HP (kJ/day). Previously, feed and feces were dried in a forced air oven at 55°C for 48 h and then ground to pass a 1-mm screen. Urine and milk were dried by lyophilization. Chemical analyses were conducted according to the methods of Association of Official Analytical Chemists (**AOAC**) (2012) for DM (no. 934.01), ash (no. 942.05) and EE (no. 920.39). The GE content of feed, feces, urine and milk (**E-milk**) was analyzed by combustion in an adiabatic bomb calorimeter (Gallenkamp Autobomb; Loughborough, UK). The dietary NDF of diets was measured in an ANKOM fiber analyzer (A220; ANKOM Technologies, Fairport, NY, USA) according to AOAC (2000) official methods (no. 973.18). The nitrogen was analyzed by the Dumas principle (TruSpec CN; LECO Corporation, St. Joseph, MI, USA).

Model description

The model simulates a goat on a farm in an intensive regime where the animals are grouped according to the level of production. The model was conceptually based on the dynamic model from Fernández (2018), but the approach to drive the energy partitioning among different pools and fluxes was completely different.

The present model consisted of a dynamic system of differential equations, and a fourth-order Runge-Kutta method with an integration step size of 0.05 day was used for numerical integration. The model was run until steady state was achieved and day were used as a unit of time. The model contains three pools (kJ/kg $BW^{0.75}$) represented by capital letters and with a box (1. digesta [D] = digestive tract, 2. assimilation [A] = metabolism and 3. body reserves [R] = body retention and/or mobilization of energy), and the inputs and outputs to and from the pools were fluxes (kJ/kg $BW^{0.75}$ per day) and are represented by arrows and denoted by the abbreviation *F* (Figure 1). Therefore, the pool will change with time depending on the magnitude of the fluxes (energy transfer among the pools), and the change is described by a

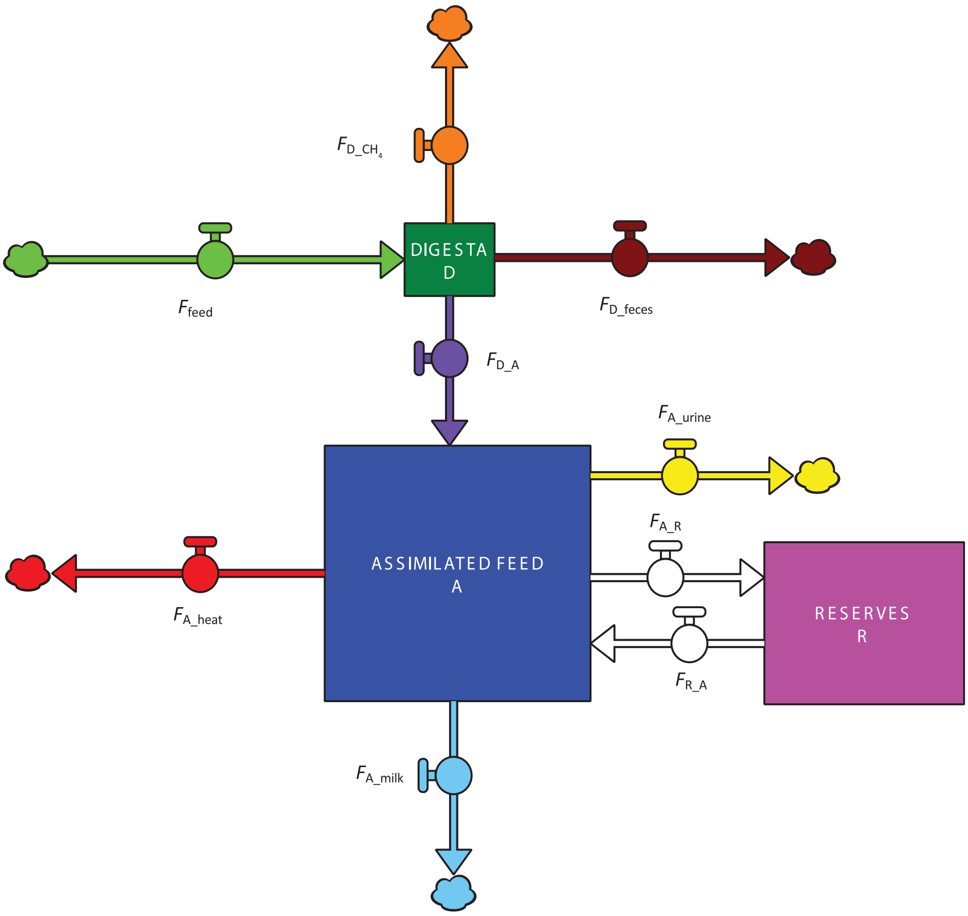

Figure 1 (colour online) Diagrammatic representation of the energy partitioning mathematical model in dairy goats (using Stella Architect software). See Table 2 for legend.

differential equation of the form: dPOOL/dt = $F_{in} - F_{out}$. We developed a model assuming mass action ($F = k \times$ POOL; being k the fractional rate) and saturating flux (i.e. Michaelis–Menten ($F = Mx/(K + \text{POOL})$; where Mx is the maximal energy rate and K the affinity constant). Knowledge of the flux and the pool allowed estimation of fractional rate k. Each element of the model is specified by an initial condition derived from actual measurements and published literature, and fractional rates are derived mainly from experimental and empirical information. Schematic representation of the model is shown in Figure 1. Description of pools and the associated differential equations describing the pool-size change over time follow below and the abbreviations are referenced in Table 2.

1. *Digesta pool,* Q_D (kJ/kg $BW^{0.75}$). The digesta pool includes one input and three outputs. The input in this pool (energy intake, F_{feed}) was determined from DM intake (DMI, kg/day) multiplied by the energy content of the diet (GE, kJ/g DM) and divided by the metabolic BW (kg $BW^{0.75}$), all determined experimentally. Outputs are waste energy from the digestive tract to feces (F_{D_feces}). Apparent total tract digestibility of energy was obtained experimentally (Table 1) and defined as $F_{D\_A} = k_d \times$ Q_D, with fractional rate being $k_d = 0.68$. Apparent total tract digestibility of energy was adjusted during model evaluation. Although CH_4 is influenced by many factors, DMI, NDF and EE were selected for this model. Enteric CH_4 prediction models are often based on various animal or feed characteristic inputs but are dominated by DMI (Hristov *et al.*, 2017). As Niu *et al.* (2018) reported, CH_4 emissions are strongly related to feed intake, NDF and dietary lipid. In the present model, emissions of energy as CH_4 ($F_D\_CH_4$) were dependent on DMI, NDF and EE, according to the literature reviewed. A reference value of DMI (R_{DMI}, average value obtained from the trial; 2034 g DM/day), R_{NDF} (also a reference value from the trial, 40%) and R_{EE} represents the EE or fat content of the diet. Due to the model being based on goats fed mixed diets indoors, the diet always had a minimum amount of fat; hence, a reference value of 3% fat was used. The fractional rate of CH_4 production '(kCH_4) was obtained experimentally (0.067), and the DMI exponent (z) was a value ranging between 0 and 2.

Digesta Pool, Q_D (kJ/kg $BW^{0.75}$).
Differential equation:

$$dQ\_D/dt = F_{feed} - F_{D\_feces} - F_{D\_A} - F_D\_CH_4$$

Inputs:

$$F_{feed} = (\text{DMI} \times \text{GE})/BW^{0.75}$$

Outputs:

$$F_{D\_feces} = (1 - k_d) \times Q\_D$$

$$F_{D\_A} = k_d \times Q\_D$$

Table 2 *Pools, fluxes and symbols used in the energy partitioning dairy goat model*

Label	Description
Energy pools (kJ/kg $BW^{0.75}$)	
Q_D	Digesta
Q_A	Assimilation
Q_R	Body reserves
Energy fluxes (kJ/kg $BW^{0.75}$ per day)	
F_{feed}	Gross energy intake to digestive tract
F_{D_feces}	Fecal energy
F_{D_A}	Digestible energy flux to metabolism
F_{R_A}	Energy mobilization
F_{A_urine}	Energy in urine
F_{A_R}	Assimilated energy flux to body reserves
F_{A_heat}	Heat energy
F_{A_milk}	Flux of assimilated energy to milk
$F_D\_CH_4$	Energy from methane
Fractional rates (/day)	
k_d	Fractional rate of F_{D_A}
k_u	Fractional rate of F_{A_urine}
k_g	Fractional rate of F_{A_R}
kCH_4	Fractional rate of $F_D\_CH_4$
Reference constants	
R_{DMI} (g/kg DM)	Average DM intake
R_{NDF} (%)	Average NDF inclusion in mixed diets
R_{EE} (%)	Average fat inclusion in mixed diets
R_{BW} (kg)	Average BW from the trial
z	DM intake exponent
J	Average heat production from development database
E_{milk} (kJ/kg $BW^{0.75}$ per day)	Maximum energy in milk
K (kJ/kg $BW^{0.75}$ per day)	Affinity constant in Michaelis–Menten equation for milk
Inputs	
BW (kg)	Input value of BW
GE (MJ/kg DM)	Diet input value of gross energy
DMI (g/kg DM)	Diet input value of DM intake
NDF (%DM)	Diet input value of NDF
EE (%DM)	Diet input value of fat
MEI (kJ/kg $BW^{0.75}$ per day)	Metabolizable energy intake

$$F_{D\_CH_4} = k_{CH_4} \times \left(\frac{\text{DMI}}{R_{DMI}}\right)^z \times \frac{\text{NDF}}{R_{NDF}} \times \frac{R_{EE}}{\text{EE}} \times Q\_D$$

The digesta pool size was expressed by the integral equation:

$$D = \int_{t0}^{t} \frac{dQ\_D}{dt} + iQ\_D$$

Representing the quantity of energy accumulated from initial time (t_0) to final time (t), with iD being the initial pool size (assumed equal to 0).

2. *Assimilation pool*, Q_A (kJ/kg $BW^{0.75}$). The assimilation pool represents the energy available for maintenance and production and included two inputs and four outputs. Fractional rates of inputs and outputs were determined experimentally from the trial described above. Inputs were the flux of digestible energy defined below (F_{D_A}) and the flux of energy mobilized from body reserves, and the latter flux can be assumed identical to energy gain (outflow from assimilation pool to reservoir energy (F_{A_R}) with a $k_g = 0.014$). The outputs also comprise the waste of energy lost in urine (F_{A_urine}) with an observed fractional rate $k_u = 0.057$. The HP lost to the environment (F_{A_heat}) was described by a Michaelis–Menten-type equation with the experimental values from observed MEI and J was the average HP observed (715 kJ/kg $BW^{0.75}$ per day). 'The energy flux output used for milk production (F_{A_milk}) was described as a saturating relationship between MEI and E-milk outflow. In this Michaelis–Menten equation, E-milk is the maximum energy content in milk observed in the trial (551 kJ/kg $BW^{0.75}$ per day) and K is the affinity constant (an initial value of 401 kJ/kg $BW^{0.75}$ per day 'proposed by Aguilera *et al.* (1990), as ME for maintenance, was suggested). Both fluxes (F_{A_heat} and F_{A_milk}) were corrected with BW using an observed average reference BW (R_{BW}) value of 48 kg.

Assimilation pool, Q_A (kJ/kg $BW^{0.75}$).
Differential equation:

$$dQ\_A/dt = F_{D\_A} + F_{R\_A} - F_{A\_R} - F_{A\_urine} - F_{A\_heat} - F_{A\_milk}$$

Inputs:

$$F_{D\_A} = k_d \times Q\_D$$

$$F_{R\_A} = -F_{A\_R}$$

Outputs:

$$F_{A\_R} = k_g \times Q\_A$$

$$F_{A\_urine} = k_u \times Q\_A$$

$$F_{A\_heat} = \frac{1}{1 + \left(\frac{J}{MEI}\right)} \times \frac{BW}{R_{BW}} \times Q\_A$$

$$F_{A\_milk} = \frac{Emilk}{K + MEI} \times \frac{BW}{R_{BW}} \times Q\_A$$

The assimilation pool size was expressed by the integral equation:

$$A = \int_{t0}^{t} \frac{dQ\_A}{dt} + iQ\_A$$

which represents the quantity of energy accumulated from initial time (t_0) to final time (t), with iA being the initial pool size (assumed to be 293 kJ/kg $BW^{0.75}$; 'Kleiber, 1972).

3. *Body Reserves pool,* Q_R (kJ/kg $BW^{0.75}$). The body reserves pool includes one input and one output. Due to the model being developed for dairy goats in mid-lactation, we assumed identical fluxes.

Body Reserves pool, Q_R (kJ/kg $BW^{0.75}$).
Differential equation:

$$dQ\_R/dt = F_{A\_R} - F_{R\_A}$$

Inputs:

$$F_{A\_R} = k_g \times Q\_A$$

Outputs:

$$F_{R\_A} = -F_{A\_R}$$

The body reserve pool size was expressed by the integral equation:

$$R = \int_{t0}^{t} \frac{dQ\_R}{dt} + iQ\_R$$

Representing the quantity of energy accumulated from initial time (t_0) to final time (t), with iR being the initial pool size (assumed to be 20 kJ/kg $BW^{0.75}$; AFRC, 1997).

Parameter estimation
The dynamic model used the function *ode()* of the deSolve (solving differential equations) package for numerical solutions of initial first-order problems and was implemented in R software (2016). The solution was achieved using the lsoda integration method with absolute and relative error tolerance of 10^{-6}. The R codes to build the model are presented in Supplementary Material S1. The parameter estimation was performed by minimizing the negative log likelihood using the function *optim()* from R (2016, v.1.1.447) and the method used for optimization was Broyden Fletcher Goldfarb Shanno algorithm (**L-BFGS-B**).

To characterize model inadequacy (i.e. bias) in the range of our observations, the observed values of E-CH_4 emissions, HP and E-milk were compared with model predictions and the discrepancy was calculated as the root mean square prediction error (**RMSPE**). The RMSPE was decomposed into error due to the overall bias of prediction (mean bias), error due to deviation of the regression slope from unity (slope bias) and error due to disturbances or random variations (random bias) (Bibby and Toutenburg, 1977). The model adequacy of the best-fitting model was further assessed outside the range of our observations by fitting a regression line between observed and predicted values and considering the intercept and slope deviation from 0 and 1, respectively. This exercise extrapolates to zero and beyond the maximum observed values and, thus, quantifies the applicability domain for the model under consideration. Afterward, residual plots ((observed – predicted) *v* predicted values) verifying the assumptions that errors are normally and identically distributed around zero with constant variance were examined. Since residuals are not correlated with predictions, if the model is unbiased, the slope of the regression of residuals on predictions must be zero.

Furthermore, RMSPE and concordance correlation coefficient (**CCC**) were also used to evaluate the precision and accuracy of predicted *v* observed values for the model (Lin, 1989). The CCC estimate represents the product of two components. First component is the Pearson correlation coefficient that measures precision (deviation of observations from the best fit line). Second component is the bias correction factor that indicates accuracy (i.e. how far the regression line deviates from the unity line).

Evaluation of the mathematical model

Lactation trial data. The model was evaluated with data from eight energy balance experiments (two unpublished results) using mixed diets (forage mixed with concentrate) conducted at the Universitat Politècnica de Valencia (López and Fernández, 2013; Ibáñez *et al.*, 2014; López *et al.* 2014; Criscioni *et al.*, 2016; Fernández *et al.*, 2018 and 2019). These trials evaluated the response of lactating goats in terms of DMI, energy and N balance, apparent total tract digestibility and milk performance when cereals were replaced with horticultural by-products. Fibrous by-products are cheaper than cereal grains and are an interesting alternative to reduce waste and to feed dairy goats. The trial of López and Fernández (2013) replaced corn grain with a mixture of soy hulls and corn gluten feed, Ibáñez *et al.* (2014) replaced corn grain with beet pulp, López *et al.* (2014) studied the effect of replacing corn grain with citrus pulp, Criscioni *et al.* (2016) replaced only the forage (alfalfa with maralfalfa), Fernández *et al.* (2018) used lemon leaves as forage instead of alfalfa hay (goats fed with the same compound feed) and Fernández *et al.* (2019) used orange leaves as forage instead of alfalfa hay (goats fed with the same compound feed). One unpublished study replaced barley with beet pulp (Pérez-Baena I) and the other (Martí JV) replaced barley with lemon pulp. All studies demonstrated successfully the possibility to substitute cereal grains with fibrous by-products. To maintain diets isoenergetic, fat was added to treatments containing fibrous by-products. Half the daily ration was offered at 0800 h and half at 1600 h, respectively. Goats had free access to water. The trials encompassed a total of 122 individual multiparous Murciano-Granadina goats in mid-lactation. Animals had *ad libitum* access to diets, which were offered at 110% of intake. A summary of the data used in the model evaluation is given in Table 3.

Model evaluation. Residual analysis was assessed for adequacy of the model. The observed and model prediction values were compared for E-milk, HP and E-CH_4. An

Table 3 *Descriptive statistics of variables in the evaluation database used to evaluate the partitioning energy model for methane, heat production and milk for dairy goats (observed in n = 122 goats)*

Variable	Lactating dairy goat fed mixed diet (n = 122) Mean	Min.	Max.	SD
Diet composition				
Forage to concentrate ratio 40/60				
DM percentage	91.4	88.6	94.1	0.87
CP (% DM)	15.7	13.2	18.2	2.25
EE (% DM)	2.2	1.6	5	0.77
NDF (% DM)	34.6	21.0	58.9	7.64
GE (MJ/kgDM)	17.1	16.3	18.0	0.53
Energy balance (kJ/kg $BW^{0.75}$)				
Intake				
GEI	1717	1462	2180	138.2
Energy loss				
Methane	92	43	171	21.79
Fecal	490	300	794	125.0
Urinary	46	25	116	12.61
Energy not for work				
Heat production	670	556	845	53.4
Energy for work				
MEI	1089	949	1201	52.04
Reserves	3	−176	120	61.7
Energy in milk	416	359	468	23.2
Goat characteristics				
DMI, g/day	1718	1294	2199	171.2
BW (kg)	44	33	61	4.7
Milk yield (kg/day)	1.8	1.4	2.5	0.21

EE = ether extract; GE = gross energy; GEI = gross energy intake; MEI = metabolizable energy intake; DMI = DM intake.

assessment of the error of the predicted relative to the observed values was made by calculation of the RMSPE. The prediction error was assessed by calculating the MSPE. The MSPE was decomposed into mean, slope and random bias, as previously described. Residual plots verifying the assumptions that errors are normally and identically distributed around zero with constant variance were examined. The CCC, described above, evaluates the degree of deviation between the best fit line and the identity line (y = x); thus, the CCC of a model that is closer to 1 is an indicator of better model performance.

Results

Model development

The model had five parameters and was fitted using observations from a single study (48 data points). The energy balance study in goats included energy intake and output of CH_4, fecal, urinary and milk energy. Initial and final values of the optimized parameters, obtained by RMSPE, with their SD and CV are shown in Table 4. The parameters kCH_4 and *K*

Table 4 *Initial and final parameter estimations and standard deviation of optimized energy partitioning dairy goat model parameters, other parameters and pools*

Parameters	Initial values	Final values	SD	CV
kCH_4	0.067	0.037	0.0212	41
z	0.300	0.274	0.0184	6
J	715	654	43.1	6
E_{milk}	551	584	23.3	4
K	401	280	85.6	25
Others paremeters (per day)		Reference		
k_d	0.68	Observed		
k_u	0.057	Observed		
k_g	0.014	Observed		
kCH_4	0.067	Observed		
Reference constants				
R_{DMI} (g/kg DM)	2034	Observed average value (development database)		
R_{NDF} (%)	40	Observed average value (development database)		
R_{EE} (%)	3	Observed average value (development database)		
R_{BW} (kg)	48	Observed average value (development database)		
Pools (kJ/kg $BW^{0.75}$)				
Q_D	0	–		
Q_A	293	Kleiber (1972)		
Q_R	20	AFRC (1997)		

Parameter abbreviation is given in Table 2.

Table 5 *Partitioning energy in the dairy goat model using performance data from the developmental data set (n = 48): prediction errors and decomposition associated with prediction of the outputs (kJ/kg $BW^{0.75}$ per day)*

Variable	Observed mean	Predicted mean	RMSPE (%)	Mean bias (%)	Slope bias (%)	Random bias (%)	CCC
Methane energy	85	84	11.9	1.27	0.22	98.51	0.773
Heat production	715	715	4.3	1.12	0.01	98.87	0.943
Milk energy	457	457	5.6	0.14	0.10	99.96	0.680

RMSPE = root mean square prediction error as a percentage of observed mean; CCC = concordance correlation coefficient.

had a CV of 41% and 25%, respectively, and less than 7% were found for parameters z, J and E_{milk}. The prediction errors are shown in Table 5. The RMSPE was 11.9% for loss of E-CH_4, 5.6% for E-milk and 4.3% for HP. Evaluation through CCC was in agreement with RMSPE, with the largest CCC for HP (0.943) followed by E-CH_4 (0.773) and then E-milk (0.680). Some mean bias was detected for HP (1.12%) and E-CH_4 (1.27%) but was around zero for E-Milk (0.14%). The slope bias was zero for HP (0.01%) and close to zero for E-milk (0.10%) and E-CH_4 (0.22%). Random bias was >98% for E-CH_4, HP and E-milk indicating non-systematic error, and the equation in the model fitted the data properly. Figure 2 displays observed *v* predicted values and the corresponding unity regression equation (i.e. observed = predicted). The model presented the least bias for the CH_4 energy data in the range 60 to 85 kJ/kg $BW^{0.75}$ per day, but above this range it underestimated (Figure 2a). It also had a nearly unbiased fit to HP data from 550 to 850 kJ/kg $BW^{0.75}$ per day (Figure 2b). For energy in milk, with a range of 430 to 500 kJ/kg $BW^{0.75}$ per day, the model bias was minimal, but below and above this range it overestimated and underestimated, respectively (Figure 2c). The residual standard error for E-CH_4, HP and E-milk showed that the model was off by 10.08, 31.92 and 0.49 kJ/kg $BW^{0.75}$ per day, respectively.

Analyses of residuals are shown in Figure 3. Results are consistent with the biases illustrated in Figure 2. For the ranges between 60 and 85 kJ/kg $BW^{0.75}$ per day (Figure 3a), 550 and 850 kJ/kg $BW^{0.75}$ per day (Figure 3b) and 430 and 500 kJ/kg $BW^{0.75}$ per day (Figure 3c) for E-CH_4, HP and E-milk fluxes, the residuals appeared to be randomly distributed about zero. Slopes of regression lines for residuals *v* predicted were negative for the three energy fluxes, indicating that the model underpredicted fluxes as the predicted flux increased. Therefore, extrapolating outside the above ranges may yield increasingly biased predictions.

Model evaluation

Data from a total of 122 individual animals from eight energy balance experiments were used to evaluate the model. With exception of E-CH_4 with an RMSPE value of 21.9%, model prediction errors <4% of the observed values were reasonable for all predicted outputs (Table 6). A value of 21.9% in

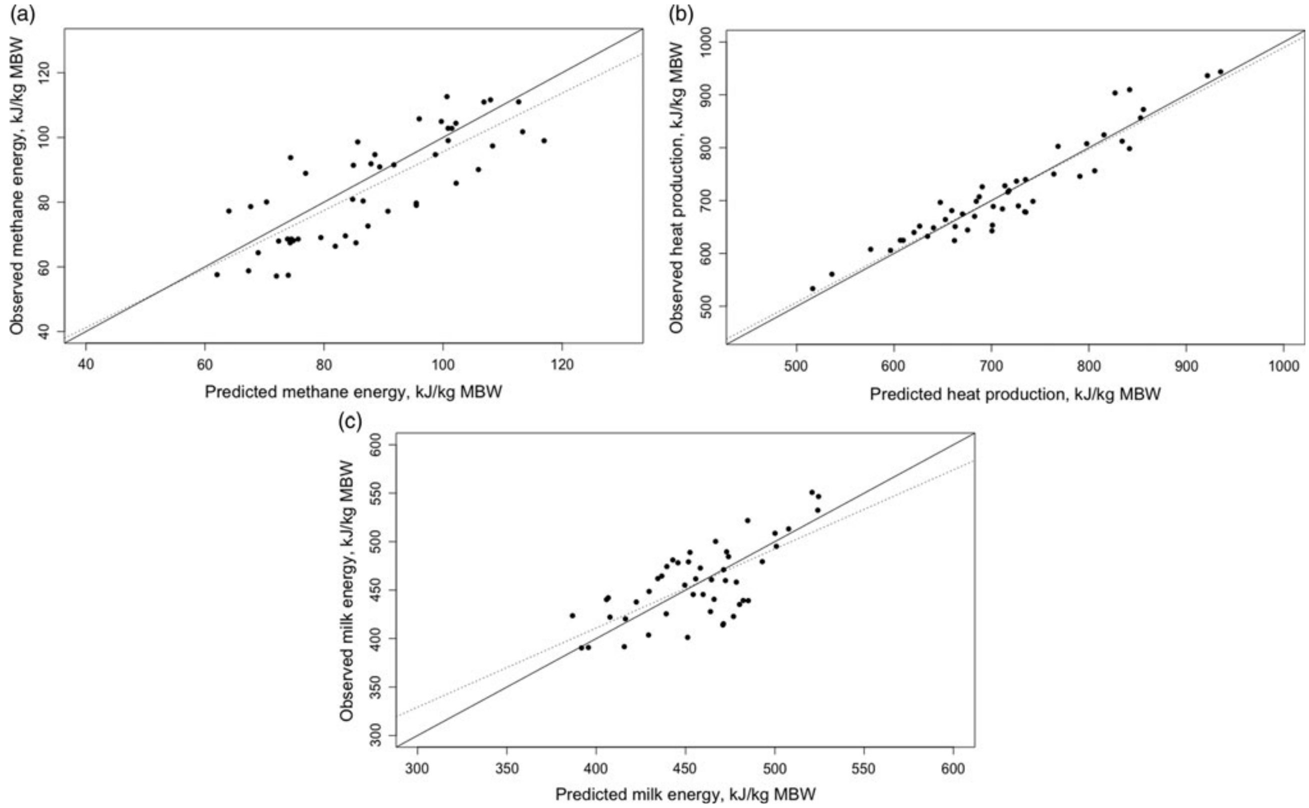

Figure 2 Observed *v.* predicted values of methane (a), heat production (b) and energy in milk (c) used for model development in dairy goats (kJ/kg $BW^{0.75}$ day; $BW^{0.75}$ = MBW). The regression equations were as follow: methane Y = 4.96 + 0.91X (standard error = 9.00 and 0.10 for the intercept and slope, respectively; residual standard error = 10.08; R^2 = 0.64); heat production Y = 26.02 + 0.96X (standard error = 36.02 and 0.05 for the intercept and slope, respectively; residual standard error = 31.92; R^2 = 0.90); milk energy Y = 76.43 + 0.83X (standard error = 57.68 and 0.12 for the intercept and slope, respectively; residual standard error = 0.48; R^2 = 0.49).

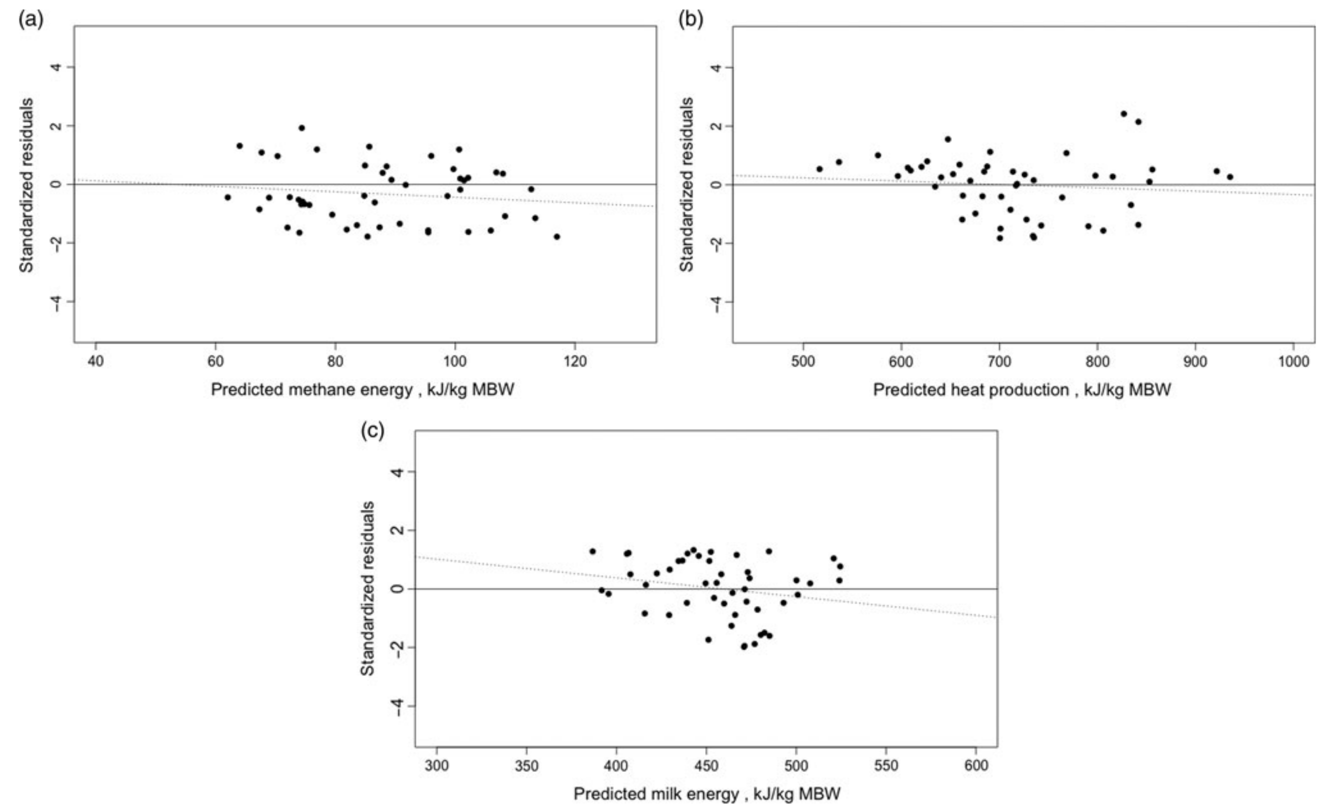

Figure 3 Residual plot of methane (a), heat production (b) and energy in milk (c) used for model development in dairy goats (kJ/kg $BW^{0.75}$ day; $BW^{0.75}$ = MBW).

Table 6 *Energy partitioning dairy goat model using performance data from the evaluation data set (n = 122): prediction errors and decomposition associated with prediction of outputs (kJ/kg BW $^{0.75}$ per day)*

Variable	Observed mean	Predicted mean	RMSPE (%)	Mean bias (%)	Slope bias (%)	Random bias (%)	CCC
Methane energy	92	91	21.9	8.01	24.2	71.75	0.600
Heat production	670	662	2.5	0.00	13.8	86.22	0.955
Milk energy	416	415	3.49	0.00	6.43	93.57	0.831

RMSPE = root mean square prediction error as a percentage of observed mean; CCC = concordance correlation coefficient.

E-CH_4 indicated that some variation remains to be explained. Evaluation through CCC was in agreement with RMSPE, with largest CCC for HP (0.955) and E-milk (0.831) and the smallest for E-CH_4 (0.600). Mean bias represents the accuracy of the model being around zero for HP and E-milk, but some disturbances were detected for E-CH_4 (8.01%). The slope bias was different from zero for E-CH_4, HP and E-milk (24.24%, 13.76% and 6.43%, respectively), meaning lack of precision with the external data set. Random bias was 93.57% for E-milk, 86.22 for HP and 71.75 for E-CH_4. Lower than 85% indicated systematic errors for E-CH_4 and that mechanisms in the model could be improved.

Plots of observed *v* predicted values in E-CH_4, HP and E-milk are shown in Figure 4. This figure includes eight data sets for energy balance, and data points from the same experiment share the same color and are connected by solid lines. Figure 4a shows overestimation in two studies (Martí *et al.*, 2012 and Pérez-Baena *et al.*, 2012) and underestimation in another two studies (Fernández *et al.*, 2018 and 2019). It had a nearly unbiased fit to HP data, but the study of López *et al.* (2014) showed underprediction for higher values of HP (Figure 4b). The same study (López *et al.*, 2014) overpredicted E-milk and the study of Criscioni *et al.* (2016) underpredicted at lower energy content in milk, and for greater energy content overpredicted E-Milk (Figure 4c).

Analyses of residuals (involves regressing residuals against predicted values) are shown in Figure 5, and for

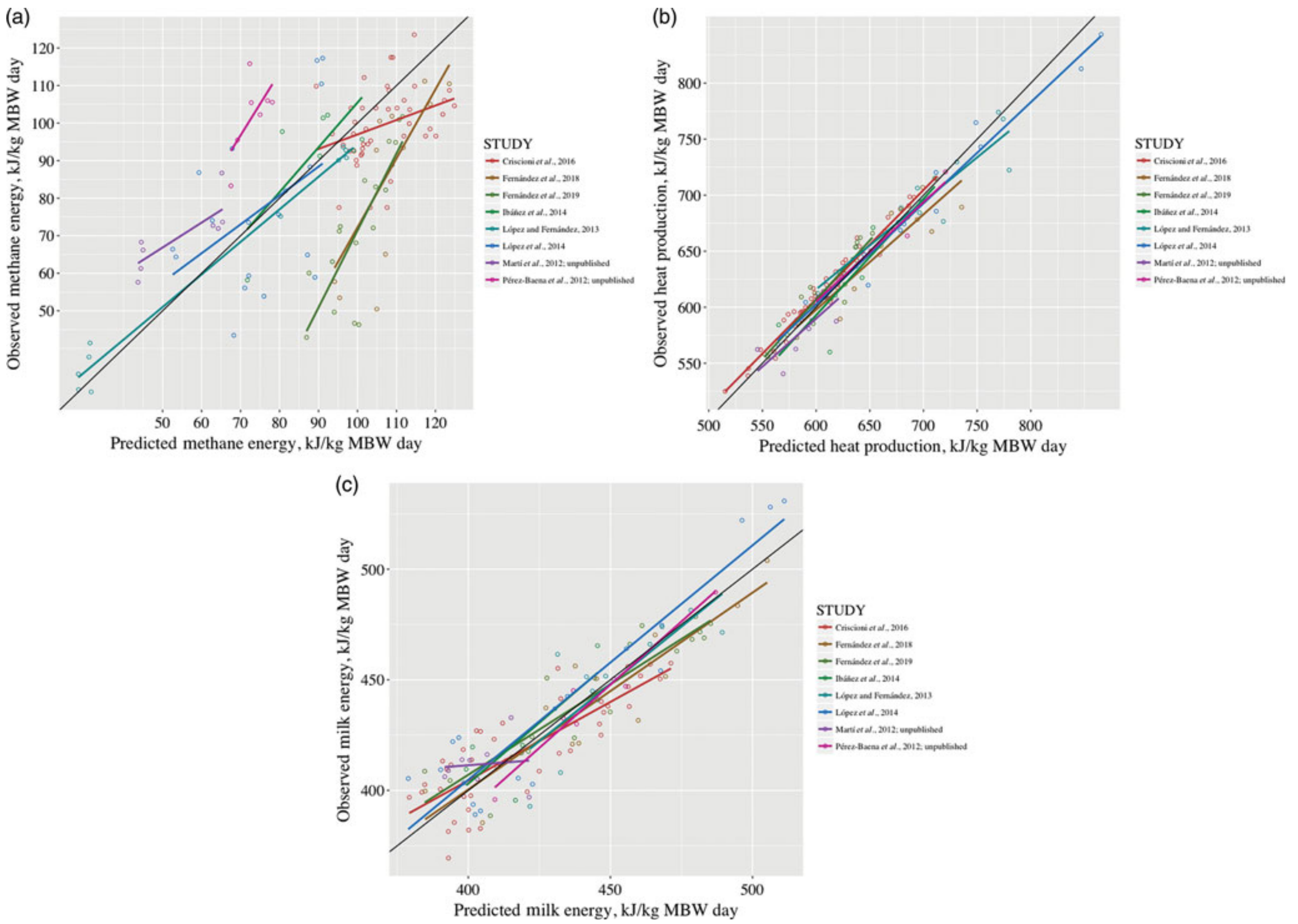

Figure 4 (colour online) Observed *v.* predicted values of methane (a), heat production (b) and energy in milk (c) used for model evaluation in dairy goats (kJ/kg BW$^{0.75}$ day; BW$^{0.75}$ = MBW).

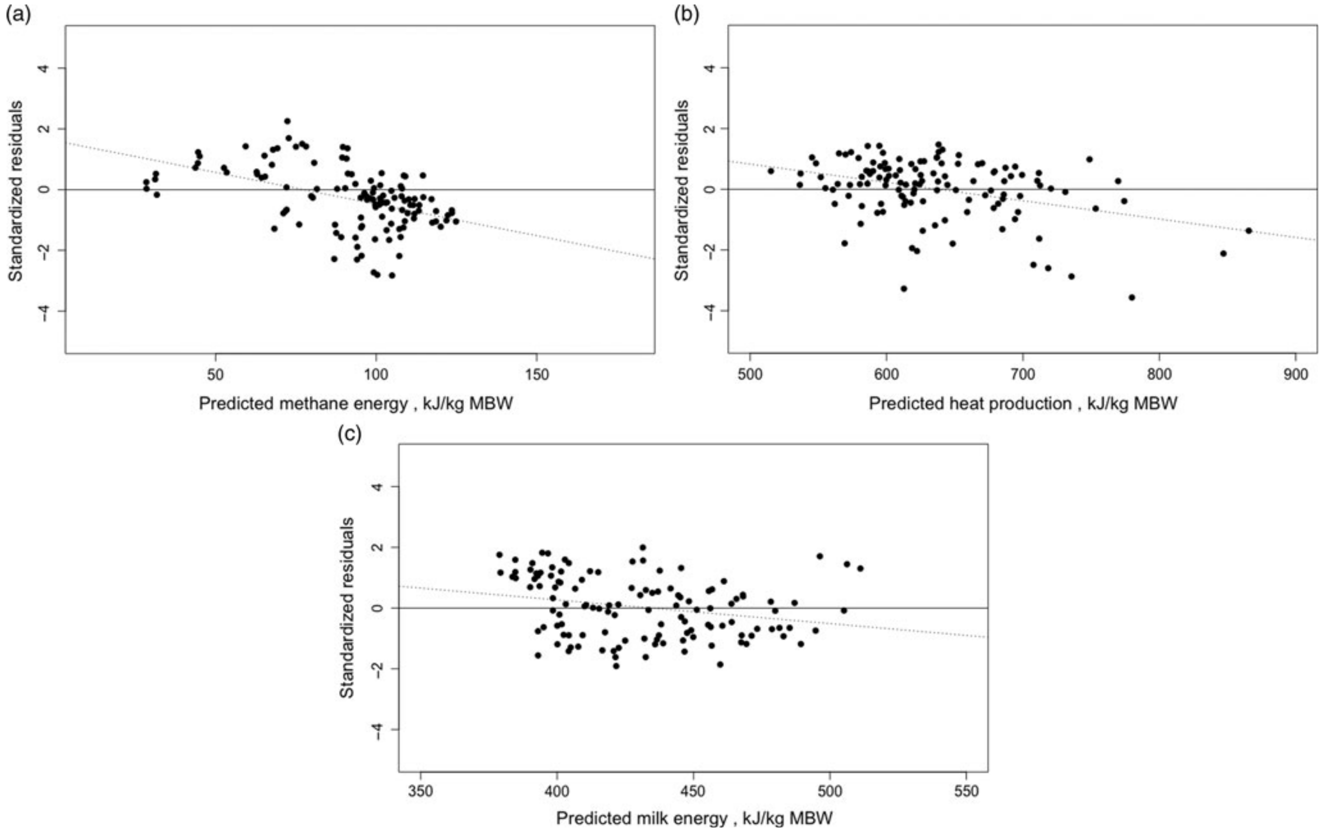

Figure 5 Residual plot of methane (a), heat production (b) and energy in milk (c) used for model evaluation in dairy goats (kJ/kg $BW^{0.75}$ day; $BW^{0.75}$ = MBW).

an unbiased model the slope of residuals regressed on prediction must be zero. The slope was negative for E-CH_4, HP and E-milk (Figure 5a, b and c, respectively), indicating that the model underpredicted as predicted energy increased.

Discussion

In constructing a dynamic model of energy partitioning, Fernández (2018) took a slightly different approach to the present model because of distinctive objectives. Fernández (2018) designed a model to investigate the hourly shape of change in CH_4 emission. The model had a constant pool called feed available, so a stock, not a flux to nurture the model. Due to the feed available was a stock, the amount of food declined each hour at a constant rate by action of the different fluxes, and this pool approached to zero when the hours advance in time. When no more feed was into the pool, the complete partitioning of energy among the others pools and their fluxes were achieved. Therefore, the constant amount of feed in Fernández's study (2018) determine the condition of the system. However, the present model work at steady state and the unit of time used was a day. The most important difference was the model had a daily flux of feed, and this forcing function influenced the entire components of the system; energy in milk, CH_4 and HP predictions. This flux of feed was the daily intake, action that causes the pools to increase or decline over time and drive the energy partitioning of the system. The present model assesses the daily variation in CH_4 emissions, milk and loss of heat when daily changes in DMI, lipid and fiber were taking place. Moreover, the present model was not an extension of Fernandez (2018) because the numbers of pools and fluxes were different. Thus, Fernández (2018) model contained six pools (feed available, digestive tract, rumen, metabolism, reservoir and milk), and the parameters were estimated by bootstrapping method. The present model contains three3 pools and parameters was estimated by L-BFGS-B.

The main objective of the model developed in this article was to predict and quantify the partitioning of energy by lactating goats fed mixed diets. It was assumed that dietary energy is transferred to the body, and part of the energy is wasted energy (CH_4, HP, feces and urine) and some is recovered in milk.

The evaluation database (Table 5) was used to assess different existing CH_4 emissions models. Using the International Panel on Climate Change (IPCC, 2007) equation for ruminants (CH_4 (MJ/day) = 0.065 × GEI) resulted in a value of 1.91 MJ CH_4/day. Using the FAO (2010) equation for ruminants (CH_4 (MJ/day) = (9.75 − ((0.005 × DM digestibility, g/kg)/100)) × GEI) resulted in a value of 1.82 MJ CH_4/day. The linear model of Patra and Lalhriatpuii (2016) for goats predicted 1.31 MJ CH_4/day (CH_4 (MJ/day) = (0.242 + 0.0511 × digestible energy intake) and the Mitscherlich model predicted 1.27 MJ CH_4/day

(CH_4 (MJ/day) = 1.721 × (1 − $e^{(-0.0721 \times \text{ME intake})}$)). Table 6 reports the observed CH_4 emission with the evaluation data set and the prediction with the present model, with results indicating similar levels of production: 1.56 MJ CH_4/day and 1.54 MJ CH_4/day, respectively. Although these models have been suggested in the preparation of inventories of enteric CH_4 production, the IPCC (2007) and FAO (2010) overestimated CH_4 production, whereas the Patra and Lalhriatpuii (2016) model would have underestimated the CH_4 emissions.

The present model is essentially focused on predicting changes between the energy consumed by the animal and its partitioning; energy transferred to milk and energy lost in CH_4 and HP. The first input in this model was BW and DMI, followed by some chemical characteristics of the diet such as EE and NDF. Ruminal volume and weight are proportional to BW; smaller animals, with lower maintenance energy requirements ingest less feed and have less CH_4 production. Simulations for DMI of 1.4, 1.7 and 2.0 kg/day with the present model resulted in a non-linear response in CH_4 emissions (24, 28 and 36 g/day, respectively) and milk production (2.2, 2.4 and 2.7 kg/day respectively). There was a significant positive relationship between DMI and CH_4 production, demonstrating that as dairy goats consumed more feed, more CH_4 is produced due to greater availability of substrates for microbial fermentation. Patra and Lalhriatpuii (2016) reported a strong relationship between CH_4 production and DMI or GEI (R^2 ranged from 0.75 to 0.85), demonstrating that DMI was the strongest driver of CH_4 emissions, followed by nutrient composition of the DMI, similar to other ruminants. Other studies also reported that feed intake (DM or energy) was the key explanatory variable for prediction equations of CH_4 emission in cattle with R^2 from 0.68 to 0.85 (Mills *et al.* 2003; Yan *et al.*, 2009; Ramin and Huhtanen, 2013). Niu *et al.* (2018) confirmed that DMI is the most important variable to predict enteric CH_4 production in dairy cattle. Thus, the CH_4 production in goats was expressed relative to DMI and the value obtained with the preset model was 890 kJ/kg DMI, which was similar to the average value reported by Patra and Lalhriatpuii (2016) in goats (940 kJ/kg DMI). Working with Alpine goats during lactation, Tovar-Luna *et al.* (2010) studied the effects of dietary concentrate level on energy utilization when diets contained 60% or 20% of concentrate. At mid-lactation and when fed 60% concentrate, the CH_4 emissions ranged from 860 to 930 kJ/kg DMI. Because of that our mixed diets contained 60% concentrate, and the CH_4 production from our simulation was 900 kJ/kg DMI, which was within the range reported by Tovar-Luna *et al.* (2010). Ellis *et al.* (2007) and Yan *et al.* (2009) reported higher CH_4 emissions in cattle, ranging from 1120 to 1490 kJ/kg DMI. In the study conducted by Kebreab *et al.* (2008), the range of predicted daily emissions for lactating dairy cows was greater and ranged from 835 to 1948 kJ CH_4/kg DMI. Therefore, the data suggest that small ruminants like goats produce less CH_4 per unit of DMI compared to cattle. Reasons for these differences across ruminant species would require further investigation.

Within diet composition, the carbohydrates fermented in the rumen produce volatile fatty acids and hydrogen, which has a direct impact on CH_4 emissions. Studies focused on the effect of type of carbohydrates indicate that diets rich in non-structural carbohydrates such as starch are more likely to favor propionate formation, resulting in less hydrogen and CH_4 production, whereas diets rich in structural carbohydrates (NDF) generally favor acetate and butyrate production by net hydrogen producers (Bannink *et al.*, 2008). With inputs of 44 kg of BW, 1717 g DMI/day, 17 MJ GE/ kgDM, 35% NDF and 3% EE, the model predicted 61 kJ E-CH_4/kg $BW^{0.75}$ per day, and when NDF was 45% the E-CH_4 was 77 kJ/kg $BW^{0.75}$ per day. The model proposed by Patra and Lalhriatpuii (2016) for goats based on NDF intake (CH_4 (MJ/day) = 0.387 + 1.167 × NDF intake (kg/day)) predicted values of 64 and 75 kJ E-CH_4/kg $BW^{0.75}$ per day, for 35% and 45% NDF, respectively. Thus, dietary NDF concentration is also a key dietary variable for predicting enteric CH_4 production, and goats fed high NDF diets tend to produce more CH_4 per unit of DMI, which can also result from the higher ruminal pH. Substituting a high-fiber diet for the optimal amount of more digestible carbohydrate or low-fiber sources increases milk production and reduces CH_4 production (Niu *et al.*, 2018).

Although Patra and Lalhriatpuii (2016) did not include the concentration of EE in their model, Grainger and Beauchemin (2011) reported that increasing the level of starch and lipids, along with decreasing NDF and ADF in diets, reduced CH_4 production. Including DMI and EE intake in the equations improved the prediction of CH_4 in cattle (Ellis *et al.*, 2007). Although some studies excluded EE concentration as an explanatory variable, Grainger and Beauchemin (2011) indicated that EE in diets inhibits the growth and activity of methanogens, thus, lowering CH_4 production in the rumen. When the dynamic model from the present study was run with inputs of 44 kg of BW, 1717 g DMI/day, 17 MJ GE/ kgDM, 35% NDF and the EE changed from 3.2% to 5.6%, as the experiment of Bava *et al.* (2001), the E-CH_4 simulated was 55 and 33 kJ/kg $BW^{0.75}$ per day, respectively (a difference of 22 kJ/kg $BW^{0.75}$ per day). Similar variation was found in the experiment of Bava *et al.* (2001) comparing forage with non-forage diets in lactating dairy Saanen goats (with 3.2% and 5.6% of EE, respectively). At early lactation, they detected E-CH_4 values of 138 and 104 kJ/kg $BW^{0.75}$ per day (difference of 34 kJ/kg $BW^{0.75}$ per day) and at mid-lactation the E-CH_4 values were 131 and 115 kJ/kg $BW^{0.75}$ per day (difference of 16 kJ/kg $BW^{0.75}$ per day); the average value between the two stages of lactation was 25 kJ/kg $BW^{0.75}$ per day. The amount of E-CH_4 was greater due to breed (Saanen) was greater due to bigger size; higher BW (55 kg, on average), intake (2.8 kg/DM, on average), GE in the diet (19 MJ/kg DM) and milk production. Aguilera *et al.* (1990) working with Granadina goats (small body size) at mid- and late-lactation reported CH_4 production ranging from 111 and 97 kJ/kg $BW^{0.75}$ per day, respectively . These values were slightly higher than those in our simulation, with 3.2% of

EE; the diet in Aguilera *et al.* (1990) was not mixed and consisted mainly of alfalfa pellets, and only barley was used as a supplement. In addition, in that study, no information was available about the fat and NDF inputs into the model.

Fernández (2018) developed a dynamic model with six pools for CH_4 emissions in dairy goats at mid-lactation. Under the conditions defined above, when diet contained 3.2% of EE the E-CH_4 was 82 kJ/kg $BW^{0.75}$ per day; whereas when EE was 5.6%, the E-CH_4 was 72 kJ/kg $BW^{0.75}$ per day. Clearly, increasing the dietary EE reduced CH_4 emissions but the values were higher compared with the present model (difference of 10 kJ/kg $BW^{0.75}$ per day.) The Fernández (2018) model seems to overpredict the CH_4 emission with values similar to Aguilera *et al.* (1990) in which diets with greater forage content were fed. Unlike the present model that include a correction for NDF, the Fernández (2018) model did not include any correction for dietary fiber.

Thus, Fernández (2018) designed a model to investigate the shape of change in CH_4 emission over time (h) with a constant decline in food from the stock over time. Also, it was possible to obtain the amount of energy accumulated in the pool milk after 24 h. The present model had a daily entrance of food (this flux represents the action of feeding, not a stock of food) and integrated the daily flux of energy in milk, the heat lost and assessed the environmental impact (predicting daily CH_4 emission), when variation in DMI, EE and NDF took place in the diet. In agreement with the common understanding that enteric CH_4 production is primarily driven by the amount and composition of feed consumed (Kebreab *et al.*, 2008; Knapp *et al.*, 2014; Hristov *et al.*, 2017; Niu *et al.*, 2018), the present model was a step ahead of the Fernández model (2018).

The study of Blaxter and Clapperton (1965) used more than 2500 determinations of 24-h CH_4 production by indirect calorimetry, and although the linear model obtained included energy digestibility and level of feeding, no goats were included in the model. The last version of Institute Nationale Recherche Agronomique (INRA, 2017) proposed an empirical general linear equation to estimate energy losses in CH_4 based on organic matter intake, BW, level of feeding and dietary concentrate level, and this equation was based mainly on the feeding trials not on indirect calorimetry. The INRA (2017) proposed a general equation for all ruminant species.

The national greenhouse inventory guidelines IPCC (2007) outlined methods for estimating CH_4 emissions from enteric fermentation. The FAO (2010) developed some empirical equations for estimating CH_4 emissions from ruminants as well. Both express CH_4 either as g CH_4/kg DMI 'or as a percentage of GEI (also called Ym factor (IPCC, 2007); the proportion of the GEI which is lost as CH_4). Using IPCC Tier 2 (IPCC 2007) methodology for dairy cattle, a Ym of 6.5% was suggested. With diets consisting primarily of grains, the percentage of GEI that is converted to CH_4 in the rumen is typically less than 4% compared with 6.5%, which is common for animals fed primarily forage (Beauchemin *et al.*, 2009). Kebreab *et al.* (2008), using a mechanistic model (COWPOLL) for dairy cows, reported a lower value for CH_4 emissions (5.6% of GE, on average) than IPCC (2007). Merino *et al.* (2011) reported that Ym ranged from 4% to 7% in dairy ewes. The Ym value in goats at mid-lactation from the studies mentioned above (Bava *et al.*, 2001; Tovar-Luna *et al.*, 2010) ranged from 3.9% to 5%. The average Ym obtained for model development in goats by Patra and Lalhriatpuii (2016) was 5.25%. The Ym value obtained in our goat mathematical simulation model was 4.5%, which is lower than the IPCC (2007) recommendation. It appears that CH_4 production is lower in goats than cattle, and we speculate that it might be due to faster passage rate of feeds in goats and consequently lower CH_4 production per unit of feed intake.

To summarize, CH_4 emissions are strongly related to feed intake, fiber and dietary lipid, and all may help quantify and mitigate CH_4 emissions. However, CH_4 production in the rumen also depends upon other dietary factors, rumen function, microbiota profiles and fermentation dynamics. Thus, it may not follow a linear trend over a wide range of values. Niu *et al.* (2018) collated an intercontinental (Europe, the USA and Australia) database in dairy cattle where a sequential approach was taken by incrementally adding key variables to develop models with increasing complexity; information on DMI, NDF, milk yield and composition is required for better estimation.

More studies in dairy goats, including other ingredients and different chemical composition of diets to predict CH_4 emissions, are needed. The energy model in the present study combines both, diet characteristics and goat energy partitioning, allowing to attain other outputs besides CH_4 emissions such as energy transfers to milk, energy waste in feces and urine and the loss of energy from daily performance. The model described in this study should be considered a suitable option for preparation of enteric CH_4 emission inventories for goats.

Conclusions

A dynamic energy-partitioning model to predict CH_4 production in goats and the energy transferred to milk and lost as heat was developed and evaluated. The goat model was setup to simulate indoor facilities in which goats are fed mixed rations. Integration of information generated from other experiments and literature into the simulation model will contribute to a more dynamic understanding of the energy transfers and conversions in this system.

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Declaration of interest

The authors have no conflict of interest to report

Ethics statement

The experimental procedures carried out were approved by the Committee on Animal Use and Care at the Universitat Politècnica de Valencia (Spain) (2017/VSC/PEA/00182). Animals were cared for by trained personnel and managed in accordance with the Spanish guidelines for experimental animal protection (Royal Decree No. 1201 2005) and the European Convention for the Protection of Vertebrates used for Experimental and other Scientific Purposes (European Directive 86/609).

Software and data repository resources

None of the data were deposited in an official repository.

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.1017/S1751731120001470

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