



Exploring methane phenotypes and their relationship with productive traits in the Spanish Holstein Population

E. Teran,^{1*} A. García Rodríguez,² I. Goiri,² J. A. Jiménez-Montero,³ and O. González-Recio^{1,4}

¹Departamento de Mejora Genética Animal, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria – CSIC, 28040 Madrid, Spain

²NEIKER – Basque Institute for Agricultural Research and Development, Basque Research and Technology Alliance (BRTA), 01192, Arkaute, Spain

³Confederación de Asociaciones de Frisona Española (CONAFE), 28340 Madrid, Spain

⁴The Roslin Institute and Royal (Dick) School of Veterinary Studies R(D)SVS, The University of Edinburgh, Easter Bush, Midlothian, EH25 9RG, UK

ABSTRACT

The goal of this study was to evaluate alternative phenotypes for methane emissions in dairy cattle and to estimate their genetic relationships with productive traits. Methane (CH₄) and carbon dioxide (CO₂) concentration in exhaled breath and eructation events were measured with sniffers from 2,961 dairy cows across 34 commercial farms in 5 Spanish regions between 2018 and 2023. Records for CO₂ concentrations were available for 23 farms. Traits derived included the average of CH₄ concentration, area under the curve of CH₄ concentration from eructation events, average maximum values of CH₄ concentration in eructation events, number of eructation events per minute, average of CO₂ concentration, CH₄:CO₂ ratio from average gas concentrations, and 2 methane production traits (g/d) derived from the ratio. A Bayesian approach was used to estimate variance components and genetic correlations. Heritability estimates for methane phenotypes ranged from 0.07 (highest posterior density interval, HPD = 0.03: 0.11) to 0.12 (HPD = 0.06: 0.17), with moderate-to-high repeatability (0.49–0.58). The number of eructation events per minute showed higher heritability (0.30; HPD = 0.24: 0.37) and repeatability (0.75; HPD = 0.73: 0.76). The phenotypic and genetic correlations between methane concentrations traits were high, ranging from 0.78 to 0.99, except for the number of eructation events per minute, which correlated positively with peak-based traits at the phenotypic level, but lowly or even negatively at the genetic level with most methane phenotypes. The phenotypic and genetic correlation between ratio and other methane concentration traits was moderate (0.46; HPD = 0.13: 0.73) to high (0.94; HPD = 0.85: 0.99), but strong and positive (0.92; HPD = 0.84:

0.98, or 0.99; HPD = 0.98: 0.99) with methane production. Methane production traits showed high phenotypic correlation (0.56–0.74) and moderate (0.44; HPD = 0.07: 0.79) to high (0.99; HPD = 0.98: 0.99) genetic correlation with methane concentration traits. The genetic correlation estimates with productive traits were low (0.12; HPD = –0.06: 0.42) to high (0.78; HPD = 0.47: 0.98) for all methane and carbon dioxide traits, with stronger associations observed with fat yield. Sniffer devices provide robust methane phenotypes under commercial conditions, enabling accurate genetic parameter estimation. We show strong correlations among methane traits, positive links with production traits, and highlight a new methane production phenotype that avoids bias in genetic correlation estimates when productive traits are used in the conversion from parts per million to grams per day. These results support the inclusion of methane traits in breeding programs to balance productivity with environmental sustainability.

Key words: methane, sniffers, dairy cattle, genetic correlation

INTRODUCTION

Methane from livestock sector accounts for 6.3% of anthropogenic GHG emissions, with ruminants being the main emitters (IPCC, 2022). Currently, several strategies exist for mitigating the effects of methane emissions from ruminants, with genetic selection emerging as progressively significant because of its long-term cumulative effects. However, to implement this strategy, some factors should be considered: (1) the limitations of the methodology used to measure methane to obtain a large amount of data in different breeding systems, (2) lack of a standardized phenotype, and (3) no well-established relationship with other traits of interest in selection indices.

Many indirect and direct methods have been used over the past 2 decades to estimate individual methane

Received August 1, 2025.

Accepted March 20, 2026.

*Corresponding author: ester.teran@inia.csic.es

The list of standard abbreviations for JDS is available at adsa.org/jds-abbreviations-26. Nonstandard abbreviations are available in the Notes.

emissions, including respiration chambers, GreenFeed systems, and noninvasive gas detector devices. Although respiration chambers are considered the reference method to measure methane production from ruminants because of their higher precision (Hill et al., 2016), they interact with the animal's natural behavior, are expensive, and have low throughput, which make them unfeasible for use in breeding programs. For these reasons, nondispersive infrared methane detection devices, such as GreenFeed and sniffers, are currently becoming more common for breeding purposes. In particular, sniffers provide a non-invasive and low-cost strategy, both in terms of installation and maintenance, making it suitable for application in commercial farms (Lassen et al., 2012; López-Paredes et al., 2020). Sniffers are commonly installed next to an automated milking system (AMS), and they measure gases from the breathing of ruminants during milking or feeding, thereby minimizing any disturbance to the animals. They allow measurement of multiple records per cow over extended periods, spanning several days, weeks, or even months. Previous studies have shown that methane from sniffers is a heritable trait, showing moderate estimates: 0.12 (López-Paredes et al., 2020), 0.21 (Lassen and Løvendahl, 2016), 0.27 (Pszczola et al., 2017). Recently, van Breukelen et al. (2023) found higher heritability (0.30) for methane production estimated from sniffers and GreenFeed. These results show that methane emission can be reduced through genetic selection using sniffer records. However, one limitation showed by these devices is the high variability between measurement, attributed mainly to the geometry of the feed bin, muzzle movement, and muzzle position (Huhtanen et al., 2015). For that reason, some studies have tried to validate estimations obtained with sniffers by comparing them with devices that are more precise. The results showed high correlations with measurements from respiration chambers and GreenFeed systems. For instance, Garnsworthy et al. (2012) and Difford et al. (2018a) reported high phenotypic correlations between data derived from sniffers and data estimated in respiration chambers ($R^2 = 0.77$ to 0.79), supporting the reliability of sniffers. Likewise, van Breukelen et al. (2023) demonstrated a high genetic correlation ($r_g = 0.71 \pm 0.13$) between daily estimates obtained with sniffers and GreenFeeds. Another limitation of sniffers is that they measure methane emissions in concentration, requiring a conversion to other units more interpretable as methane production. The predominant equation employed for deriving individual estimates of methane production was described by Madsen et al. (2010), which is evaluated through the relationship with heat-producing units (HPU), thereby integrating data pertaining to ECM, live weight, and days in pregnancy (Pedersen et al., 2008). Other alternatives to estimate CO_2 production were studied based on diet, productive

traits, and weight to precisely estimate individual values independent of HPU (Kjeldsen et al., 2024). A significant drawback of these conversion formulas is that they are derived using productive data, which may introduce biases in the correlations observed between methane emissions and productive traits, leading to potential double accounting when they are included selection indices and statistical artifacts in the genetic correlations.

Another important challenge for the inclusion of methane emissions in the breeding programs is the lack of a standardized trait to define these emissions. Methane production appears to be a good candidate for inclusion in the breeding goals and selection indices because it is interpretable and is the most "clean" trait for reducing methane (de Haas et al., 2017). However, sniffers assess methane in concentration (ppm) rather than in terms of methane production (g/d), requiring approximations to methane production per cow (g/d or L/d; Madsen et al., 2010; Kjeldsen et al., 2024). Some definitions from sniffers are based on overall averaged records, and others are based on the eructation events. An earlier study from López-Paredes et al. (2020) reported moderate to strong genetic correlations between methane concentration from eructation events and methane production (0.96 ± 0.18) using an equation in Chagunda et al. (2009). In addition to methane production, different methane phenotypes are currently being studied through many approaches. For instance, the estimation of methane intensity (g/kg or L/kg of product) is derived from the measurements of methane emissions per unit of product. Another common phenotype is methane yield (g/kg of DMI or L/kg of DMI), estimated per unit of DMI (Breider et al., 2019). However, these last 2 phenotypes are discouraged in selection indexes because these ratio traits may encompass traits that are already represented within the index, and may exhibit variance components that are driven by one of the traits, resulting in unpredictable outcomes over time (Basarab et al., 2013). Residual methane is an alternative phenotype that has been proposed but is not free of down sides (Manzanilla-Pech et al., 2022b). Residual methane is an estimate that may come with some error, and some genetic correlation may still exist.

Finally, to incorporate methane in breeding programs, its relationship with other traits of interest, mainly production, must be taken into account (Wall et al., 2010). Currently, only a limited number of studies have assessed this genetic correlation. For example, López-Paredes et al. (2020) identified positive genetic correlations between methane production estimated with sniffers and kilograms of milk, fat, and protein, indicating that selection for lower methane emissions would affect these productive traits. However, these correlations were low, with large uncertainty in the estimates. Lassen and Løvendahl (2016) also found a positive cor-

relation between methane production and ECM (0.43 ± 0.10), meaning that selection against methane emissions might negatively affect milk production. Recently, van Breukelen et al. (2025) also obtained close to zero genetic correlation between methane and milk production traits, being higher with fat yield (0.12 ± 0.08 at first parity and 0.23 ± 0.10 at second parity).

Therefore, the objectives of this study were to (1) investigate the genetic parameters associated with different trait definitions for methane by using an updated dataset of measurements in commercial farms and (2) obtain genetic correlation with milk yield traits.

MATERIALS AND METHODS

Data Recording

Methane records from 2,961 Holstein cows in 34 commercial farms from 5 different regions of Spain (Galicia, Cantabria, País Vasco, Navarra, and Cataluña) were collected from April 2018 to June 2023. Eligibility criteria to include a farm in this study were as follows: they needed to be enrolled in the official recording scheme of type and milk trait conducted by the Confederation of Spanish Friesian Associations, they must have an AMS, and the farmers had to consent to participate. Some farms were measured more than once. Methane and carbon dioxide concentrations (ppm) were measured every second using a nondispersive infrared methane detection device (Guardian NG infrared gas monitor and Gascard NG infrared gas sensor, respectively; Edinburgh Instruments Ltd., Livingston, UK) during 3 to 4 wk. The range of measurement of sniffers was 0 to 10,000 ppm for methane and 0 to 50,000 ppm for carbon dioxide. The devices were installed in the AMS, collecting breath and eructation events from the feed bin during the visit of cows (on average 3 times a day), thereby minimizing possible effects associated with diurnal feeding variation among herds and cows. Some farms had more than one AMS and several sniffer devices were installed in more than one AMS simultaneously. The lag period for the gas to traverse from the feed bin to the sniffer was quantified. This lag measurement was used to synchronize records from the AMS and sniffers. The entry and exit times for each cow registered by the AMS was associated with the methane emissions of the corresponding cow during that time. Each period between entry and exit time was defined as a visit. After synchronization, a total of 221,761 visits from 3,951 cows were obtained for all the cows during the period studied. The carbon dioxide concentration was available only for farms measured after 2021 (67% of the total farms studied).

Only animals with data from milk recordings of the test record during the period of methane measurements were

retained. Milk yield was obtained from the AMS. Protein and fat percentage from the official test-day record were used to calculate protein and fat yield. Records from cows with >365 DIM were excluded from the analysis.

Definition of Methane Traits

An in-house program was used to determine eructation peaks per visit, using a similar method as that described by Huhtanen et al. (2015), considering the slope changes between running windows containing 5 consecutive measurements to determine the beginning and end time points of each eructation event. Visits with at least one peak were retained and only the first 5 min of the visit were considered because we observed that after this time cows had eaten all the allocated concentrate feed in the AMS, and most cows lose interest in the feed bin, which caused the measurements not to be representative after this period. All records were adjusted for background noise. Background methane was represented by the average of the 5 lowest measurements during each visit, from entrance in the AMS to exit. This background was subtracted from each concentration record. The carbon dioxide background was adjusted in the same manner.

A schematic representation of the pipeline from data collection to phenotype definition is provided in Figure 1. Additionally, a graphical representation of phenotypes defined in the following list is provided in Figure 2.

Four phenotypes for CH₄ were defined based on concentration (ppm), as follows:

- The mean ppm value for all CH₄ records, which is the average of all the measurements per second divided by the duration of the visit to the AMS. This trait was named mean CH₄ (**AVGCH4**),
- The sum of all ppm records for methane within the eructation peaks for CH₄. This is equivalent to an area under the curve of eructation events. The summation was then averaged by minute (**AUC**). The peak magnitude was defined as the summation of the averages of the 2 highest values within each peak, across all peaks of the visit, expressed per minute (**MAXPK**),
- The number of peaks per minute (**NPK**) was defined as the frequency of eructation events per minute and was calculated as the number of eructation events during the AMS visit divided by the visit time and expressed per minute.

Also, one phenotype for CO₂ was defined:

- The mean CO₂ was calculated as the average of all the measurements during the visit to the AMS (**AVGCO2**).

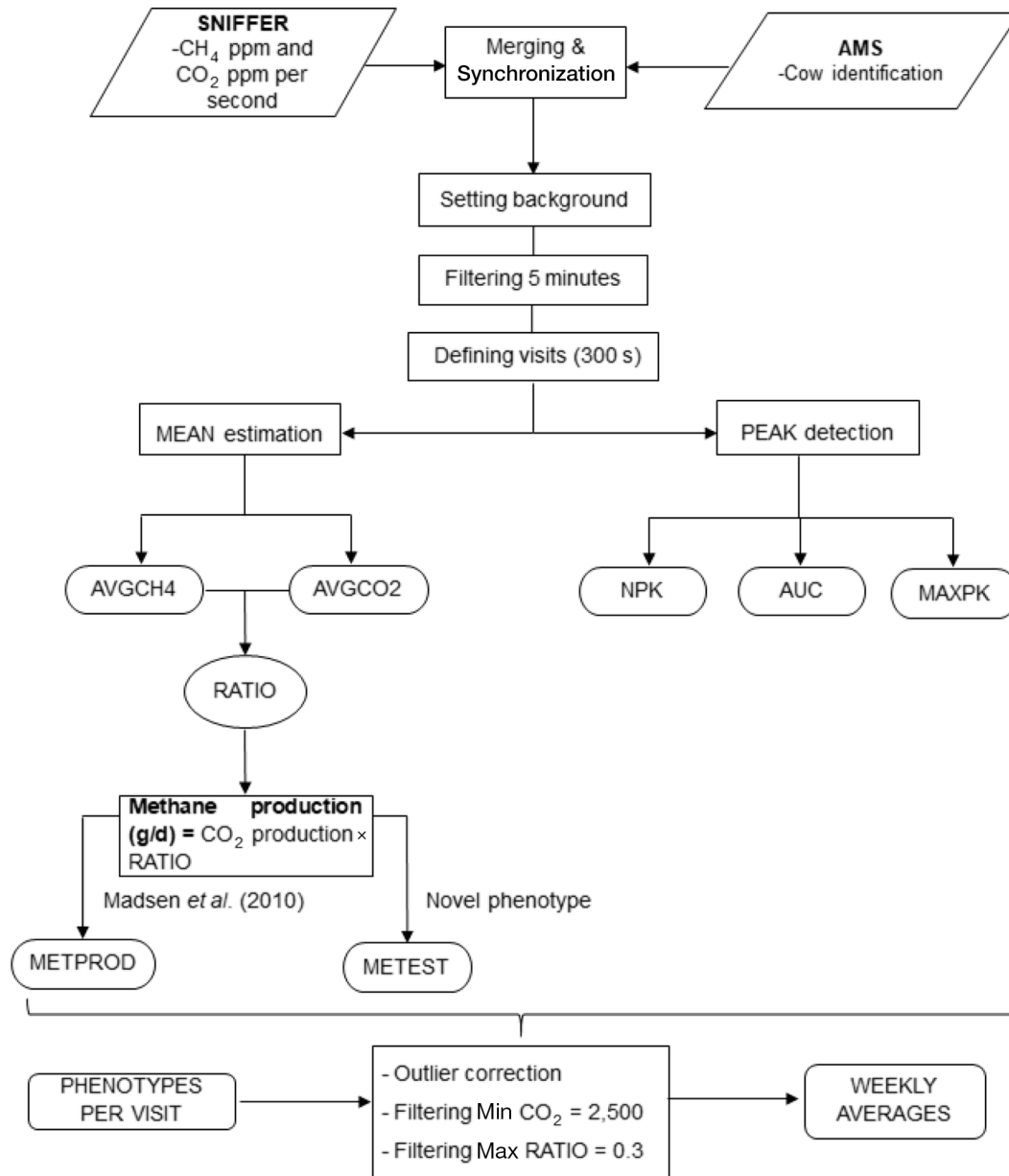


Figure 1. Schematic flowchart illustrating the process from methane data acquisition to phenotype definition. Parallelograms represent data entry points, rectangles denote the processes involved, and ovals indicate the terminal outcomes (phenotypes). Ultimately, the phenotypes recorded during each visit are averaged to obtain the final weekly traits. The METPROD values were obtained using Madsen et al. (2010). Max = maximum; Min = minimum.

An additional trait was computed, which was based on the ratio between AVGCH₄ and AVGCO₂ (**CH₄:CO₂**).

In addition, AVGCH₄ and AUC were also calculated by considering a frequency of sniffer measurements at 5 s intervals (**AVGCH₄_5s** and **AUC_5s**) to evaluate the influence of measurement frequency on the definition of the phenotypes because previous studies have reported sniffers records with a 5-s interval.

Two other phenotypes of methane production were derived from the ratio of CH₄ and CO₂ concentration, BW, and productive traits. The first definition of methane production in grams per day (**METPROD**) was based on the equation proposed by Madsen et al. (2010). They defined the methane production as follows:

$$\text{Methane production (L/d)} = a \times (b - d)/(c - e), \quad [1]$$

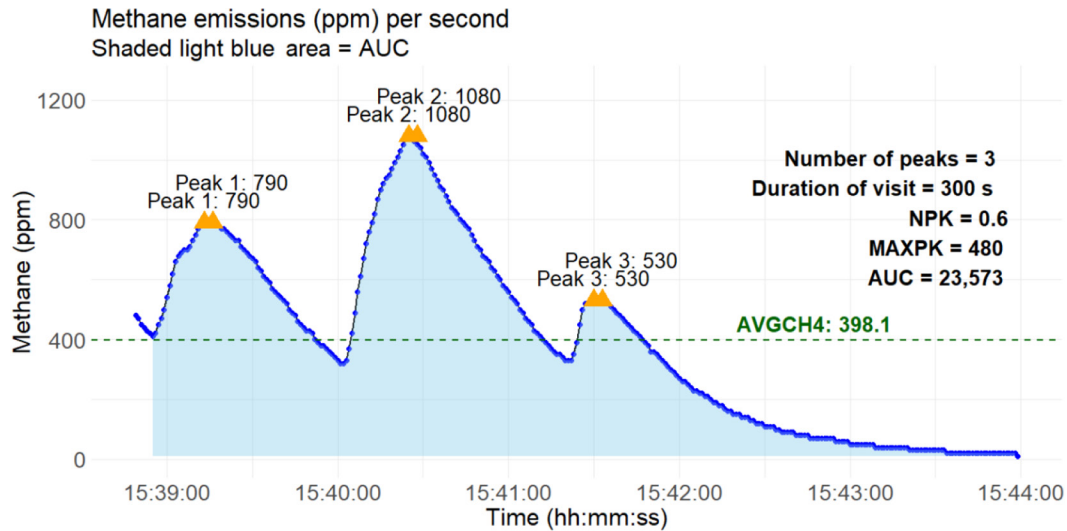


Figure 2. Methane emissions per second. The plot represents a visit of 300 s where 3 peaks were detected. The green dashed line represents AVGCH₄, estimated as the average methane emission per visit. The light blue shaded area corresponds to the AUC phenotype, calculated as the sum of the areas of all peaks detected per visit, expressed per minute. Yellow triangles indicate the 2 maximum points within each peak; these values were averaged, and the resulting means were summed and expressed per minute to obtain the MAXPK phenotype.

where a is the CO₂ (L/d) produced by the animal, b is the CH₄ concentration in mix air in ppm, c is the CO₂ concentration in mix air in ppm, d is the CH₄ concentration in background air in ppm, and e is the CO₂ concentration in background air in ppm. Because d and e are considered insignificant (1.8 and 380 ppm, respectively) compared with respiration air in cattle (approximately 500 and 5,000 ppm on average), they were not estimated.

To estimate the individual CO₂ production per day (a in Equation 1), the value of 180 L/HPU per 24 h (Pedersen et al., 2008), divided by 1,000, was used. The HPU equation incorporates information from ECM, live weight, and days in pregnancy as follows:

$$\begin{aligned} \text{CO}_2 \text{ production (L/d)} &= 180 \times 24 \times 10^{-3} \\ &\times 5.6 \times \text{kg body mass}^{0.75} + 22 \times \text{ECM} + 1.6 \times 10^{-5} \\ &\times \text{days in pregnancy}^3. \end{aligned} \quad [2]$$

Using Equation 1, the trait of methane production is expressed as follows:

$$\begin{aligned} \text{METPROD} &= 0.714 \times \text{CH}_4\text{:CO}_2 \times 180 \times 24 \times 10^{-3} \\ &\times 5.6 \times \text{kg body mass}^{0.75} + 22 \times \text{ECM} + 1.6 \times 10^{-5} \\ &\times \text{days in pregnancy}^3, \end{aligned} \quad [3]$$

where 0.714 is the conversion factor from liters to grams of methane (Brouwer, 1965), using the methane molar volume (22.4 L/mol) and the methane molar mass (16.042

g/mol). The CH₄:CO₂ of AVGCH₄ and AVGCO₂, represents b and c in Equation 1.

The second phenotype of methane production was an alternative trait (**METEST**). This phenotype is derived using a method similar to Equation 1 of Madsen et al. (2010), but with the difference that CO₂ is adjusted to the mean and SD of the expected CO₂ production within each comparison group (herd-robot-week-year). Consequently, methane production was indirectly modified through the adjustment of CO₂. The METEST equation can be expressed as follows:

$$\begin{aligned} \text{Methane production (L/d)}_{\text{adjusted}} &= a_{\text{adjusted}} \\ &\times (b - d)/(c - e), \end{aligned} \quad [4]$$

where a_{adjusted} represents the conversion of CO₂ (ppm) to CO₂ production (L/d) adjusted to the mean and SD of the expected CO₂ production within comparison group.

The first step was to convert CO₂ concentration (ppm) into CO₂ production (L/d). Assuming that the sniffer collects 1 L of gas per minute and sniffers are set to measure gases at a 1-s interval, the conversion from CO₂ concentration to CO₂ production (L/d) would be

$$\text{CO}_2 \text{ (L/d)} = \text{CO}_2 \text{ (ppm/s)} \times \frac{1 \text{ L}}{10^6 \text{ ppm}} \times \frac{86,400 \text{ s}}{1 \text{ d}}. \quad [5]$$

Next, Equation 2 from Pedersen et al. (2008) was applied to predict the expected CO₂ production per comparison group (herd-robot-week-year):

$$\begin{aligned} \text{CO}_2 \text{ production (L/d)}_{\text{group}} &= 180 \times 24 \times 10^{-3} \times 5.6 \\ &\times \text{kg body mass}^{0.75} + 22 \times \text{ECM} + 1.6 \times 10^{-5} \\ &\times \text{days in pregnancy}^3. \end{aligned}$$

After that, the captured CO₂ production (L/d) from the sniffer was standardized to mean (μ) and SD of expected CO₂ production, as follows:

$$\begin{aligned} \text{CO}_2 \text{ adjusted} &= \text{SD}_{\text{group}} \text{ expected CO}_2 \text{ (L/d)} \\ &\times \frac{\text{CO}_2 \text{ (L/d)}_i - \mu \text{CO}_2 \text{ (L/d)}}{\text{SD CO}_2 \text{ (L/d)}} + \mu_{\text{group}} \text{ expected CO}_2 \text{ (L/d)}. \end{aligned} \quad [6]$$

Then, Equation 4 was used to obtain methane production (L/d):

$$\begin{aligned} \text{Methane production (L/d)} &= \text{CO}_2 \text{ adjusted (L/d)} \\ &\times \text{CH}_4:\text{CO}_2. \end{aligned}$$

Finally, to estimate METEST (g/d), the coefficient of methane density, 0.714, was used to convert L/d to g/d.

Data Filtering

After defining the phenotype, some steps for data curation were undertaken. Visits that did not detect any eruption peak were removed. Visits with CO₂ concentration <2,500 or CH₄:CO₂ values exceeding 0.30 or methane production (METPROD and METEST) values exceeding 1,200 were discarded, being considered biologically improbable. A z-score test was performed to test for normal distribution, and it was significant. For this reason, the outlier detection was performed using the quantile method (first and 99th percentiles), where values lower or greater than these percentiles were discarded. A total of 194,575 records per visit (accounting for 87% of the initial dataset) and 3,475 cows (also representing 87% of the initial dataset), were kept following the implementation of filters and the correction of outliers.

Next, all measurements were weekly averaged, retaining only data from cows with more than 5 visits per week. In the final dataset only groups of herd-robot-week-year with at least 5 weekly averages and cows with at least 2 averaged values (obtained over a span of at least 2 wk) were kept. After the implementation of all filters mentioned, data of methane concentration was available for 2,961 cows, whereas data of CO₂ was available for 1,576 of them. Data for METPROD and METEST were available for 1,265 and 1,576 cows, respectively.

Genomic and Pedigree Information

The pedigree was traced back to 19 generations, with an average of 7 equivalent generations and 44,364 individuals. Genomic information was available for 2,077 cows with phenotype. Additionally, 538 genotypes for sires and grandsires were included. Animals were genotyped with the EuroG MD beadchip developed by EuroGenomics. Missing genotypes were imputed as described in Jiménez-Montero et al. (2013). Those SNPs that had allele frequency <0.05, call rate <0.90, or were monomorphic or located in the sex chromosomes were filtered out. Moreover, the parent-progeny Mendelian conflicts were verified, excluding those animals with more than 10% of SNPs with conflict or SNPs that presented conflict in more than 100 animals. After quality control 40,489 SNPs were kept for further analysis.

Variance Component Estimation

A Bayesian model was implemented to estimate variance components for methane phenotypes as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_h\mathbf{h} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_p\mathbf{p} + \mathbf{e}, \quad [7]$$

where $\mathbf{y}$ is a $n \times 1$ vector of methane phenotypes; $\mathbf{b}$ denotes the vector for fixed effects estimates: number of calving (first, second, and third and greater), month of calving (1 to 12), and lactation stage (set at 3 levels = 0–90, 91–150, and 151–365 d), with corresponding incidence matrix $\mathbf{X}$; $\mathbf{h}$ is the vector of the contemporary group (herd-week-year-robot) effect as random with incidence matrix $\mathbf{Z}_h$; $\mathbf{a}$ is the vector of direct animal genetic effects with incidence matrix $\mathbf{Z}_a$, assumed to be distributed as $\mathbf{a} \sim N(0, \mathbf{H}\sigma_a^2)$, where $\mathbf{H}$ is the numerator relationship matrix based on the pedigree and genomic relationship (Misztal et al., 2009; Aguilar et al., 2010; Christensen and Lund, 2010; Legarra et al., 2014) and σ_a^2 is the additive genetic variance. Then, $\mathbf{p}$ is the vector of permanent effect with corresponding incidence matrix $\mathbf{Z}_p$, and $\mathbf{e}$ denotes the vector of residuals distributed as $N(0, \mathbf{I}\sigma_e^2)$, where $\mathbf{I}$ is the identity matrix and σ_e^2 is the residual variance.

The heritability was calculated as intraherd heritability (van Engelen et al., 2015) as

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2}. \quad [8]$$

Table 1. Descriptive statistics of number of records, number of cows, and mean and SD of methane and carbon dioxide phenotypes averaged by week

Trait ¹	No. of records (% weekly records before filtering)	No. of cows (% cows before filtering)	Mean (SD)
AVGCH4 (ppm)	11,377 (66)	2,961 (85)	358 (189)
AVGCH4_5s (ppm)	11,377 (66)	2,961 (85)	359 (190)
AUC (ppm)	11,377 (66)	2,961 (85)	12,825 (7,607)
AUC_5s (ppm)	11,377 (66)	2,961 (85)	2,717 (1,867)
MAXPK (ppm)	11,377 (66)	2,961 (85)	452 (316)
NPK	11,377 (66)	2,961 (85)	0.59 (0.15)
AVGCO2 (ppm)	6,513 (62)	1,576 (81)	5,371 (1,722)
CH4:CO2	6,513 (62)	1,576 (81)	0.07 (0.01)
METPROD (g/d)	5,211 (62)	1,265 (81)	337 (89)
METEST (g/d)	6,513 (62)	1,576 (81)	309 (80)

¹AVGCH4 = average of CH₄; AVGCH4_5s = average of CH₄ estimated every 5 s; AUC = area under the curve; AUC_5s = area under the curve estimated every 5 s; MAXPK = summation of the averages of the 2 highest measurements from each peak within a visit; NPK = number of peaks per minute; AVGCO2 = average of CO₂; CH4:CO2 = ratio of AVGCH4 and AVGCO2; METPROD = methane production estimated with the Madsen equation; METEST = methane production adjusted by the CO₂ expected by comparison group.

The repeatability was calculated as

$$t = \frac{\sigma_a^2 + \sigma_p^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2} \quad [9]$$

For genetic parameter estimations, some phenotypes with high phenotypic values were transformed to avoid large variance values. The phenotypes modified were AUC and AUC_5s, which were divided by 100 and 10, respectively.

Genetic correlations between methane phenotypes were estimated using bivariate analysis with the same effects as in Equation 7. Genetic correlations between methane phenotypes and productive traits of milk (kg), fat (kg) and protein (kg) were also estimated. The analysis was implemented with gibbs.f90 from the BLUPF90+ suite of programs (Misztal et al., 2018). The number of samples used in this method was 500,000, thinned every 10 samples, with a burn-in of 50,000. For all analyses, convergence was evaluated using several criteria: the effective sample size exceeded the recommended threshold (≥ 100), Geweke diagnostic Z-scores were within the range -1.96 to $+1.96$, and visual inspection of the Markov chains indicated adequate convergence. The genetic correlation was estimated as

$$r_g = \frac{\sigma_{a1a2}}{\sqrt{\sigma_{a1}\sigma_{a2}}}, \quad [10]$$

where σ_{a1a2} is the additive covariance between trait 1 and 2 and σ_{a1} and σ_{a2} are additive variances of trait 1 and 2, respectively.

RESULTS AND DISCUSSION

This study deals with different methane phenotypes derived from direct methane records and was conducted on a total of 11,377 records (66% of the weekly averages before filtering) from 2,961 cows (85% of weekly averages before filtering) across 34 commercial farms. Records were distributed across 3 lactation stages (levels 1, 2, and 3), with 3,421, 2,257, and 5,699 records, respectively, and across 3 lactation numbers (parities 1, 2, and 3), with 4,092, 3,243, and 4,042 records, respectively. A detailed frequency of records per lactation week is presented in Figure 3. Genetic parameters were estimated between traditional and novel traits using pedigree with an average of 7 equivalent generations and genotypic data for more than 70% of the sampled individuals. The findings from this research are expected to provide valuable insights into the knowledge of genetic relationship between different definitions of methane traits from sniffers data to be used in breeding programs.

Descriptive statistics of weekly averages of methane phenotypes are presented in Table 1. The AVGCH4 and AVGCH4_5s, showed similar estimates ($\pm$ SD), 358 ($\pm$ 189) and 359 ($\pm$ 190), respectively. These estimates were in line with previous estimation of methane concentration in dairy cattle (van Breukelen et al., 2023), using a different sniffer brand (WD-WUR v1.0, manufactured by Carltech BV). However, they were lower than other estimates obtained with the same brand of sniffers (Diford et al., 2018a), but these differences can be explained by the high variation (SD) obtained in the present study, associated with the variation across farms. In contrast, the average of AUC by second ($12,825 \pm 7,607$) differed from the same trait calculated every 5 s ($2,717 \pm 1,867$), with the latter being lower. This difference can

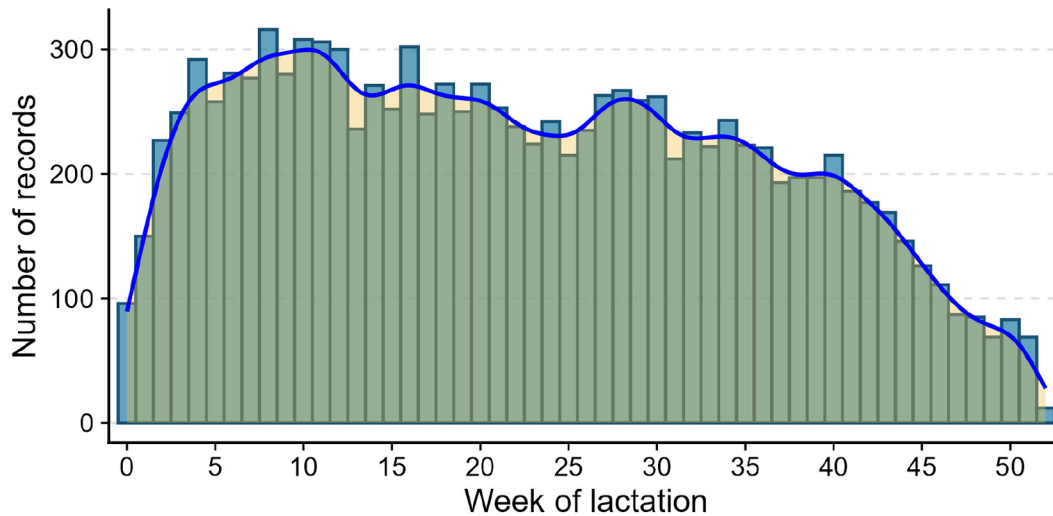


Figure 3. Number of records per week of lactation.

be explained because this phenotype is calculated by the summation of all the values within the peaks, and measurements per second represent more values than measurements every 5 s. The AUC phenotype is similar to the peak area integral estimated by Garnsworthy et al. (2012), but AUC is calculated over all peaks, while the second one is estimated by peak. The MAXPK showed a lower value than AUC because the first is calculated by summation of the average of only 2 points of each peak. In contrast, the frequency of eructation per minute (NPK) was approximately 0.6, which was slightly lower than similar studies in cattle (Garnsworthy et al., 2012; Bell et al., 2014). This may be explained by different methods used to detect the peaks.

The AVGCO₂ concentration showed an average of $5,371 \pm 1,722$, which is lower than that reported by Huhtanen et al., 2015; $7,600 \pm 2,223$) and higher than the findings of van Breukelen et al. (2022; $3,820 \pm 1,660$). These discrepancies may be attributed to different device settings or varying methodologies used to establish background levels. For instance, Huhtanen et al. (2015) determined background based on air concentrations recorded immediately before and following the cow's visit, whereas our study defined the background as the 5 lowest concentrations recorded during each visit. Furthermore, the range of the CO₂ detection device is an important variable influencing CO₂ averages. For example, van Breukelen et al. (2022) used a sniffer with a measuring range for CO₂ concentrations up to 10,000 ppm, in contrast to the device employed in our study, which measures up to 50,000 ppm. The CH₄:CO₂ was 0.07 ± 0.01 , which is similar to the results of Lassen and Løvendahl (2016), but lower to the 0.13 ± 0.12 reported by van Breukelen et al. (2022). The underlying reasons

for these variations may be attributed to either elevated CH₄ levels, diminished CO₂ concentrations, or a combination of both factors.

For methane production, both METPROD and METEST showed similar mean values, $337 (\pm 89)$ and $309 (\pm 80)$ g/d, respectively, with a high phenotypic correlation between them ($R^2 = 0.90$). These estimates are lower than those reported in studies of high-producing Holstein cows, where mean methane emissions often exceed 400 g/d. For example, van Breukelen et al. (2023) reported weekly mean values of 435 ± 98 g/d using GreenFeed, whereas methane production derived from the Madsen et al. (2010) equation applied to sniffer data yielded 331 ± 218 g/d, highlighting the influence of measurement method on observed averages. Similarly, Hristov et al. (2018) reported mean methane emissions of 344 ± 103 g/d using respiration chambers, 435 ± 78 g/d with GreenFeed, and 316 ± 89 g/d using the SF₆ tracer technique. In contrast, Garnsworthy et al. (2019) reported methane values exceeding 400 g/d across multiple measurement methods, including respiration chambers, GreenFeed, SF₆, and laser devices. The lower averages observed in our study likely reflect differences in diet, production systems, and population characteristics. Unlike many controlled experiments, the present study is based on a large and heterogeneous commercial population, capturing a broad range of production levels and management conditions.

The curve of METEST along the lactation showed a steep increase at wk 10 (Figure 4), which is in line with the standard lactation curve in dairy cows (Silvestre et al., 2009). Then another small, less pronounced increase occurred from wk 15 and 25. After wk 25, it starts to decrease until approximately wk 50. This trend is ob-

Table 2. Estimated additive (a), permanent (pe), herd-robot-week-year (h), and residuals (e) variances for the methane and carbon dioxide phenotypes analyzed

Trait ¹	σ_a^2	σ_{pe}^2	σ_h^2	σ_e^2
AVGCH4 (ppm)	1,294	7,216	32,329	6,210
AVGCH4_5s (ppm)	1,308	7,313	32,472	6,280
AUC ² (ppm)	275	1,326	4,559	1,158
AUC_5s ³ (ppm)	1,078	5,288	18,086	4,602
MAXPK (ppm)	3,712	24,069	90,367	21,812
NPK	0.59×10^{-2}	0.86×10^{-2}	0.36×10^{-2}	0.48×10^{-2}
AVGCO2 (ppm)	49,101	497,520	21×10^5	379,010
CH4:CO2	0.18×10^{-4}	0.55×10^{-4}	0.11×10^{-3}	0.77×10^{-4}
METPROD (g/d)	476	2,159	3,188	1,893
METEST (g/d)	428	1,518	2,862	1,782

¹AVGCH4 = average of CH₄; AVGCH4_5s = average of CH₄ estimated every 5 s; AUC = area under the curve; AUC_5s = area under the curve estimated every 5 s; MAXPK = summation of the averages of the 2 highest measurements from each peak within a visit; NPK = number of peaks per minute; AVGCO2 = average of CO₂; CH4:CO2 = ratio of AVGCH4 and AVGCO2; METPROD = methane production estimated with the Madsen equation; METEST = methane production adjusted by the CO₂ expected by comparison group.

²Variance component estimated from the trait AUC divided by 100.

³Variance component estimated from the trait AUC_5s divided by 10.

served when methane is predicted from equations that include BW and milk yield (Garnsworthy et al., 2012) and may be associated with decreased milk production in late lactation. However, METEST values do not directly depend on productive traits, therefore the trend of the curve might be associated with the ingesta during gestation, which is positively correlated with methane emissions (Harder et al., 2019).

Genetic Parameters

The variance components explained by additive, permanent, contemporary group, and residual effects are shown in Table 2. The contemporary group accounted for the largest proportion of variance in CH₄ and CO₂ con-

centrations, reflecting the inherent variability of sniffers due to feed-bin characteristics, airflow, and uncontrolled animal movement (Huhtanen et al., 2015). In contrast, methane production traits showed lower variance explained by the contemporary group, because they are pre-adjusted for comparison groups. For example, METEST is standardized by expected CO₂ production, while CH4:CO2 and NPK are less sensitive to dilution effects.

Heritability estimates for methane phenotypes ranged from 0.07 to 0.12 (Table 3), consistent with previous reports in this population (0.11–0.12; López-Paredes et al., 2020) and other dairy populations (0.10–0.20; Dillard et al., 2018b; Lassen and Løvendahl, 2016; van Engelen et al., 2018). Higher estimates (~0.32) have also been reported using sniffers and GreenFeed (van Breuke-

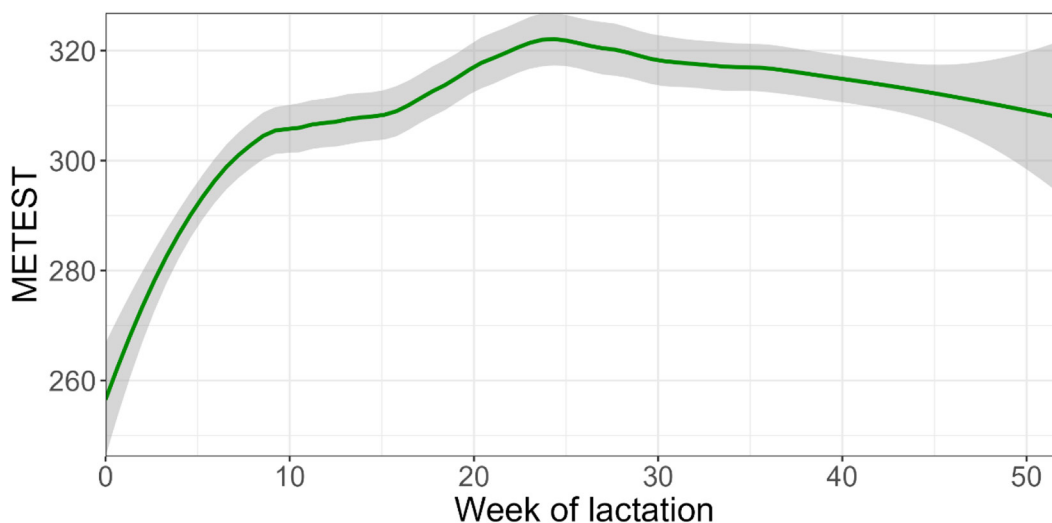


Figure 4. Average METEST (g/d) per week of lactation in the 23 commercial farms evaluated. The solid line is the loess regression of the averages of METEST and the gray shadow shows the 95% CI.

len et al., 2023). Milk production traits, in comparison, displayed moderate heritability, as previously described (Kadarmideen et al., 2003; Pritchard et al., 2013). Heritability of CO₂ concentration was lower than both methane traits and previous estimates (van Engelen et al., 2018; van Breukelen et al., 2023), suggesting a stronger environmental influence. Nevertheless, CO₂ remains useful as a technical control because very low CO₂ values may indicate unreliable measurements (Oikawa et al., 2022).

Phenotypes measured at different sampling intervals (1 s vs. 5 s) yielded similar heritability and repeatability values, indicating that recording frequency does not bias genetic parameter estimates. This finding supports comparability across studies using different sampling intervals and highlights opportunities to optimize device storage (Lassen and Løvendahl, 2016; van Breukelen et al., 2024). Measurement periods of 3 to 4 wk per farm enabled at least 2 weekly averages per animal, yielding moderate-to-high repeatability (0.49–0.58), with the highest for NPK (0.75; Table 3). These values align with previous findings, which emphasize the influence of measurement duration: shorter periods (~3 d) yield lower repeatability (0.39; Lassen et al., 2012), and longer periods (>60 d) increase it (0.66; van Breukelen et al., 2023). Using GreenFeed, Manafiazar et al. (2017) also reported high repeatability for CH₄ (0.79) and CO₂ (0.86).

Methane concentration traits showed very high phenotypic (0.90–0.99; $P < 0.001$) and genetic (0.78 [highest posterior density interval, **HPD** = 0.67–0.88] to 0.99 [HPD = 0.98–0.99]) correlations (Table 4). Peak-derived traits were more strongly correlated with each other than with average-derived traits, and both measurement frequencies (1 s vs. 5 s) showed correlations of 0.99 (HPD = 0.98–0.99). The NPK showed weaker correlations (phenotypic: 0.20–0.40; genetic: 0.45–0.49) and a negative genetic correlation with AVGCH₄ (–0.21).

The CH₄:CO₂ trait showed high phenotypic and genetic correlations with methane concentration, particularly with AVGCH₄ (0.70 [$P < 0.001$]) and 0.94 [HPD = 0.85–0.99], respectively). Correlations with NPK were near 0 (phenotypic) or negative (genetic), similar to the pattern with AVGCH₄. The CH₄:CO₂ is relevant as a correction for technical variability and for estimating methane production, but its use in genetic selection is debated because of nonlinear relationships with its components (Løvendahl et al., 2018) and unequal variance contributions (Zetouni et al., 2017). In this study, the stronger correlation with AVGCH₄ than with AVGCO₂ (0.88 vs. 0.28) suggests that selection on CH₄:CO₂ would primarily target methane.

Methane production traits (METPROD and METEST) showed moderate-to-high correlations with methane concentration (phenotypic: 0.56–0.74; genetic: 0.44–0.99), with the highest values for average-derived traits. The

Table 3. Heritabilities (h^2) and repeatabilities (t) of methane and carbon dioxide phenotypes, with 95% CI in parentheses

Trait ¹	h^2	t
AVGCH ₄ (ppm)	0.09 (0.05 to 0.13)	0.58 (0.56 to 0.60)
AVGCH ₄ _5s (ppm)	0.09 (0.05 to 0.13)	0.58 (0.56 to 0.60)
AUC (ppm)	0.10 (0.06 to 0.14)	0.58 (0.56 to 0.60)
AUC_5s (ppm)	0.10 (0.05 to 0.14)	0.58 (0.56 to 0.60)
MAXPK (ppm)	0.07 (0.03 to 0.11)	0.56 (0.54 to 0.58)
NPK	0.30 (0.24 to 0.37)	0.75 (0.73 to 0.76)
AVGCO ₂ (ppm)	0.05 (0.01 to 0.10)	0.59 (0.56 to 0.61)
CH ₄ :CO ₂	0.12 (0.06 to 0.17)	0.49 (0.46 to 0.52)
METPROD (g/d)	0.10 (0.03 to 0.17)	0.58 (0.55 to 0.61)
METEST (g/d)	0.11 (0.05 to 0.17)	0.52 (0.49 to 0.55)
Milk yield (kg)	0.21 (0.16 to 0.26)	0.78 (0.78 to 0.79)
Protein yield (kg)	0.20 (0.14 to 0.25)	0.78 (0.77 to 0.79)
Fat yield (kg)	0.22 (0.16 to 0.27)	0.82 (0.81 to 0.83)

¹AVGCH₄ = average of CH₄; AVGCH₄_5s = average of CH₄ estimated every 5 s; AUC = area under the curve; AUC_5s = area under the curve estimated every 5 s; MAXPK = summation of the averages of the 2 highest measurements from each peak within a visit; NPK = number of peaks per minute; AVGCO₂ = average of CO₂; CH₄:CO₂ = ratio of AVGCH₄ and AVGCO₂; METPROD = methane production estimated with the Madsen equation; METEST = methane production adjusted by the CO₂ expected by comparison group.

AVGCH₄ was strongly correlated with METPROD (0.88; HPD = 0.71–0.99) and METEST (0.99; HPD = 0.98–0.99), and the 2 methane production traits themselves showed high correlation (phenotypic: 0.90 [$P < 0.001$]; genetic: 0.86 [HPD = 0.72–0.98]).

Correlations between CO₂ and methane concentrations were high with averages-derived traits (0.69–0.73), consistent with previous studies in dairy (Madsen et al., 2010) and beef cattle (Renand et al., 2019; Ryan et al., 2022). However, the correlation with peak-derived traits was weak (0.18–0.30). Positive phenotypic and genetic correlations were also observed between CO₂ and methane production, reflecting that cows exhaling more CO₂ also emit more CH₄. Because CO₂ production reflects metabolic rate (Madsen et al., 2010; Huhtanen et al., 2015), higher CO₂ implies increased feed fermentation and greater methane output. Supporting this, Donoghue et al. (2020) reported strong genetic correlations between CO₂ and methane production in beef cattle. High correlations were also observed between gas-emission traits and growth and body composition, consistent with their shared biological basis.

Genetic Correlations with Productive Traits

Genetic correlations between methane and production traits were generally positive and moderate, both for concentration (0.16–0.47) and production (0.32–0.78). In contrast, NPK showed negative correlations with milk (–0.24), fat (–0.09), and protein (–0.26) yields, consistent with its weaker association with total methane output. The AVGCH₄ was more strongly correlated with production

Table 4. Phenotypic (below diagonal) and genetic r_g (above diagonal) correlations between methane and carbon dioxide phenotypes, with 95% CI in parentheses¹

Trait	Methane concentration						Methane production			
	AVGCH4 (ppm)	AVGCH4_5s (ppm)	AUC (ppm)	AUC_5s (ppm)	MAXPK (ppm)	NPK	AVGCO2 (ppm)	CH4:CO2	METPROD (g/d)	METEST (g/d)
AVGCH4 (ppm)	—	0.99 (0.99 to 1.00)	0.82 (0.74 to 0.91)	0.82 (0.70 to 0.90)	0.78 (0.67 to 0.88)	-0.21 (-0.45 to 0.05)	0.69 (0.41 to 0.94)	0.94 (0.85 to 0.99)	0.88 (0.71 to 0.99)	0.99 (0.98 to 0.99)
AVG_5s (ppm)	0.99***	—	0.82 (0.71 to 0.90)	0.82 (0.70 to 0.90)	0.78 (0.67 to 0.87)	-0.21 (-0.46 to 0.04)	0.73 (0.43 to 0.95)	0.94 (0.85 to 0.99)	0.89 (0.73 to 0.99)	0.99 (0.99 to 1.00)
AUC (ppm)	0.94***	0.94***	—	0.99 (0.99 to 1.00)	0.99 (0.99 to 1.00)	0.49 (0.29 to 0.68)	0.18 (-0.54 to 0.66)	0.46 (0.13 to 0.73)	0.44 (0.07 to 0.79)	0.57 (0.32 to 0.77)
AUC_5s (ppm)	0.94***	0.94***	0.99***	—	0.82 (0.70 to 0.90)	0.49 (0.28 to 0.68)	0.26 (-0.34 to 0.76)	0.46 (0.13 to 0.73)	0.44 (0.06 to 0.79)	0.54 (0.26 to 0.77)
MAXPK (ppm)	0.90***	0.90***	0.93***	0.93***	—	0.45 (0.25 to 0.65)	0.30 (-0.41 to 0.81)	0.55 (0.24 to 0.81)	0.47 (-0.10 to 0.92)	0.65 (0.39 to 0.85)
NPK	0.20***	0.20***	0.39***	0.36***	0.40***	—	-0.39 (-0.82 to 0.10)	-0.14 (-0.41 to 0.13)	-0.41 (-0.79 to -0.04)	-0.19 (-0.50 to 0.11)
AVGCO2 (ppm)	0.85***	0.85***	0.77***	0.77***	0.74***	-0.01 ($P = 0.61$)	—	0.27 (-0.35 to 0.71)	0.50 (-0.09 to 0.97)	0.40 (-0.15 to 0.83)
CH4:CO2	0.70***	0.70***	0.68***	0.68***	0.64***	0.02 ($P = 0.06$)	0.35***	—	0.92 (0.84 to 0.98)	0.99 (0.98 to 0.99)
METPROD (g/d)	0.63***	0.62***	0.60***	0.60***	0.56***	0.04**	0.31***	0.89***	—	0.86 (0.72 to 0.98)
METEST (g/d)	0.74***	0.74***	0.72***	0.72***	0.67***	0.02*	0.43***	0.94***	0.90***	—

¹AVGCH4 = average of CH₄; AVGCH4_5s = average of CH₄ estimated every 5 s; AUC = area under the curve; AUC_5s = area under the curve estimated every 5 s; MAXPK = summation of the averages of the 2 highest measurements from each peak within a visit; NPK = number of peaks per minute; AVGCO2 = average of CO₂; CH4:CO2 = ratio of AVGCH4 and AVGCO2; METPROD = methane production estimated with the Madsen equation; METEST = methane production adjusted by the CO₂ expected by comparison group.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, Pearson test.

Table 5. Estimated genetic correlations between methane and carbon dioxide phenotypes and productive traits with 95% CI in parentheses¹

Trait	Milk yield (kg)	Fat yield (kg)	Protein yield (kg)
AVGCH4 (ppm)	0.47 (0.25 to 0.70)	0.38 (0.14 to 0.62)	0.32 (0.05 to 0.57)
AVGCH4_5s (ppm)	0.47 (0.25 to 0.70)	0.38 (0.13 to 0.61)	0.32 (0.05 to 0.57)
AUC (ppm)	0.21 (−0.04 to 0.44)	0.20 (−0.05 to 0.45)	0.09 (−0.17 to 0.36)
AUC_5s (ppm)	0.21 (−0.04 to 0.45)	0.20 (−0.05 to 0.45)	0.22 (−0.11 to 0.54)
MAXPK (ppm)	0.22 (−0.05 to 0.48)	0.18 (−0.10 to 0.45)	0.16 (−0.09 to 0.42)
NPK	−0.24 (−0.44 to −0.59)	−0.09 (−0.29 to 0.12)	−0.26 (−0.45 to −0.05)
AVGCO2 (ppm)	0.72 (0.12 to 0.99)	0.53 (0.04 to 0.90)	0.59 (−0.34 to 0.99)
CH4:CO2	0.29 (−0.03 to 0.59)	0.42 (0.09 to 0.70)	0.33 (−0.01 to 0.65)
METPROD (g/d)	0.78 (0.47 to 0.98)	0.73 (0.43 to 0.99)	0.69 (0.32 to 0.98)
METEST (g/d)	0.32 (−0.01 to 0.68)	0.48 (0.12 to 0.74)	0.36 (0.01 to 0.69)

¹AVGCH4 = average of CH₄; AVGCH4_5s = average of CH₄ estimated every 5 s; AUC = area under the curve; AUC_5s = area under the curve estimated every 5 s; MAXPK = summation of the averages of the 2 highest measurements from each peak within a visit; NPK = number of peaks per minute; AVGCO2 = average of CO₂; CH4:CO2 = ratio of AVGCH4 and AVGCO2; METPROD = methane production estimated with the Madsen equation; METEST = methane production adjusted by the CO₂ expected by comparison group.

traits (0.32–0.47) than peak-derived phenotypes (0.09–0.22; Table 5). The strongest correlations (0.18–0.73) were observed with fat yield, which was consistent with previous studies (Lassen and Løvendahl, 2016; Breider et al., 2019; Pszczola et al., 2019), and likely reflect the biological link between VFA production and methane release during fermentation (Dijkstra et al., 2011).

Carbon dioxide also showed moderate-to-high positive genetic correlations with production traits (0.53–0.72), particularly fat yield, highlighting its role as an indicator of feed digestion and metabolic activity. In contrast, both phenotypic and genetic correlations between CO₂ and NPK were low and negative, aligning with the limited contribution of eructation frequency to total methane emissions.

The literature consistently reports positive genetic correlations between methane and milk yield traits, despite variation in measurement methods, trait definitions, and models. For example, Pszczola et al. (2019) found positive correlations with fat (0.21) and milk (0.15) yield using methane production derived from Madsen's equation, although this approach can inflate correlations, as discussed throughout this manuscript. Manzanilla-Pech et al. (2022a) reported a moderate correlation (0.44) between methane (from Madsen's equation) and ECM, whereas Rojas de Oliveira et al. (2024) found methane predicted from mid-infrared spectroscopy correlated positively with fat (0.38) but slightly negatively with milk and protein yield. Similarly, Kandel et al. (2017) reported a weak positive correlation with fat (0.11) but negative values for milk and protein, with large SE. More recently, van Breukelen et al. (2025) reported weak positive correlations between methane concentration from sniffers and milk traits.

Methane production traits also correlated positively with production traits, although estimates differed between calculation methods. The METPROD values showed moderate-to-high correlations with milk, fat, and

protein yields (0.69–0.78) recorded in the AMS, likely reflecting its dependence on productive traits in the conversion equation (Madsen et al., 2010), which estimates CO₂ production from HPU (Pedersen et al., 2008). The inclusion of ECM in this equation likely inflates correlations with milk and component yields. In contrast, METEST, which adjusts methane concentration using predicted CO₂ while accounting for contemporary group effects, showed weaker correlations with yield traits in the AMS (0.32–0.48) but still strong genetic alignment with AVGCH4 (0.99; HPD = 0.98–0.99). Thus METEST may be a more advantageous option in comparison to alternative methane traits that depend on productive traits. Previous studies have indicated the bias associated with estimated genetic correlations between methane production (estimated using productive traits) and productive traits such as ECM, BW, and DMI (Breider et al., 2019; Manzanilla-Pech et al., 2022a). These skewed correlations present 2 significant challenges. The first implies that by selecting for methane reduction, one would indirectly also be selecting for other traits of interest, affecting negatively the genetic progress in production. The second challenge arises when the trait is incorporated into selection indexes because it is effectively counted twice, making it difficult to disentangle methane from productive traits and assign an independent weighting. Conversely, METEST does not directly incorporate production traits, is less biased by milk yield, and may be more suitable for breeding objectives, where correlations with production traits can be modeled explicitly within selection indexes, allowing the reduction in methane emissions with minimal effects on the genetic progress of productive traits (González-Recio et al., 2020).

This study, based on a large-scale commercial cohort, enabled precise estimation of heritability and correlations while accounting for diverse management practices. It also provided a robust evaluation of technical variability

ity in the sniffer method. Nonetheless, some limitations remain. Validation of novel methane phenotypes against gold-standard methods (e.g., GreenFeed, g/day) is necessary because assumptions such as constant airflow sampling (1 L/min) may not hold in practice. In addition, although the adjustment of the novel phenotype by CO₂ production per comparison group makes it indirectly independent of individual production records, caution is required regarding the number of observations per group used for this adjustment. In particular, a sufficiently large proportion of available records within each group, preferably exceeding 50% or a comparable threshold, is recommended to ensure stable and reliable representation of the group. Further, the implications of including methane traits with moderate correlations to production traits in breeding goals require careful evaluation. Despite these limitations, our findings provide valuable insight into methane phenotype definitions and their potential integration into selection programs.

CONCLUSIONS

This study demonstrates that sniffer devices enable the collection of large-scale methane phenotypes under commercial conditions, providing reliable estimates of genetic parameters. The extensive dataset allowed precise estimation of correlations, showing strong genetic links among methane traits, whether derived from overall measurements or from eructation events. Genetic correlations with production traits were consistently positive, with the strongest and most antagonistic relationship observed with fat yield. The CH₄:CO₂ trait proved to be heritable, repeatable, and strongly correlated with methane concentration, confirming its utility for deriving methane production traits, although its role in selection programs remains debated. Importantly, we propose a novel methane production phenotype (METEST) that does not directly rely on individual milk yield traits. The METEST showed favorable genetic properties and reduced bias compared with conventional methods, highlighting its potential for inclusion in sustainability-oriented breeding indexes. Together, these findings provide new insights into methane trait definition and measurement and support the integration of robust methane phenotypes into breeding programs aimed at reducing environmental impact without substantially compromising productivity, given the moderate genetic correlations between methane and productive traits (0.28–0.52).

NOTES

This research was funded by RTA2015-00022-C03 (METALGEN; Madrid, Spain) project from the Spanish

National Plan of Research, development, and innovation 2013-2020, the Agreement CON23-227 between CSIC-INIA (Madrid, Spain) and ASCOL (Oviedo, Spain) for the implementation of the NEOWAS (Brussels, Belgium) project on genetic analysis and development of methane emission equations in dairy cattle and the Department of Economic Development and Competitiveness (Basque Government, Vitoria-Gasteiz, Spain). Farmers and breeders' associations are acknowledged for data sharing and infrastructure. Data were analyzed using the CESGA Supercomputing infrastructure (Galicia, Spain). This work has received funding from the European Union's Horizon Europe research and innovation program under the grant agreement No 101059609 (Re-Livestock project; Brussels, Belgium). No human or animal subjects were used, so this analysis did not require approval by an Institutional Animal Care and Use Committee or Institutional Review Board. The authors have not stated any conflicts of interest.

Nonstandard abbreviations used: AMS = automatic milking system; AUC = area under the curve per visit; AUC_5s = area under the curve per visit estimated in a 5-s interval; AVGCH4 = methane average per visit; AVGCH4_5s = methane average per visit estimated in a 5-s interval; AVGCO₂ = carbon dioxide average per visit; CH₄:CO₂ = ratio of AVGCH4 and AVGCO₂; HPD = highest posterior density interval; HPU = heat-producing unit; Max = maximum; MAXPK = summation of the averages of the 2 highest measurements from each peak within a visit; METPROD = methane production (g/d) estimated with Madsen's equation; METEST = methane production (g/d) estimated adjusting by production traits; Min = minimum; NPK = number of peaks per minute.

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ORCIDS

- E. Teran,  <https://orcid.org/0000-0002-8476-7940>
 A. García Rodríguez,  <https://orcid.org/0000-0001-5519-6766>
 I. Goiri,  <https://orcid.org/0000-0002-6522-0085>
 J. A. Jiménez-Montero,  <https://orcid.org/0000-0002-8121-1509>
 O. González-Recio  <https://orcid.org/0000-0002-9106-4063>