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1 **Evaluation of the performance of existing mathematical models predicting enteric** 2 **methane emissions from ruminants: animal categories and dietary mitigation strategies**

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Abstract

 The objective of this study was to evaluate the performance of existing models predicting enteric methane (CH4) emissions, using a large database (3183 individual data from 103 *in vivo* studies on dairy and beef cattle, sheep and goats fed diets from different countries). The impacts of dietary strategies to reduce CH⁴ emissions, and of diet quality (described by organic matter digestibility (dOM) and neutral-detergent fiber digestibility (dNDF)) on model performance were assessed by animal category. The models were first assessed based on the root mean square prediction error (RMSPE) to standard deviation of observed values ratio (RSR) to account for differences in data between models and then on the RMSPE. For dairy cattle, the CH⁴ (g/d) predicting model based on feeding level (dry matter intake (DMI)/body weight (BW)), energy digestibility (dGE) and ether extract (EE) had the smallest RSR (0.66) for all diets, as 39 well as for the high-EE diets ($RSR = 0.73$). For mitigation strategies based on lowering NDF or improving dOM, the same model (RSR = 0.48 to 0.60) and the model using DMI and neutral- and acid-detergent fiber intakes (RSR = 0.53) had the smallest RSR, respectively. For diets with high starch (STA), the model based on nitrogen, ADF and STA intake presented the smallest RSR (0.84). For beef cattle, all evaluated models performed moderately compared with the models of dairy cattle. The smallest RSR (0.83) was obtained using variables of energy intake, BW, forage content and dietary fat, and also for the high-EE and the low-NDF diets (RSR = 0.84 to 0.86). The IPCC Tier 2 models performed better when dietary STA, dOM or dNDF were high. For sheep and goats, the smallest RSR was observed from a model for sheep based 48 on dGE intake ($RSR = 0.61$). Both IPCC models had low predictive ability when dietary EE, NDF, dOM and dNDF varied (RSR = 0.57 to 1.31 in dairy, and 0.65 to 1.24 in beef cattle). The performance of models depends mostly on explanatory variables and not on the type of data

 (individual vs. treatment means) used in their development or evaluation. Some empirical models give satisfactory prediction error compared with the error associated with measurement methods. For better prediction, models should include feed intake, digestibility and additional information on dietary concentrations of EE and structural and nonstructural carbohydrates to account for different dietary mitigating strategies.

Keywords

Model evaluation; methane emission; ruminant; dietary strategy

Abbreviations

 ADF, acid-detergent fiber; ADFI, ADF intake; AU, Australia; BW, body weight; CCC, concordance correlation coefficient; CH4, enteric methane; CV, coefficient of variation; dGE, digestibility of GE; DM, dry matter; DMI, DM intake; dNDF, digestibility of neutral-detergent fiber; dOM, digestibility of organic matter; ECT, error in central tendency; ED, error due to the disturbance; EE, ether extract; ER, error due to the regression; EUR, Europe; FA, fatty acids; FPCM, fat and protein corrected milk; GE, gross energy; GEI, GE intake; GHG, greenhouse gas; IPCC, Intergovernmental Panel on Climate Change; MSPE, mean square prediction error; NDF, neutral-detergent fiber; NDFI, NDF intake; OM, organic matter; RMSPE, root MSPE; 67 RSR, RMSPE to standard deviation of observed values ratio; SF_6 , Sulphur hexafluoride tracer; STA, starch; US, United States of America; Ym, percentage of GE converted into CH4;

1. Introduction

 Accurate estimation of enteric methane (CH4) emissions from ruminants is important for national greenhouse gas (GHG) inventories and for assessing dietary mitigating strategies. In many countries, the IPCC (2006) Tier 1 or Tier 2 methodologies are used to report their national inventories of GHG emissions. The IPCC Tier 2 model, although more detailed than Tier 1, 74 relies on gross energy intake (GEI) which can lead to inaccuracy in predicting CH_4 emissions for diets of different nutrient composition (Ellis et al., 2010). The determination of CH⁴ emissions from individual animals requires specialized equipment (Hammond et al., 2016) and expensive methodologies (Kebreab et al., 2006). Many empirical models have been developed for specific ruminant categories to estimate CH⁴ emissions from dairy cattle (Charmley et al., 2016; Niu et al., 2018), beef cattle (Ellis et al., 2009; Cottle and Eckard, 2018) and small ruminants (Patra et al., 2016; Patra and Lalhriatpuii, 2016) or for all ruminants (Blaxter and Clapperton, 1965; IPCC, 1997 and 2006; Sauvant et al., 2011; Ramin and Huhtanen, 2013).

 Most prediction models are based on feed intake (dry matter intake (DMI) or GEI). However, these models do not adequately account for the effect of other dietary factors such as lipid supplementation (Bannink et al., 2006), neutral detergent fiber (NDF) content, organic matter digestibility (dOM) (Archimède et al., 2011; Appuhamy et al., 2016), content of starch (STA) and sugars (Hindrichsen et al., 2005) and the presence of plant secondary compounds (Jayanegara et al., 2012). Consequently, alternative models that take into account feed properties and animal characteristics to improve prediction of CH⁴ emissions under different nutritional mitigation strategies have been proposed. Some models can be applied across all ruminant categories (Blaxter and Clapperton, 1965; IPCC, 2006; Ramin and Huhtanen, 2013; Bell et al., 2016) whereas others are specific to one ruminant category (Charmley et al., 2016; Escobar-Bahamondes et al., 2017a; Cottle and Eckard, 2018).

 There is global interest in the use of nutrition and feeding management to decrease CH⁴ emissions from ruminants (Knapp et al., 2014). Consequently, if the national inventory calculations are based on empirical models, these should be assessed for their reliability under different nutritional mitigation strategies and different production conditions. The objectives of this study were to evaluate the performance of existing models using a large database of individual records for specific 1) ruminant categories (dairy cattle, beef cattle, sheep or goats) and 2) nutritional strategies that mitigate CH⁴ emissions (lipid and STA supplementation, low NDF content in the diet, or enhanced diet digestibility).

2. Materials and methods

2.1. Database

 A database of 3183 individual observations from the GLOBAL NETWORK project (https://globalresearchalliance.org/research/livestock/collaborative-activities/global-research- project/) was used to evaluate the performance of models that predict CH⁴ emissions from ruminants. This individual database (Table 1) included 103 studies from three regions: Europe

 (EUR; 2707 observations from 92 studies), United States of America (US; 198 observations from 5 studies) and Australia (AU; 278 observations from 6 studies). Enteric CH⁴ emissions

109 included in the present database were measured using respiration chambers (65% of data), $SF₆$

tracer technique (30%) and automated head chamber (GreenFeed™, C-Lock Inc., Rapid City,

 SD, US; 5%), on different animal categories (dairy cattle, 67%; beef cattle, 18%; sheep, 13%; goat, 2%), using various experimental designs (randomized block design (average adaptation duration 47 days), latin square design (average adaptation duration 19 days), change-over or

switch-back design (average adaptation duration 15 days)).

Data pre-processing

 Data pre-processing was performed, because the collected data were sometimes incomplete (missing values or variables of interest), inconsistent (different names or units for the same variable) and noisy (containing errors or outliers). We corrected the inconsistent data by using the same name and unit across all studies. Outliers in the database were screened as described by Niu et al. (2018). No data on gross energy content and chemical composition of the diets were available for the AU dairy cattle data. All data on dietary composition for beef cattle, sheep and goat subsets were from EUR. Finally, the dietary treatments were classified according to the purpose of each study into four CH⁴ mitigation strategies (A to D), as classified by Martin et al., (2010) and Hristov et al., (2013). These were: (A) lipid supplementation (EE content of the diet); (B) low fiber content in the diet (NDF content of the diet); (C) high STA content in the diet, and (D) high-quality diet (in terms of dOM and dNDF).

2.2. Selection of Models

 To select the models, we used web search online databases (Science Direct, Web of Science) for articles written in English and published from 2000 to 2017 using the following key words: "methane", "*in vivo*", "prediction", "model" (or "equation") and "ruminant" (or "cattle" or "dairy" or "beef" or "sheep" or "goat"). Only models with predictor variables or required information that were available in our database were selected (Table 2). Therefore, due to the lack of information, the models of CH⁴ emissions from ruminants fed plants rich of secondary compounds were not evaluated. Some models were specific to one ruminant category (e.g., Charmley et al. (2016)), whereas others were applicable to more than one category. In addition to the IPCC models, the models from Sauvant et al. (2011) were evaluated with data from all ruminant categories. The models from Ramin and Huhtanen (2013) were evaluated with dairy and beef cattle and sheep. The models containing variables associated with dietary lipid content were used to evaluate their predictive ability for lipid supplementation mitigation strategy. The models that take into account dietary NDF, dOM or dNDF were used to evaluate their ability 141 to predict CH₄ when ruminants are fed a high-quality diet (Low NDF content or high dOM and dNDF). The models that use STA content or dietary concentrate content as variables, were 143 tested for their predictive ability when a large level of STA was used to reduce CH₄ emissions. The published models were grouped based on the region of data origin (EUR, US or AU) and the type of data used in their development (individual data or treatment means). All models were used in their original version except one model from Nielsen et al. (2013) based on DMI, EE and NDF contents, where we used the modified version of Appuhamy et al. (2016). Some models are based on fatty acids (FA) instead of ether extract content, so the total FA content in the diet was estimated using the adapted model of Giger-Reverdin et al. (2003):

150 %FA/EE = $100 - (32 - 5.86 \times EE + 0.261 \times EE^2 + 0.287 \times forage)$

The unit of EE and forage proportion used in this equation is % DM.

The CH⁴ unit used in the present evaluation is g/d; hence, when original equations used MJ/d,

a conversion factor (55.65 kJ per g of CH4; Brouwer 1965) was used. When the equation was

154 reported in L/d, it was converted to g/d using the molar density of CH₄ (0.714 g/L).

Choices of data for model evaluation

 Before model evaluation, data were checked to ensure there was no overlap between model development and validation sets. Consequently, data originally used in model development by the respective groups of researchers were excluded before evaluation of that particular model. For example, the 154 observations used by Charmley et al. (2016) to develop their models were removed before evaluating the performance of models from Charmley et al. (2016). For the same reason, the models developed by Niu et al. (2018) were not tested, as these models were derived from a large share of the database used in the present evaluation.

 Next, we selected the data based on each model's specifications with respect to ruminant category and CH⁴ mitigation strategy. For instance, ruminant category-specific models were evaluated only using the data from the respective ruminant category, whereas generic models were evaluated first using the data from each ruminant category separately and then using the data of all ruminant categories.

 The evaluation of models by CH⁴ mitigation strategies was carried out within each ruminant category (dairy cattle, beef cattle, sheep and goats). Using the dietary content of EE, NDF and 170 STA values, the database was separated into two subsets for each strategy to assess, respectively, the mitigation strategies of lipid supplementation, enhancement of diet quality by lowering dietary fiber and the use of the high-STA diets. In addition, the performance of models was assessed by variation in the diet quality (variations in dOM and in dNDF). The separation into two subsets for lipid supplementation was set by mean of EE content. For the mitigation strategy

 based on the use of STA, the two subsets were obtained from subtracting the standard deviation from the mean of STA content. For NDF content in dairy cattle diets, the fixed threshold of 350 g/kg DM was used, due to the non-normal distribution of NDF data for this animal category. Consequently, given the distribution of data the resulting thresholds were 39.3 g of EE/kg DM, 350 g of NDF/kg DM, and 101 g of STA/kg DM, for dairy cattle and 40 g of EE/kg DM, 338 g of NDF/kg DM and 110 g of STA/kg DM for beef cattle. Within each strategy, the datasets obtained were then qualified as low or high when dietary contents were lower or higher than those thresholds, respectively. The existing models were originally developed from either individual animal or treatment mean datasets. To test the effect of data type (individual vs. means) on the performance of models, our individual database was transformed into a "means" database by obtaining arithmetic means of the individual observations within the same treatment and within each experiment. Four individual and four mean models with the smallest RSR predicting CH4 emissions from dairy cattle were evaluated using individual and mean databases.

2.3. Criteria for model evaluation

 The CH⁴ prediction models were evaluated using the following criteria. The prediction model associated with the lowest root mean square prediction error (RMSPE) to standard deviation of observed values ratio (RSR) and the lowest RMSPE is considered the best performing:

Mean Square Prediction Error

 The mean square prediction error (MSPE) was calculated according to Bibby and Toutenburg (1977):

196
$$
MSPE = \frac{1}{n} \sum_{i=1}^{n} (O_i - P_i)^2
$$

197 Where n is the number of observations, $\mathbf{0}_i$ is the ith observed value and \mathbf{P}_i is the ith predicted 198 value. Usually, square root of the MSPE (RMSPE) is used to evaluate model prediction because 199 it has the same unit as the observed values:

$$
RMSPE = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (O_i - P_i)^2}
$$

201 In the present research, RMSPE was also expressed as a percentage of mean observed CH⁴ 202 emissions in order to compare models developed for different ruminant categories or CH⁴ 203 mitigation strategies:

204
$$
RMSPE\% = \frac{\frac{1}{n}\sqrt{\sum_{i=1}^{n}(O_i - P_i)^2}}{\frac{1}{n}\sum_{i=1}^{n}O_i} \times 100
$$

205

 A smaller value of RMSPE and RMSPE% indicates better performance of model prediction. The MSPE value is determined by three types of error: error in central tendency (ECT: measure of precision) or mean bias, error due the regression (ER; measure of accuracy) or slope bias, and error due to the disturbance (ED) or random error (Bibby and Toutenburg, 1977). These terms were calculated as:

$$
ECT = (\bar{P} - \bar{O})^2
$$

$$
ER = (S_p - r \times S_o)^2
$$

$$
ED = (1 - r^2) \times S_o^2
$$

214 Where \bar{P} and \bar{O} are the predicted and observed mean values, S_p is the SD of predicted values,

215 S_o is the SD of observed values, and *r* is the Pearson correlation coefficient.

216 *Concordance Correlation Coefficient*

- 217 The concordance correlation coefficient (CCC; Lin, 1989) was calculated as the product of *r*
- 218 and a bias correction factor (C_b) , measure of accuracy):

220 where C_b indicates how far the best fit line deviates from the concordance or unity line of the 221 observed values versus predicted values plot. The C_b ranges from 0 to 1 with greater values indicating less deviation from the concordance line. Large value of CCC indicates better performance of model prediction.

RMSPE to standard deviation of observed values ratio (RSR)

When different data are used to compare the performance of models, the ratio of RMSPE and

SD, should be used because it takes into account the data variability (Moriasi et al., 2007).

 $PSR = RMSPE/SD$ of observed values of CH₄

 In this study, the performance of models with different numbers of data was ranked first by RSR and then by RMSPE%.

3. Results

3.1. Descriptive statistics of data

 The descriptive statistics of our database by ruminant category are presented in Table 1. Overall, the database included a wide range in animal body weight, feed intake, diet composition, and CH⁴ emission. The dairy cattle included in the database produced, on average, 389 g of CH4/d 235 (n = 2147), 20.5 g of CH₄/kg DMI (n = 1975) and 14.3 g of CH₄/kg of fat and protein corrected 236 milk (FPCM; $n = 1733$). Enteric CH₄ emissions expressed as a percentage of GEI (Ym) was 6.12%. Only 14.5, 0 and 11.5% of the EUR, US and AU dairy diets were 100% forage-based, respectively. On average, EUR, US and AU dairy cattle were fed diets with 37.4, 48.9 and 37.8 g of EE/kg DM, respectively.

 Beef cattle produced 202 g CH4/d on average and the Ym was 6.99%. The forage proportion was 0.70 of the diet resulting in an average DMI of 8.8 kg/d. Some high-grain diets (concentrate 242 proportion > 0.85) were included (6% of data). Most common ingredients in beef diets were corn, wheat and grass silage (present in 60% of the observations) and cereal straw (32% of the observations). The CH⁴ emissions and Ym value were 19.3 g/d and 5.45% for sheep, and 14.2 245 g/d and 4.20% for goats, respectively. The average proportion of forage in the diet was 0.76 for sheep and 0.36 for goats. The contents of EE, NDF and dOM in diets for sheep and goats were 31 vs. 29 g/kg DM, 504 vs. 380 g/kg DM and 645 vs. 757g/kg DM, respectively.

3.2. Performance of the models

3.2.1. Dairy Cattle

 Of the 40 existing equations evaluated using the dairy cattle data, only the 11 models with the 251 smallest RSR (RSR \leq 1) as well as the IPCC 1997 and IPCC 2006 Tier 2 models (used as reference) are listed in Table 3. Overall, equations based on feed intake (DMI, GEI and feeding level (DMI/BW)) had the smallest RSR of predicting CH⁴ emissions from dairy cattle. All models revealed a positive relationship between feed intake and daily CH⁴ emissions. Two models (Ramin_1 and Ramin_2) from Ramin and Huhtanen (2013) had low RSR (0.66 and 0.76, respectively) and RMSPE% (15.6 and 21.2%), and more than 90% of the prediction error due to random error. These two models also showed small mean bias (0.70 and 6.30%, respectively) with CCC values of 0.75 and 0.57, for Ramin_1 and Ramin_2 respectively. Mills_3, a nonlinear equation from Mills et al. (2003; see Table 2), resulted in the third ranked RSR (0.78), and in 21.8% of RMSPE%. A similar result was obtained by IPCC_1997, which 261 had the fourth ranked RSR (0.79) and the CCC value of 0.68. The mean bias obtained from the 262 prediction of IPCC 1997 was 0.10%, which was smaller than the mean bias observed in Mills $\overline{3}$ (11.7%), but the slope bias was greater (12.8 vs. 1.5%, respectively). Ellis et al. (2007) proposed models with different levels of complexity for dairy cattle and one of those models (Ellis_3), 265 presented the fifth ranked RSR (RSR = 0.80 , RMSPE% = 22.7% and CCC = 0.60). Decomposition of the error indicated an 11.5% mean bias. This model included DMI, NDF intake (NDFI) and acid detergent fiber intake (ADFI) and had smaller RSR than the three simple models that only included one of the three predictors (models not shown in Table 3; RSR of Ellis_3 vs. Ellis_1, Ellis_2 and Ellis_4 was 0.80 vs. 0.87, 1.06 and 1.28, respectively). In addition, Ellis' simple models produced a larger mean bias than the complex model. The models of Charmley et al. (2016) for dairy cattle based on GEI or DMI produced similar RSR (0.81), which was similar to the RSR produced by IPCC_1997. The decomposition of RMSPE made by the models of Charmley et al. (2016) showed that at least 81.0% of the error was due to 274 random effects. The linear models by Mills et al. (2003; Mills_2 and Mills_1) had the 9th and $10th$ ranked RSR and CCC values of 0.62 and 0.68, respectively. The Mills 2 model was associated with the second smallest RMSPE% (17.8%) among all models, however it was 277 ranked 9th considering its greater RSR, due to the small variability of observed CH₄ values. The 278 11th and 12th ranked models in Table 3 are complex models from Ramin and Huhtanen (2013) and Sauvant et al. (2011). They represent the only models including dOM in the diet. The updated Tier 2 model of IPCC (IPCC_2006) relating GEI and CH⁴ outputs was the last ranked model with a RSR of 0.87.

 The two subsets of low- and high-EE (under and over 39.3 g of EE/kg DM, respectively) diets in the dairy cow data were created to enable assessment of the ability of the models to predict difference in emissions caused by differences in concentrations of dietary lipids. These two data subsets had mean dietary EE contents of 30.4 vs. 51.7 g/kg DM, respectively, and mean CH⁴ yields and intensities of 20.9 vs. 18.8 g/kg DMI, and 15.7 vs. 12.4 g/ kg of milk, respectively (see Appendix A). A numerical difference in Ym was also observed (6.42 vs. 5.68%, for the low- vs. the high-EE subsets, respectively). Models that specifically included lipid content as one of the variables showed the smallest RSR and RMSPE among all models tested with the high-EE subset (Figure 1). The models Ramin_1 and Ramin_3 maintained their RSR and 291 RMSPE% (RSR = 0.73 and 0.83, respectively, and RMSPE% = 16.1 and 20.3%, respectively) in the high-EE diets compared with their RSR and RMSPE% using all dairy diets, whereas the RSR of IPCC_1997 increased from 0.79 to 1.05. The Moraes model showed large RSR (0.95), with considerable mean bias (27.8%). All models gave larger CCC values using all dairy diets than when only the high-EE diets were used.

 The subsets of low-NDF and high-NDF diets (under and over 350 g NDF/kg DM, respectively) of dairy cattle had mean NDF contents of 285 and 433 g/kg DM, respectively (Appendix B). 298 Other factors varied between the low- and the high-NDF subsets as CH₄ emissions (405 vs. 385) g/d), CH⁴ yield (18.6 vs. 22.5 g/kg DMI), CH⁴ intensity (12.9 vs. 16.2 g/kg of milk), Ym (5.64 vs. 6.79%), DMI (22.2 vs. 17.4 kg/d) and GEI (409 vs. 331 MJ/d), respectively. Using the low- NDF subset, Ramin_1 resulted in RSR of 0.48, RMSPE% of 10.1% and a CCC of 0.88. Using the high-NDF subset, Ellis_3 had the smallest RSR (0.54) and RMSPE% (17.6%) (Figure 2). Based on the obtained RSR and RMSPE%, the IPCC Tier 2 models performed better with the high-NDF (RSR = 0.68 and 0.57, RMSPE% = 16.9 and 14.3%, for IPCC_1997 and IPCC_2006, 305 respectively) than with the low-NDF diets $(RSR = 1.06$ and 1.31 , $RMSPE\% = 23.7$ and 29.2% . for IPCC_1997 and IPCC_2006, respectively). The existing models, except Ramin_1, had smaller RSR at high NDF level in the diet (from 0.54 to 0.63) than at low NDF level (RSR > 0.95).

 The two subsets representing low- and high-STA diets (under and over 101 g of STA/kg DM) for dairy cattle are presented in Appendix C. The low- and the high-STA diets had average STA concentrations of 56 and 215 g/kg DM of STA respectively. The CH⁴ emissions, yields and intensities in the low- and the high-STA subsets were 364 vs. 415 g/d, 22.7 vs. 20.4 g/kg DMI and 17.1 vs.14.1 g/kg of milk, respectively. The feed intakes (on DM basis) in the low- and the high-STA subsets were 16.1 vs. 20.8 kg/d and the Ym values were 6.73 vs. 6.17%, respectively. In general, all models had smaller RMSPE% for the low-STA diets (RMSPE%: 11.9 to 16.4%) than for the high-STA diets (RMSPE%: 18.2 to 26.1%). However, the RMSPE decomposition revealed greater mean bias and smaller slope bias in the low- than the high-STA subsets (Figure 3). The ranking of models did not change between the low- and the high-STA subsets with the exception of IPCC_2006, which had the smallest RSR (0.80) for the low-STA diets but the greatest RSR (1.04) for the high-STA diets.

 The two subsets representing the low- and the high-quality diets using either dOM (under and over 720 g/kg DM, respectively) or dNDF (under and over 600 g/kg DM) are described in 323 Appendices D and E, respectively. At the low- and the high-dOM (mean: 679 and 767 g/kg DM, respectively), Ellis_3 and Ramin_1 models had the smallest RSR and the greatest CCC for predicting CH⁴ emissions from dairy cattle (Figure 4; Table 4). At the low dNDF, the same two models showed small RSR and RMSPE%, and greatest CCC (RSR = 0.67 and 0.78, RMSPE% $327 = 19.9$ and 16.7% , $CCC = 0.71$ and 0.70, respectively). Ramin 1 had a smaller RMSPE% compared with Ellis_3, but the adjustment of the RMSPE by the SD of observed values of CH⁴ made Ellis_3 the highest ranked model. The evaluated models in both subsets (the low- and the high-dNDF diets) generally showed acceptable RSR and RMSPE% and were more accurate for the high-dNDF diets. All RSR obtained from the high-dNDF subset were smaller than those obtained from the low-dNDF subset. The RSMPE% obtained by the best five models in the high-dNDF subset had a small range (13.3 to 18.4%). Ellis_3 showed good predictive ability in both subsets considering its small RSR (0.67 and 0.59 in the low- and the high-dNDF subsets, respectively), RMSPE% < 20% and almost null mean and slope biases (Figure 5). Ramin_3 gave the smallest RSR for the high-dNDF subset, resulting in similar RSR with Ellis_3 (0.59) but smaller RMSPE%. Mills_2 had 13.5% of RMSPE% and the third smallest RSR although it had a 24.6% mean bias. The IPCC_2006 was associated with the fourth RSR for the high-dNDF diets.

3.2.2. Beef cattle

 For beef cattle, 21 models were evaluated using the beef cattle data. Table 5 presents the 10 342 models with the smallest RSR ($RSR \leq 1$) to predict CH₄ emissions from beef cattle. The model from Escobar-Bahamondes et al. (2017a) resulted in the smallest RSR (0.83) and RMSPE%

 (27.2%) among all models, with 93.6% of the RMSPE due to random errors and CCC value of 0.40. Among the feed intake-based models, Ramin_2, Yan_1, Yan_2 and IPCC_2006 had similar results. The RSR of these models ranged from 0.84 to 0.87 and RMSPE% from 32.7 to 34.0%. The remaining models presented in Table 5 had low predictive ability considering the 348 large RMSPE% ($>$ 33%) and the large mean bias (from 17.5 to 22.1%).

 The descriptions of the low- and the high-EE subsets (under and over 40 g of EE/kg DM, respectively) of beef cattle are shown in Appendix F. The average of EE content in each subset was 25.3 and 58.4 g/kg DM, respectively. The emissions and yields of CH⁴ in the low- and the high-EE diets were 252 vs. 188 g/d, and 26.9 vs. 23.4, respectively. When models were evaluated using each subset separately (Table 6), the ranking was the same, with the Escobar- Bahamondes et al. (2017a) model having the smallest RSR followed by the models of Grainger and Beauchemin (2011), IPCC_2006 and IPCC_1997. The RSR values of all models were slightly smaller at the low- than at the high-EE diets. Large prediction errors were observed for all models at high EE content (RMSPE% > 33%). The predictions by Tier 2 models of IPCC are associated with large RMSPE% (from 33 to 37%) and large mean biases (from 31 to 45%) in the high-EE subset. The CCC of all predicting models were smaller for the high-EE than for the low-EE diets. Similar to lipid supplementation strategy, the models were evaluated when low- or high-NDF diets were fed to beef cattle (under and over 338 g of NDF/kg DM, respectively). In both the low- and the high-NDF diets (Appendix G), again the Escobar- Bahamondes et al. (2017a) model showed the smallest RSR in the prediction of CH⁴ emissions from beef cattle. The RSR of this model was slightly smaller at high NDF than at low NDF content (0.84 vs. 0.86, respectively). The IPCC_2006 and IPCC_1997 models were associated with large RSR (from 0.88 to 0.98), RMSPE% (from 31 to 40.5%) and mean biases from 3.1 367 to 31.6%. When differences in dietary STA were taken into account (threshold $= 110$ g of STA/kg DM; see Appendix H), the IPCC models presented the smallest RSR among all models, 369 although their prediction of CH₄ emissions was associated with large RSR (> 1) and RMSPE% $370 \leq 32\%$; and small CCC (0.38). Diet composition and CH₄ emissions in each data subset of the low- and the high-dOM or dNDF (under and over 745 and 600 g/kg DM, for dOM and dNDF respectively) for the beef data are shown in Appendices I and J, respectively. The smallest RSR was obtained by Ellis_5 model at the low-dOM and by IPCC_1997 at the high-dOM diets (RSR $374 = 0.71$. However, using dNDF as an indicator of diet quality, the smallest RSR was obtained by IPCC_2006 with both, the low- and the high-dNDF diets (Table 6).

3.2.3. Small ruminants

 The six evaluated models with RSR < 1 using sheep data, ranked by RSR, are shown in Table 7. The Patra_3 model had the smallest RSR (0.61) with the RMSPE% being 19.2%, most of which was due to random sources. The correlation coefficient (*r*) between observed and predicted values by Patra_3 was 0.81, resulting in the largest CCC (0.75) in Table 7. The 381 IPCC_1997 and Patra_2 models were both based on GEI and were ranked $2nd$ and $3rd$, respectively. The RSR and RMSPE% obtained from IPCC_1997 and Patra_2 were similar (0.77 vs. 0.78; RMSPE% = 26.8 and 27.2%, respectively). In comparison to the IPCC_1997 and Patra_2 models, the other models were all associated with greater RSR (0.85 on average) and greater RMSPE% (around 30%). IPCC_1997 had greater precision and accuracy in predicting CH⁴ than IPCC_2006.

 The evaluated models were less accurate at predicting CH⁴ emissions for goats than they were for sheep (Table 8). Three models from Patra and Lalhriatpuii (2016) resulted in large RSR (from 0.86 to 0.98) and large RMSPE% (from 38 to 43%). The model from FAO reports (2010) based on digestibility of dry matter was associated with a large RSR (1.22) and RMSPE% (65.4%).

3.2.4. Individual animal data vs. treatment means models

 Results of the comparison between models developed from individual records or treatment means are shown in Table 9. The four models with the smallest RSR values based on individual records in dairy cattle (all diets) were IPCC_1997, Charmley_2, Charmley_1, and IPCC_2006, and the four models with the smallest RSR values based on treatment mean records were Ramin_1, Ramin_2, Ellis_3, and Sauvant_1. The range in values of RSMPE% for individual record models was smaller than that for mean record models (21.2 to 23.4% vs. 15.6 to 27.4%, respectively). When both types of models (individual and treatment means) were evaluated using the 'treatment means' database, the RMPSE% of individual and means models varied from 16.9 to 18.7% and from 13.7 to 20.2%, respectively. Moreover, the values of RMSPE% for each individual record and mean record model were decreased when evaluated using the mean database compared with when evaluated using the individual database.

 The SD of the observed values of CH⁴ emissions in the 'treatment means' database was smaller than that determined in the individual record database. In general, the ranking of the means models was higher than that of individual record models when evaluated either by the individual or 'treatment means' databases.

4. Discussion

 In the current research, we aimed to identify the models that had the smallest prediction error of CH⁴ emissions and fitted our data, based on the smallest RSR and RMSPE%. We evaluated a large number of published models to estimate CH⁴ emissions for different ruminant categories under diverse dietary regimes. The database generated by the GLOBAL NETWORK project comprised > 3000 individual data from 103 studies and is the largest ever used in such model evaluation. Previous studies have evaluated models for a single ruminant category (e.g., either dairy cattle, beef cattle or feedlot cattle; Kebreab et al., 2008; Ellis et al., 2010; Escobar- Bahamondes et al., 2017b) or models based on regional data obtained from the scientific literature and based on treatment means (Appuhamy et al., 2016). This is the first evaluation of models using a large database based on data from individual animals of all major livestock species and breeds and the data were from experiments that have been conducted in various countries in which diverse nutritional strategies to mitigate CH⁴ emissions have been tested. The domain of application of each model has been respected and the performance obtained reflects the goodness of fit between the CH⁴ predictions and CH⁴ observed values in our database. It should be pointed out that some dietary variables used by the evaluated model were not measured in all included studies, therefore the models were evaluated against different numbers of observations. In this study, we present the results of evaluations using maximal data for each model and chose the statistical parameter "RSR" to compare models evaluated using different datasets.

 Some of the selected models are specific to certain ruminant categories, whereas others are developed to estimate CH⁴ emissions in different ruminant categories (IPCC, 1997 and 2006; Sauvant et al,. 2011; Ramin and Huhtanen, 2013). At the moment, although the IPCC Tier 2 models are primarily used to provide estimates of CH⁴ emissions in national inventories of CH⁴ emissions, their adequacy for dairy cattle (Appuhamy et al., 2016; Niu et al., 2018), as well as for feedlot and beef cattle (Kebreab et al., 2008), and for small ruminants (Patra et al., 2016; Patra and Lalhriatpuii, 2016) has been debated. In this research, we have compared the accuracy of the IPCC Tier 2 models with those of other models from the scientific literature using data for different nutritional strategies for CH⁴ mitigation, as well as different ruminant categories.

4.1. Dairy cattle

 The smallest error of prediction of CH⁴ emissions from dairy cattle (by the smallest RSR and RMSPE%) were obtained from the models developed in Ramin and Huhtanen (2013), Mills et al. (2003), IPCC (1997) and Charmley et al. (2016). In general, they all use feed intake (DMI, GEI or feeding level (DMI/BW)) as a predictor variable. This is in agreement with feed intake being the key factor driving CH⁴ emissions (Reynolds et al., 2011; Hristov et al., 2013; Niu et al., 2018). Moreover, the DMI can explain at least 70% of variation in CH⁴ emissions from cattle (Ricci et al., 2013) through a positive linear relationship between DMI and the daily CH⁴ 445 emissions rate (g/d), using the slope to reflect the changes in CH₄ with DMI or the CH₄ yield (g CH4/kg DMI) with or without intercept (Dijkstra et al., 2011; Charmley et al., 2016). However, Ramin_2 and Mills_3 performed better than other DMI-based models since it included a curvilinear effect of DMI at large feed intake (Figure 6). The curvilinear effect may be due to the high passage rate of solid matter out of the rumen (Knapp et al., 2014) and the effect of a high proportion of concentrate which are hallmarks of diets associated with large feed intake (Rotz et al., 2011). These two models also captured the effect of the shift in fermentation pattern from more acetogenic to more propiogenic at increased DMI (Robinson et al., 1986), especially for diets containing a large fraction of rapidly fermentable carbohydrates by the indirect effect of pH on volatile fatty acids (Bannink et al., 2008). Janssen (2010) 455 discussed the negative effect of a large concentration of dissolved H_2 in the rumen on the CH₄ formation, especially in animals having a large intake of readily fermentable feed. However, Ramin_2 resulted in smaller CCC than Mills_3 due to its under-prediction of CH⁴ emissions when emissions are greater than 600 g/d.

 The overall smallest RSR and RMSPE, and the largest CCC and r were obtained from the prediction made by the model Ramin_1. This performance can be explained by the inclusion of three factors that affect ruminal CH⁴ production: the feeding level (DMI/BW), energy digestibility (dGE) and dietary lipid (EE) content. The importance of dGE as a key factor to estimate CH⁴ emissions has been long known (Blaxter and Clapperton, 1965). Other studies have suggested that the use of dOM instead of energy digestibility to better predict CH⁴ emissions from ruminants (Bell et al., 2016) because CH⁴ is produced in the rumen by the fermentation of OM (Sauvant et al., 2011). However, in the present evaluation, two models include dOM (e.g., Ramin_3 and Sauvant_1) as a predictor, but they showed less precision and accuracy than the model of Ramin_1 which is based on dGE.

 In agreement with Niu et al. (2018), the Ym value of 6% of GEI being converted into CH⁴ and introduced in IPCC_1997 model, provided a more accurate prediction for dairy cattle across regions than the Ym of 6.5% introduced in IPCC_2006 model. Kebreab et al. (2008) and Appuhamy et al. (2016) pointed out that the Tier 2 model of the IPCC (2006) could over- estimate CH⁴ emissions in dairy cattle. The average Ym for dairy cattle in our database was 6.12%, which was closer to the IPCC_1997 value. More complex models based on Tier 3 methodology indicate that a Ym value of 6% is more realistic than a 6.5% (Bannink et al., 2011). Both IPCC models are based on GEI only and do not capture the effect of changes in the composition of the diet and therefore show a limited ability to estimate the difference in CH⁴ emissions under different nutritional strategies (Ellis et al., 2010). Also, the present results support this argument when the IPCC models were challenged against data from diets with different concentrations of lipid, STA or digestible DM.

Dietary lipid content

482 The negative effect of high dietary EE concentration on the absolute CH₄ emissions (g/d) did not become apparent from the data analysis because of the concomitantly greater feed intake in the high- than in the low-EE subset (22.7 vs. 18.2 kg of DM/d, respectively). The daily CH⁴ emissions are determined primarily by the amount of feed intake and, for this reason, the effect of lipid supplementation is better assessed based on CH⁴ yield. On this basis, the CH⁴ yield for the low- and the high-EE diets were 20.9 and 18.8 g/kg of DMI. In addition, a numerical effect of EE on Ym was observed, with Ym about 12.5% smaller in the high- than in the low-EE 489 subsets (Ym = 5.68 vs. 6.42%). Moreover, the average of fiber intake (NDF intake, g/d) was larger in the high-EE than in the low-EE subsets, which likely counterbalanced the effect of lipid supplementation. Dietary lipids have been reported to reduce CH⁴ emissions (Beauchemin et al., 2008; Moate et al., 2011). Some authors reported that lipid sources (Knapp et al., 2014) or fatty acids profile (Giger-Reverdin et al., 2003) have an effect as well, but this was not a major source of variation based on the meta-analysis made by Beauchemin et al. (2008). In the current research, the results related to lipid supplementation strategy are in agreement with the results reported by Beauchemin et al. (2008), Martin et al. (2010) and Moate et al. (2011) who showed that the addition of 10 g EE/kg DM led to 5.6% and 3.8% and 3.5% lower CH⁴ yield 498 (g/kg DM), respectively. The negative effect of dietary lipids on daily CH₄ emissions (g/d) was also reported in the meta-analysis of Eugène et al. (2008), where the average EE contents in the low- and the high-EE subsets were 25 and 64 g/kg DM, respectively. However, that effect was due to the lower DMI associated with the high dietary lipid content. The Ramin_1 model includes both DMI and dietary lipid content (EE), and this may explain the small prediction error (RSR and RMSPE %) of Ramin_1 with both the global dairy dataset and with the high- EE subset. Some models from Grainger and Beauchemin (2011) and Nielsen et al. (2013) performed well with the low-EE dataset but not the high-EE dataset. The model by Nielsen et al. (2013) uses total fatty acid content instead of EE content. In the current research we estimated in total fatty acid content from EE content using an equation from Giger-Reverdin et al. (2003), and this may have introduced error and hence lower prediction performance by these models.

 The IPCC_1997 and IPCC_2006 models had small RSR (0.78 and 0.80, respectively), small RMSPE% (17.1 and 17.6%, respectively) and large CCC (0.71) in the low-EE subset but large 512 RSR and RMSPE% and small CCC in the high-EE subset (RSR > 1 , RMSPE% $> 25\%$ and CCC < 0.50). Cows fed the low-EE diets (EE < 39.3 g/kg DM) had a Ym value of 6.42% in our 514 database (n = 685 observations), which is close to the value of 6.5% adopted in IPCC (2006). On the contrary, the Ym of the high-EE diets was 5.68% (n = 490 observations) which is substantially smaller than the value of 6% adopted in the IPCC_1997 model.

Dietary NDF content

 When dairy cattle were fed high-quality diets (assessed by dOM or dNDF) or low-NDF diets, 519 the Ellis 3 model based on DMI, NDFI and ADFI, outperformed Ramin 1 by the smaller RSR, which is based on DMI, dGE and EE. This result indicates the importance of including variables associated with structural carbohydrates if the model is to predict the effect of NDF content on CH⁴ emissions from cattle. However, this effect may not depend only on structural carbohydrate, as it can be often confounded by effects of DMI and the negative effect of dietary lipids on dNDF, and the ratio of structural/non-structural carbohydrates in the diet (Moe and Tyrrell, 1979). Ramin_1 had a particularly good predictive ability for CH⁴ emissions from dairy cattle fed low NDF content diets indicated by a RMSPE of only 10.1% and CCC of 0.88. Both IPCC models predicted CH⁴ emissions for the high-NFD diets better than for the low-NDF diets.

Dietary starch content

 The models were also assessed for predicting CH⁴ emissions from dairy cow diets differing in STA content, which mainly originated from either cereals or silages (corn or barley). To split the database into the low- and the high-STA subsets, we chose to use dietary STA content as a criterion and not the dietary concentrate content. Consequently, STA from the inclusion of cereal in the diet, but also from corn or barley silages, which are largely present in the database, were included. When substantial amounts of STA is fed to dairy cattle, it is more appropriate to include information about feed composition or digestibility in the model as in Mills_2 and Ramin_3 models, next to the feed intake. The Sauvant_1 model contains concentrate proportion in the diet as a variable and its RSR was superior to 1 (not shown in Table 4) in predicting CH⁴ emissions from cattle fed the high-STA diets in the present work. We surmise the proportion of concentrate in the diet is not precise enough to explain variation in CH⁴ emissions, and the prediction models should introduce STA content. In addition, at the same content of STA in the 541 diet, the type of grain fed to dairy cattle has been reported to impact the CH₄ emissions (Moate et al., 2017). However, more studies are required with direct comparisons between types of starch. It is known that information about contents of dietary carbohydrate fractions (cellulose, hemicellulose, lignin, STA and sugars) is useful to predict variation in CH⁴ emissions (Moe and Tyrrell, 1979; Hindrichsen et al., 2005; Ellis et al. 2009). However, because of the unavailability of data on cellulose, hemicellulose, lignin and sugars in our database, these models could not 547 be evaluated. The IPCC 1997 and IPCC 2006 models, based on GEI, resulted in 20 to 22% of RSMPE% for the high-STA diets. This can be explained by the capacity of GEI to capture STA in the diet.

Diet quality

551 Feeding diets of high quality (i.e. digestibility) has been reported to reduce CH₄ intensity (g/kg) of milk) by increasing milk production per cow, diluting the amount of feed required per unit of milk and changing rumen fermentation conditions (Knapp et al., 2014). The quality of diets is partially determined by the cell-wall content and its digestibility (Jung and Allen, 1995). However, at similar dietary NDF content, diet quality can still vary considerably (Broderick et al., 2002), affecting feed intake, animal performance and CH⁴ emissions, yield and intensity. In the present evaluation, diet quality was assessed using dOM and dNDF of the diet. Under the variation of both diet quality factors (dOM and dNDF), Ellis_3 and Ramin_1 showed the smallest RSR. Only one of the two IPCC models had good predictions of CH⁴ emissions with small RSR and RMSPE for the high-quality diets depending on the criterion for diet quality (the IPCC_1997 model for the high-dOM subset and the IPCC_2006 model for the high-dNDF subset). In our database, dOM was affected by NDF, STA and EE contents in the diet. The Ramin_3 model contains predictors that can account for effects associated with diet quality, and it successfully reduced prediction error to 13%. A similar model, but expanded using more 565 parameters related to diet quality (i.e. dNDF), may be useful to better predict CH_4 emission.

 The current research has mostly focused on predictive equations based on major nutrient components in diets. Recently, research has shown that the inclusion of a small amount of 3- nitrooxypropanol in the diet of cattle can result in a substantial, sustained reduction in CH⁴ emissions (Hristov et al. 2015). We consider that if in the near future, 3-nitrooxypropanol is registered for use in ruminants, predictive models that include 3-nitrooxypropanol as a predictor will need to be developed.

4.2.Beef cattle

 Models evaluated in the beef category were associated with considerable prediction error (RMSPE > 34%). This suggests new equations need to be developed for beef cattle. Given that all beef data in our study were from EUR, the effort of developing and updating equations should be focused on including an evaluation for this specific region as well. Furthermore, globally, the largest beef cattle herds are outside Europe and effort should also be directed towards the development of improved predictive equations suited to these regions. The smallest prediction error (considering RSR and RMSPE) with our beef data was obtained using the model from Escobar-Bahamondes et al. (2017a). However, the CCC associated with this model was not the largest among the evaluated models for beef cattle. Originally, the Escobar- Bahamondes et al. (2017a) model was developed using data from both high-forage and high- grain diets and it had a RMSPE% of 12.1% of the observed mean CH⁴ emissions which was much smaller than the RMSPE% of 27.2% obtained in the present evaluation. However, Escobar-Bahamondes et al. (2017a) applied a cross-validation methodology using the same data they used for the model development which may partly explain this observation. The DMI- based model (Ramin_2) was less accurate for beef cattle than for dairy cattle, despite the fact that it was developed from a general database including data from both dairy and beef cattle, as well as sheep.

 Similar to the dairy cattle category, there was not a single model that predicted CH⁴ emissions with small RSR and RMSPE in all nutritional mitigation strategies for beef cattle. The low performance of models tested for the individual nutritional mitigation strategies may be because all beef data were from EUR whereas the models were developed using data from US (Ellis et 594 al., 2007 and 2009; Grainger and Beauchemin, 2011). The CH₄ emissions (g/d) from beef cattle 595 fed diets with high EE content (average $EE = 58.4$ g/kg DM) was 25% smaller than CH₄ 596 emissions from beef cattle fed the low-EE diets (average $EE = 25.3$ g/kg DM). Among all models evaluated for this ruminant category, the model from Escobar-Bahamondes et al. (2017a) achieved the most accurate prediction of CH⁴ emissions from lipid supplemented diets, and diets with different contents of NDF. This is in agreement with the results for dairy cattle where complex models based on feed intake, digestibility and diet composition were also most appropriate to predict CH⁴ emissions under different nutritional conditions. The model of Escobar-Bahamondes et al. (2017a) lacks a variable for digestibility (of energy, OM or NDF), which probably explains its large RSR and RMSPE, and its small CCC compared with the model Ramin_1 for dairy cattle.

4.3. Small ruminants

 Few specific models for small ruminants were found in the scientific literature. In addition to IPCC and global models (Sauvant et al., 2011; Ramin and Huhtanen, 2013), the equations evaluated were obtained from Patra et al. (2016) and Patra and Lalhriatpuii (2016). For sheep, the smallest prediction errors based on the values of RSR and RMSPE were obtained from Patra_3, based on digestible energy intake (DEI, MJ/d). The Patra_3 model was also associated with the largest CCC and largest correlation (r) between observed and predicted values. This is probably because it considered the relationship between energy digestibility and CH⁴ production in the rumen, first reported half a century ago (Blaxter and Clapperton, 1965). For goats, all the evaluated models showed moderate predictions given the RSR > 0.85 and the 615 RMSPE% $> 37\%$ of the mean observed CH₄ emissions. In sheep, IPCC_1997 was better at predicting CH⁴ emissionsthan IPCC_2006. In a meta-analysis, IPCC_2006 was evaluated using sheep data on 98 treatment means and the RMSPE was 23.1% of the mean CH⁴ emissions (Patra 618 et al., 2016). In our evaluation, IPCC 2006 had a slightly larger prediction error (RMSPE = 619 30% , n = 111).

4.4.Impact of the data source of models

 Models from Ramin and Huhtanen (2013) were applicable to different ruminant categories (dairy and beef cattle, and sheep). They performed globally better than some category-specific models such as those from Grainger and Beauchemin (2011), Nielsen et al. (2013) as well as Moraes et al. (2014) in the dairy category. Grainger and Beauchemin (2011) proposed both category-specific (Grainger_3 from cattle) and across categories models to estimate the effect of dietary fat on CH⁴ emissions from ruminants (Grainger_1 and Grainger_2). Similar RSR were observed from across-categories and cattle-specific models when they were evaluated using data from dairy and beef cattle fed lipid supplements. The present study only evaluated models developed since 2000. However, it is acknowledged that the model of Blaxter and Clapperton (1965) which was subsequently corrected by Wilkerson et al. (1995) as well as the model of Moe and Tyrrell (1979) were developed using data from cattle with or without small ruminants and their good predictive abilities have been well documented.

 The use of databases containing either data from individual animals or treatment means in the evaluation might lead to different conclusions about the performance of the same model (Ellis et al., 2010). However, Ellis et al. (2010) used different sources to obtain their two evaluation datasets, one for individual animal data and one for treatment mean data, and the difference in the performance of one model when evaluated against these datasets may be due to the variation in each dataset. Therefore, in the present study the treatment means database was created from the original individual animal database to avoid such bias. The models developed on either individual animal data or treatment means data had smaller RSR when challenged against data from individual animals than when challenged against treatment means data, because of the greater variability or standard deviation of observed CH4 in individual animal data compared with treatment means data (105 vs 74.3 g/d). Models derived from treatment means data had smaller RSR than models derived from individual animal data. This might result from the smoothing out of large individual variation when calculating means. Overall, our study indicates that the performance of models (given by the RSR and RMSPE) does not as much depend on the type of data used for the model development (individual animal records or treatment means records), but essentially on the explanatory variables used in the model.

4.5.Model prediction uncertainties

 Recent work from the GLOBAL NETWORK project (Hristov et al., 2018), reviewed the uncertainties and discrepancies associated with the CH⁴ measurement techniques, expressed as coefficient of variation (CV). A significant CV was associated with all measurement methods 653 for CH₄ yield (g/kg of DMI): 21, 27 and 21% for respiration chambers, SF_6 tracer technique and automated head chamber, respectively. This CV includes different sources of error (Hammond et al., 2016). The range of the prediction errors (RMSPE%) obtained in this study from the empirical models were 15.6 to 23.4% for dairy cattle (all diets), 27.2 to 36.7% for beef cattle (all diets), 19.2 to 32.7% for sheep and 37.7 to 65.4% for goats. The different ranges of prediction error between animal categories can be associated with the different amount of data available for each category. Some evaluated models had smaller prediction error than the uncertainty associated with the measurement techniques (see Tables 3, 5 and 7).

5. Conclusions

 From the empirical CH⁴ prediction models published since 2000, there is no unique model that accurately predicts CH⁴ emissions for all ruminant categories and for all nutritional strategies designed to mitigate CH⁴ emissions. With our database, the IPCC (1997) Tier 2 model generally performed better than the updated IPCC (2006) model for the different ruminant categories and nutritional strategies evaluated in this study. Using our database, both IPCC models performed moderately under different mitigation strategies because they do not account for differences in dietary lipid, NDF and STA contents, and the effects of diet quality (i.e., digestibility). The 669 models of Ramin and Huhtanen (2013) demonstrated a good predictive ability to estimate CH₄ emissions from dairy cattle. The model of Escobar-Bahamondes et al. (2017a) showed good predictive performance when applied to beef cattle fed diets with different contents of EE and NDF. The explanatory factors used in the model have more impact on its performance than the type of data (individual data vs. treatment means) used in the development or in the evaluation. Based on the results from our dataset, some empirical models give satisfactory predictions compared with the error associated with CH⁴ emissions measurement methods. More data and modeling efforts are needed to better predict CH⁴ emissions from beef cattle and small ruminants. For future model development, it is recommended to take into account nutritional strategies designed to mitigate CH⁴ emissions.

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EUR							US						AU		
	Dairy cattle						Dairy cattle						Dairy cattle		
Variables	n	Mean	SD	Min	Max	$\mathbf n$	Mean	SD	Min	Max	$\mathbf n$	Mean	SD	Min	Max
$CH4$ emission	1671	376	106	89.7	711	198	436	111	223	732	278	432	83.0	145	612
$CH4$ yield	1671	20.9	4.18	6.53	41.7	198	16.2	4.27	8.28	32.5	106	23.1	3.46	11.9	30.0
$CH4$ intensity	1441	14.1	4.48	3.22	59.3	198	11.1	3.84	4.68	31.7	94	24.1	7.82	13.0	66.2
Ym	1599	6.28	1.23	2.14	11.3	198	4.91	1.27	2.55	9.79					
BW	1617	619	77.8	365	956	195	652	75.1	487	863	158	577	64.7	416	906
FPCM	1441	29.3	8.39	7.69	537	198	41.1	8.19	13.6	69.9	94	18.5	5.10	5.69	30.4
DMI	1671	18.3	4.54	4.17	33.5	198	27.3	3.49	19.6	37.2	106	19.5	2.84	9.09	24.9
GEI	1599	343	82.4	104	605	198	498	62.6	362	669					
forage	1141	0.68	0.18	0.35	1.00	198	0.61	0.03	0.56	0.65	278	0.75	0.11	0.57	1.00
CP	1570	165	30.7	81.0	274	198	165	6.11	152	177					
\rm{EE}	977	37.4	13.1	17.0	80.1	198	48.9	5.73	38.0	55.0	108	37.8	16.5	16.9	65
ASH	1434	75.5	15.6	37.2	142	150	58.1	8.22	47.4	69.3					
NDF	1376	377	108	134	697	198	297	22.0	273	332					
ADF	1358	205	55.1	72.0	365	198	201	16.2	180	230					
STA	1209	183	89.4	10.0	566	111	249	19.5	239	298					
d OM	944	723	56.5	526	875	111	695	33.9	582	763					
dNDF	675	624	110	198	906	111	455	60.7	266	560					

Table 1. Variable summary statistics of the database for different regions and ruminant categories

Table 1 (continued)

EUR = Europe; US = United States of America; AU = Australia; CH₄ emissions = methane emissions (g/d); CH₄ yield = methane emissions per kg of DMI; CH_4 intensity = methane emissions per kg of animal product (kg of fat and protein corrected milk for dairy cattle, sheep and goats; and kg of average daily gain for beef cattle); Ym = percentage of gross energy converted to CH₄ (%); BW = body weight (kg); FPCM = fat and protein corrected milk (kg/d) = milk yield (kg/d) \times [0.337 + 0.116 \times fat (%) + 0.06 \times protein (%)] according to Gerber et al. (2011); DMI = dry matter intake (kg/d); GEI = gross energy intake (MJ/d) ; Forage = forage proportion in the diet; CP = dietary crude protein content (g/kg DM); EE = dietary ether extract content (g/kg DM); ASH: dietary ash content (g/kg DM); NDF = dietary neutral detergent fiber content (g/kg DM); ADF = Acid Detergent Fiber (g/kg DM); STA = Starch (g/kg DM); dOM $=$ digestibility of organic matter (g/kg DM); dNDF = digestibility of NDF (g/kg DM); n = number of observations; SD = standard deviation; Min = minimum; $Max = maximum$.

Source	Model	Prediction equation CH ₄ (g/d) =	Animal category	Mitigation strategy ²	Origin 3
Charmley et al. (2016)	Charmley_1	$38 + 19.22 \times DMI$	Dairy	All diets	AU
Charmley et al. (2016)	Charmley_2	$(2.14 + 0.058 \times \text{GEI})/0.05565$	Dairy	All diets	AU
Mills et al. (2003)	$Mills_1$	$(5.93 + 0.92 \times DMI)/0.05565$	Dairy	All diets	EUR
Mills et al. (2003)	$Mills_3$	$(56.27 \times (1 - \exp^{(-0.028 \times \text{DMI})})) / 0.05565$	Dairy	All diets	EUR
Nielsen et al. (2013)	Nielsen_1	$(1.23 \times DMI - 0.145 \times FA + 0.012 \times NDF)/0.05565$	Dairy	Lip, DQ	EUR
Ellis et al. (2007)	$Ellis_2$	$(3.14 + 2.11 \times \text{NDFI})$ 0. 05565	Dairy	DQ	US
Ellis et al. (2007)	$Ellis_3$	$(2.16 + 0.493 \times DMI - 1.36 \times ADFI + 1.97 \times NDFI)$ 0.05565	Dairy	DQ	US
Moraes et al. (2014)	Moraes	$(0.225 + 0.042 \times \text{GEI} + 0.0125 \times \text{NDF} - 0.0329 \times$ EE)/0.05565	Dairy	Lip, DQ	US
Mills et al. (2003)	$Mills_2$	$(7.3 + 13.13 \times NI + 2.04 \times ADFI + 0.33 \times$ STAI)/0.05565	Dairy	DQ, STA	EUR
Escobar-Bahamondes et al. $(2017a)$	Escobar	$-35.0 + 0.08 \times BW + 120 \times forage - 69.8 \times FA^{3} +$ $3.14 \times$ GEI	Beef	All diets	EUR, US, AU
Yan et al. (2009)	Yan_1	$((35.1 \times DMI)+14.7) \times 0.714$	Beef	All diets	EUR
Yan et al. (2009)	Yan_2	$(1.959 \times \text{GEI} + 8.8)) \times 0.714$	Beef	All diets	${\rm EUR}$
Ellis et al. (2007)	$Ellis_6$	$(-1.02 + 0.681 \times DMI + 4.81 \times forage) / 0.05565$	Beef	DQ	US
Ellis et al. (2007)	$Ellis_5$	$(5.58 + 0.848 \times \text{NDFI})$ 0. 05565	Beef	DQ	US
Ellis et al. (2009)	$Ellis_7$	$(4.72 + 1.13 \times STAI)/0.05565$	Beef	STA	US
Ellis et al. (2009)	Ellis ₋₈	$(-1.01 + 2.76 \times \text{NDFI} + 0.722 \times \text{STAI})/0.05565$	Beef	DQ, STA	US
Ellis et al. (2009)	$Ellis_9$	$(2.5 - 0.367 \times STAI/ADFI + 0.766 \times DMI)/0.05565$	Beef	DQ, STA	US
Charmley et al. (2016)	Charmley_3	$20.7 \times DMI$	Dairy and Beef	All diets	AU
Grainger and Beauchemin (2011)	Grainger_3	$(24.55 - 0.102 \times FA) \times DMI$	Dairy and Beef	Lip	EUR, US, AU
Moate et al. (2011)	Moate	$(\exp^{(3.15 - 0.0035 \times FA)}) \times DMI$	Dairy and Beef	Lip	EUR, US
IPCC $(1997)^4$	IPCC 1997	$(0.060 \times \text{GEI}) / 0.05565$	All categories	All diets	EUR, US, AU

Table 2: List of models evaluated in this study among animal category and mitigation strategy.

DMI = dry matter intake (kg/d), GEI = gross energy intake (MJ/d), FA = dietary fatty acids (g/kg DM), NDF = dietary neutral detergent fiber (g/kg DM), NDFI = NDF intake (kg/d), ADF = dietary acid detergent fiber (g/kg DM), ADFI = ADF intake (kg/d), EE = dietary extract ether (g/kg DM), EEI = EE intake (kg/d), BW = body weight (kg), forage = forage proportion in the diet, NI = nitrogen intake (kg/d), STA = dietary starch (g/kg) DM), STAI = STA intake (kg/d), $dGE =$ digestibility of gross energy (g/kg DM), $dOM =$ digestibility of organic matter (g/kg DM), NFC = non fibrous carbohydrates (g/kg DM), pCO = concentrate proportion in the diet, OMI = organic matter intake (kg/d), DEI = digestible energy intake (MJ/d) .

¹ Animal category in which model is applied: Dairy = Dairy cattle, Beef = Beef cattle, All categories = dairy and beef cattle and small ruminants 2 Mitigation strategy: All diets = Performance using all data of corresponding animal category, Lip = lipid supplementation, DQ = Diet quality, STA $=$ Starch content. ³ origin of data used in the model development: EUR $=$ Europe, US $=$ United States of America, AU $=$ Australia. ⁴ IPCC1997 and IPCC 2006 are used for dairy cattle, beef cattle with forage proportion in the diet < 0.90 and mature sheep (> 1 year). For feedlot cattle (concentrate proportion > 0.90) and young sheep (< 1 year) Ym values of 3 and 4.5% were used.

	Model	n	$\sqrt{a'}$ \sim $\sqrt{a'}$	RMSPE	ECT	ER	\sim \sim \sim \sim \prime ED		CCC	
Rank			RMSPE (g/d)	%	%	%	$\%$			RSR
	Ramin 1	463	61.0	15.6	0.70	2.90	96.4	0.75	0.76	0.66
$\overline{2}$	Ramin_2	1958	82.1	21.2	6.30	3.30	90.4	0.57	0.69	0.76
3	$Mills_3$	1975	84.3	21.8	11.7	1.50	86.8	0.64	0.69	0.78
4	IPCC_1997	1797	82.3	21.2	0.10	12.8	87.1	0.68	0.68	0.79
5°	Ellis_ 3	1034	88.7	22.7	11.5	0.80	87.7	0.60	0.66	0.80
6	$Charmley_2$	1797	84.5	21.8	7.60	9.60	82.8	0.66	0.68	0.81
	$Charmley_1$	1869	87.0	22.8	8.10	9.80	82.0	0.66	0.68	0.81
8	Charmley_3	1869	87.6	22.9	3.00	16.0	81.0	0.67	0.68	0.81
9	Mills 2	1320	72.5	17.8	4.00	4.40	91.6	0.59	0.62	0.82
10	Mills 1	1975	89.3	23.1	18.4	1.80	79.8	0.61	0.68	0.83
11	Ramin ₃	626	80.0	20.5	5.40	8.10	86.5	0.61	0.63	0.84
12	Sauvant_1	967	93.5	27.4	12.5	9.90	77.6	0.63	0.66	0.85
13	IPCC_2006	1797	90.8	23.4	11.0	17.4	71.6	0.65	0.68	0.87

Table 3. Evaluation of the performance of CH₄ emissions (g/d) prediction models for dairy cattle (ranked by RSR)

 \overline{Rank} = rank of the performance based on the RSR, $n =$ number of observations; RMSPE = Square root of the mean square prediction error, expressed in g/d and RMSPE% as a percentage of methane emissions mean; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance

expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed values ratio.

Mitigation			Rank Model $\mathbf n$		RMSPE	RMSPE	ECT	$\rm ER$	ED	CCC		RSR
strategy					(g/d)	$\%$	$\%$	$\%$	$\%$		\mathbf{r}	
Lipid	The low-EE		IPCC_1997	685	64.0	17.1	7.68	15.2	77.1	0.71		0.73 0.78
supplementation	diets	\overline{c}	IPCC_2006	685	65.7	17.6	3.33	23.7	73.0	0.71		0.73 0.80
	(mean 30.4 g/kg	3	Moate	609	66.2	17.9	10.7	17.3	72.0	0.70		0.72 0.81
	DM)		Grainger_3	609	72.4	19.6	23.7	16.6	59.7	0.67		0.73 0.89
		5	Grainger_1	609	73.2	19.8	25.1	16.5	58.4	0.66		0.73 0.90
		6	Nielsen_1	557	75.0	19.9	43.8	7.89	48.3	0.64		0.76 0.93
			Ramin 1	391	70.6	16.1	8.57	7.53	83.9	0.72		0.74 0.73
	The high-EE diets	\overline{c}	Ramin ₃	314	87.2	20.3	0.66	8.03	91.3	0.60		0.61 0.83
		3	Moraes	490	95.3	22.9	27.8	0.87	71.3	0.47		0.59 0.95
	(mean 51.7 g/kg	$\overline{4}$	IPCC_1997	490	105	25.3	11.4	22.9	65.6	0.49		0.52 1.05
	DM)	5	IPCC_2006	490	127	30.5	33.3	21.6	45.1	0.42	0.52 1.27	
Diet quality by	The low-NDF diets (mean 285 $g/kg DM$)		Ramin 1	67	41.9	10.1	2.31	1.96	95.7	0.88		0.88 0.48
NDF content		\overline{c}	$Ellis_3$	414	89.9	21.7	6.78	5.10	88.1	0.40		0.45 0.95
		3	IPCC_1997	701	96.1	23.7	13.6	22.8	63.7	0.49	0.53	1.06
		4	IPCC_2006	701	118	29.2	37.3	20.6	42.1	0.41	0.53	1.31
			$Ellis_3$	514	63.4	17.6	6.26	1.76	92.0	0.82		0.85 0.54
	The high-NDF	$\overline{2}$	IPCC_2006	817	56.6	14.3	3.59	11.3	85.2	0.84		0.85 0.57
	diets (mean 433	3	Sauvant_2	562	65.2	18.0	10.9	24.3	64.9	0.86		0.89 0.58
	$g/kg)$ DM)	4	Nielsen 1	430	56.8	14.2	30.8	7.09	62.1	0.84		0.88 0.60
		5	Ramin 3	381	60.7	15.1	4.11	1.91	94.0	0.77	0.79	0.63
		6	IPCC_1997	817	67.0	16.9	36.5	2.73	60.8	0.78		0.85 0.68
STA content	The low-STA		IPCC_2006	217	48.4	13.3	4.50	8.60	86.9	0.65	0.67	0.80
	diets	\overline{c}	$Mills_2$	217	53.2	14.6	14.5	1.42	84.1	0.52		0.59 0.87
	(mean 56.1 g/kg	3	Ramin ₃	144	40.3	11.9	26.7	10.4	63.0	0.58		0.65 0.95
	DM)	4	IPCC_1997	217	59.5	16.4	39.7	2.82	57.5	0.54		0.67 0.98
	The high-STA		$Mills_2$	1103	75.7	18.2	3.13	5.39	91.5	0.58		0.60 0.84
	diets	$\overline{2}$	Ramin ₃	446	90.2	22.0	4.05	8.41	87.5	0.54		0.56 0.88

Table 4. Evaluation of the performance of CH⁴ emissions (g/d) prediction models for dairy cattle fed lipid supplements, diets with different contents of NDF and STA, and diets of different quality (ranked by RSR).

 $EE =$ dietary ether extract (g/kg DM), NDF = neutral detergent fiber (g/kg DM), STA = dietary starch (g/kg DM), dOM = digestibility of organic matter (g/kg DM), dNDF = digestibility of NDF (g/kg DM), Rank = rank of the performance based on the RSR, n = number of observations; RMSPE = Square root of the mean square prediction error, expressed in g/d and RMSPE% as a percentage of methane emissions means; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed values ratio.

Rank	Model	n	RMSPE (g/d)	RMSPE %	ECT %	ER %	ED %	CCC	\mathbf{v}	RSR
	Escobar	161	66.1	27.2	0.49	5.94	93.6	0.40	0.60	0.83
2	Ramin 2	419	75.3	33.3	0.77	1.92	97.3	0.42	0.56	0.84
3	Yan_1	419	76.3	33.8	5.07	0.06	94.9	0.48	0.56	0.85
$\overline{4}$	Yan_2	403	78.0	34.0	9.29	0.77	89.9	0.49	0.57	0.87
\mathfrak{S}	IPCC 2006	380	76.6	32.7	15.0	0.43	84.6	0.46	0.60	0.87
6	$Charmley_3$	419	82.2	36.4	17.5	0.80	81.7	0.39	0.56	0.91
7	IPCC_1997	403	84.2	36.7	22.1	0.61	77.3	0.39	0.57	0.93
8	Grainger_2	177	77.1	32.9	18.6	0.43	81.0	0.40	0.52	0.95
9	Grainger_1	177	78.7	33.6	21.8	0.06	78.1	0.37	0.52	0.97

Table 5. Evaluation of the performance of CH₄ emissions (g/d) prediction models for beef cattle (ranked by RSR).

 $Rank = rank$ of the performance based on the RSR, $n = number$ of observations; RMSPE = Square root of the mean square prediction error, expressed in g/d and RMSPE% as a percentage of methane emissions means; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed values ratio.

matter (g/kg DM), dNDF = digestibility of NDF (g/kg DM), Rank = rank of the performance based on the RSR, n = number of observations; RMSPE = Square root of the mean square prediction error, expressed in g/d and RMSPE% as a percentage of methane emissions means; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed values ratio.

 $EE =$ dietary ether extract (g/kg DM), NDF = neutral detergent fiber (g/kg DM), STA = dietary starch (g/kg DM), dOM = digestibility of organic

	Rank Model	n	RMSPE (g/d)	RMSPE %	ECT %	ER %	ED %	CCC		RSR
	Patra 3	90	3.33	19.2	3.45	5.31	91.2	0.75	0.81	0.61
	IPCC 1997	111	4.35	26.8	2.30	3.82	93.9	0.64	0.66	0.77
	Patra 2	111	4.41	27.2	8.69	0.00	91.3	0.59	0.66	0.78
4	Sauvant 1	229	6.73	31.1	1.82	10.8	87.4	0.61	0.62	0.84
	Patra 1	274	6.71	32.7	0.64	2.18	97.2	0.51	0.55	0.85
6	IPCC 2006	111	4.86	29.9	18.1	6.45	75.4	0.61	0.66	0.86

Table 7. Evaluation of the performance of CH₄ emissions (g/d) prediction models for sheep (ranked by RSR).

 $Rank = rank of the performance based on the RSR, n = number of observations; RMSPE = Square root of the mean square prediction error,$ expressed in g/d and RMSPE% as a percentage of methane emissions means;; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed

values ratio.

	Rank Model	n	RMSPE	RMSPE	ECT	ER	ED	CCC		RSR
			(g/d)	%	%	%	$\%$			
	Patra 4	46	5.80	37.7	1.97	0.77	97.3	0.37	0.51	0.86
	Patra_5	46	6.23	40.5	7.76	.09	91.2	0.36	0.45	0.92
	Patra 6	46	6.59	42.8	0.45	0.03	99.5	0.06	0.16	0.98
4	FAO 2010	30	10.1	65.4	48.5	5.15	46.4	0.37	0.54	1.22

Table 8. Evaluation of the performance of CH₄ emissions (g/d) prediction models for goats (ranked by RSR).

expressed in g/d and RMSPE% as a percentage of methane emissions means;; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed values ratio.

 $Rank = rank$ of the performance based on the RSR, $n = number$ of observations; RMSPE = Square root of the mean square prediction error,

Table 9. Evaluation of models using data from individual animals or treatment means.

 $n =$ n = number of observations; RMSPE = Square root of the mean square prediction error, expressed in g/d and RMSPE% as a percentage of methane emissions means;; ECT% = error due to central tendency expressed as a percentage of RMSPE; ER% = error due to deviation of the regression slope expressed as a percentage of RMSPE; ED% = error due to the disturbance expressed as percentage of RMSPE; CCC = concordance correlation coefficient; *r* = correlation coefficient; RSR = RMSPE to standard deviation of observed values ratio.

Figure 1. Observed vs. predicted values plots, using dairy cattle data, of 8 models with the smallest RSR for the low- (black points) and the high-EE (red points) diets. The black discontinued line is the identity line $y = x$, the gray, black and red lines are the fitted regression lines for all diets, the low- and the high-EE diets, respectively.

Figure 2. Observed vs. predicted values plots, using dairy cattle data, of 8 models with the smallest RSR for the low- (black points) and the high-NDF (red points) diets. The black discontinued line is the identity line $y = x$, the gray, black and red lines are the fitted regression lines for all diets, the low- and the high-NDF diets, respectively.

Figure 3. Observed vs. predicted values plots, using all dairy cattle data and for the low- (black points) and the high-STA (red points) diets, of the 4 models Mills_2, Ramin_3, and of IPCC_1997 and 2006. The black discontinued line is the identity line y = x, the gray, black and red lines are the fitted regression lines for all diets, the low- and the high-STA diets, respectively.

Figure 4. Observed vs. predicted values plots, using all dairy cattle data and for the low- (black points) and the high-dMO (red points), of the 4 models Ellis_3, Ramin_1, and of IPCC_1997 and 2006. The black discontinued line is the identity line $y = x$, the gray, black and red lines are the fitted regression lines for all diets, the low- and the high-dOM diets, respectively.

Figure 5. Observed vs. predicted values plots, using all dairy cattle data and for the low- (black points) and the high-dNDF (red points), of the 4 models Ellis_3, Ramin_3, and of IPCC_1997 and 2006. The black discontinued line is the identity line $y = x$, the gray, black and red lines are the fitted regression lines for all diets, the low- and the high-dNDF diets, respectively.

Figure 6. Relationship between DMI (kg/d) and CH⁴ emissions (g/d) by dairy cattle in our database. The blue and green lines are two DMI-based models evaluated: Ramin_2 [CH₄ (g/d) = (20 + 35.8 × DMI - 0.5 × DMI²) × 0.714] and Mills_3 [CH₄ (g/d) = (56.27 × (1 - exp^(-0.028 × DMI)))/0.05565], respectively.