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Exploring definitions of daily enteric methane emission phenotypes for genetic evaluations using a population of indoor-fed multi-breed growing cattle with feed intake data

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Abstract

Genetic selection has been identified as a promising approach for reducing enteric methane (CH_4) emissions; a prerequisite for genetic evaluations; however, these are estimates of the necessary genetic parameters based on a population representative of where the genetic evaluations will be used. The objective of this study was, therefore, to derive genetic parameters for a series of definitions of CH_4, carbon dioxide (CO_2), and dry matter intake (DMI) as well as genetic correlations between CH_4, CO_2, and DMI in a bid to address the paucity of studies involving methane emissions measured in beef cattle using GreenFeed systems. Lastly, estimated breeding values (EBV) were generated for nine alternative definitions of CH_4 using the derived genetic parameters; the EBV were validated against both phenotypic performance (adjusted for non-genetic effects) and the Legarra and Reverter method comparing EBV generated for a subset of the dataset compared to EBV generated from the entire dataset. Individual animal CH_4 and CO_2 records were available from a population of 1,508 multi-breed growing beef cattle using 10 GreenFeed Emission Monitoring systems. Nine trait definitions for CH_4 and CO_2 were derived: individual spot measures, the average of all spot measures within a 3-h, 6-h, 12-h, 1-d, 5-d, 10-d, and 15-d period and the average of all spot measures across the full test period (20 to 114 d on test). Heritability estimates from 1,155 animals, for CH_4, increased as the length of the averaging period increased and ranged from 0.09 ± 0.03 for the individual spot measures trait to 0.43 ± 0.11 for the full test average trait; a similar trend existed for CO_2 with the estimated heritability ranging from 0.17 ± 0.04 to 0.50 ± 0.11. Enteric CH_4 was moderately to strongly genetically correlated with DMI with a genetic correlation of 0.72 ± 0.02 between the spot measures of CH_4 and a 1-d average DMI. Correlations, adjusted for heritability, between the adjusted phenotype and (parental average) EBV ranged from 0.56 to 1.14 across CH_4 definitions and the slope between the adjusted phenotype and EBV ranged from 0.92 to 1.16 (expectation = 1). Validation results from the Legarra and Reverter regression method revealed a level bias of between −0.81 and −0.45, a dispersion bias of between 0.93 and 1.17, and ratio accuracy (ratio of the partial evaluation accuracies on whole evaluation accuracies) from 0.28 to 0.38. While EBV validation results yielded no consensus, CH_4 is a moderately heritable trait, and selection for reduced CH_4 is achievable.

Lay Summary

Livestock production is a significant contributor to greenhouse gas emissions. Animal breeding programs have been proposed as a sustainable mitigation strategy to reduce enteric methane emissions in livestock production. Before creating a genetic evaluation for enteric methane production, it is important to estimate how much inter-animal genetic variability contributes to the observed differences in enteric methane production. The purpose of this study was to explore multiple enteric methane phenotypes and estimate how much phenotypic variation was due to genetic differences among 1,508 growing cattle of multiple breeds and crosses; also of interest was the extent of similarity in the genetic control of enteric methane, carbon dioxide, and feed intake (i.e., the genetic correlation) and to determine if selection of animals on the estimated genetic merit for methane emissions of their parents would manifest itself in differences in actual methane produced by those animals. Between 9% and 43% of the inter-animal differences in daily enteric methane production were due to differences in the genetic composition of those animals; the genetic control influencing methane production was similar to that of feed intake (i.e., a strong genetic correlation between methane emissions and feed intake of up to 0.72).

Key words: beef cattle, heritability, carbon dioxide, GreenFeed, validation

Abbreviations: AP, adjusted phenotype; CH_4, enteric methane; CO_2, carbon dioxide; CV_e, coefficient of residual variation; CV_g, coefficient of genetic variation; DMI, dry matter intake; EBV, estimated breeding value; GEM, GreenFeed emission monitoring; ICBF, Irish Cattle Breeding Federation; NDIR, non-dispersive infrared sensor; RFID, radio frequency identification; TBV, true breeding value; TMR, total mixed ration

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Introduction

Livestock production is a contributor to global anthropogenic emissions of potent greenhouse gases, including enteric methane (CH_4; Eisen and Brown, 2022). Enteric CH_4, as a byproduct of feed fermentation, accounts for a loss of 2% to 12% of the gross energy intake of cattle (Johnson and Johnson, 1995); 89% of total CH_4 produced by ruminants is excreted through eructation (Broucek, 2014). Reducing enteric CH_4 emissions through mitigation strategies remains a crucial step towards achieving global greenhouse gas reduction targets. Several studies have identified animal breeding as a promising approach for reducing CH_4 emissions (Donoghue et al., 2016; Hayes et al., 2016; de Haas et al., 2021), emphasizing the role of animal breeding as an important part of the global strategy to addressing the issue of CH_4 emissions in agriculture.

The advantage of animal breeding as a mitigation strategy to reduce CH_4 emissions is that it is a cost-effective, permanent, and cumulative approach (Knapp et al., 2014). In order to incorporate CH_4 as a trait in a breeding goal, it is necessary to establish a clear trait definition, which is recordable in an affordable manner, exhibits phenotypic variation, and is under genetic control (de Haas et al., 2017, 2021). Estimates of genetic parameters for the trait in question are required in the mixed model equations used in genetic evaluations. Several studies in sheep and cattle have previously demonstrated CH_4 to be moderately heritable with estimates varying depending on population and measurement method (Jonker et al., 2018; Garnsworthy et al., 2019); CH_4 heritability estimates in dairy cattle using sniffers ranged from 0.13 to 0.32 (van Breukelen et al., 2022), whereas estimates from respiration chambers in Angus cattle ranged from 0.19 to 0.32 (Donoghue et al., 2016, 2020). However, the majority of these estimates to date have been derived from dairy cow populations (Pszczola et al., 2017; Bittante and Cecchinato, 2020; López-Paredes et al., 2020; Manzanilla-Pech et al., 2021; Richardson et al., 2021; van Breukelen et al., 2022), and little is known about the heritability of CH_4 in beef populations and, in particular, beef populations where CH_4 was measured using GreenFeed Emission Monitoring (GEM) systems. Genetic correlations between CH_4 traits and feed intake estimated in Angus cattle populations (Donoghue et al., 2016, 2020; Manzanilla-Pech et al., 2016) are positive and range from moderate to strong; however, the genetic correlation between various CH_4 definitions and feed intake in multi-breed cattle populations collected simultaneously using GEM systems and automatic feed stations is unknown. Lastly, although CH_4 emissions have been demonstrated to be moderately repeatable (Ryan et al., 2022), there remains substantial diurnal variation across CH_4 estimates; consequently, the impact of averaging a number of repeated spot measures per animal on the heritability estimate and contributing variance components is also of interest.

Therefore, the objective of this study was to use a large database of GEM system data from a cattle performance test facility to: (1) estimate genetic parameters for several definitions of CH_4, carbon dioxide (CO_2), and dry matter intake (DMI); (2) estimate the genetic correlations between CH_4, CO_2, and DMI; and (3) validate the CH_4 estimated breeding values (EBV) produced by comparing parental average EBV for CH_4 against actual phenotypic CH_4. This is the first study to generate heritability estimates for CH_4 from a multi-breed population of growing beef cattle recorded using GEM systems and focuses on the practical application of research to genetic evaluations. The results from this study will help establish a method for developing EBV for an CH_4 trait.

Materials and Methods

The data used in the present study were obtained from a pre-existing database managed by the Irish Cattle Breeding Federation. Therefore, it was not necessary to obtain animal care and use committee approval in advance of conducting this study.

Phenotypic data

The dataset used in this study is an expanded dataset of that previously described in detail by Ryan et al. (2022). Briefly, CH_4 and CO_2 flux measurements were recorded between the years 2018 and 2022 using 10 GEM systems in the Gene Ireland Progeny Performance Test Center (https://www.icbf.com/?page_id=12900) located in Tully, Co. Kildare, Ireland which operates as a commercial feedlot. Details of the CH_4, CO_2 and feed intake measurements, and the diet fed and how the cattle were acclimatized to the GEM are described in detail elsewhere (Ryan et al., 2022). Briefly, a total mixed ration of ~13.95% hay, 45.35% concentrates, and 40.7% water was provided to the steers and heifers once per day during the test period with a paddle mixer wagon. The total mixed ration was estimated to have a dry matter of 51% and a metabolizable energy value of 12.1 MJ/kg DM. Young bulls were fed concentrates ad libitum, based on the consumption of feed during the acclimatization period. GEM system feed storage bins were filled with concentrates every second day. The concentrates offered within the GEM system to all test animals had dry matter of 86% and a metabolizable energy concentration of 14.1 MJ/kg DM. Measurements were recorded on animals ranging from 356 to 897 d of age at test start date and consisted of 862 steers, 488 heifers, and 158 young bulls, with all animals slaughtered immediately after the end of the test. All cattle were grouped in pens of 25 animals according to their sex, liveweight, and breed, and each group was referred to as a cohort. Cohorts were comprised of animals of the same animal type, i.e., suckler-bred beef, beef-sired animals from the dairy herds, and dairy-bred animals. The breed breakdown of the animals included in this study, by sire and dam breed, are described in Supplementary Table S1. Mean liveweight at the end of test period was 652 kg (SD = 68.6 kg) for steers, 651 kg (standard deviation = 62.5 kg) for heifers, and 672 kg (standard deviation = 65.2 kg) for young bulls.

The GEM systems used in this study were manufactured by C-Lock Inc (C-Lock Inc., Rapid City, South Dakota). All GEM systems were calibrated at the start of each test period and machine settings are described elsewhere (Ryan et al., 2022). The test period ranged from 20 to 114 d in length and was the period of time where animals had full access to the GEM system post-acclimatization. Details of the number of records and animals per GEM system machine are in Supplementary Table S2. The number of visits differed by machine due to varying lengths of time each machine was at the test center, with the oldest GEM system accumulating the greatest number of records (n = 71,135) and animals (n = 313). Animals that did not use the GEM system were not included in the analysis. Ancestry data were available on all animals, and all animals included in the analysis were parentage and breed verified using genotype data. Prior to edits, a total of 400,960 GEM system individual spot measures were available from 1,508 animals destined for slaughter.

Data edits

Test period length in the present study varied by cohort and consisted of a start date (i.e., when all animals in the pen had acclimatized to the GEM system) and an end date, immediately prior to slaughter. Test period length per cohort was determined by management decisions taken in the test station. Only CH_4 spot measures at least 2 min in duration were retained. Furthermore, the top 1% and bottom 1% of values for each trait were discarded (n = 7,878; Supplementary Figure S1). The total number of visits per animal to the GEM ranged from 1 to 459 visits throughout the test period and the total number of days each animal visited to the GEM system at least once ranged from 1 to 113 d. After edits, GEM system data were available on 1,473 animals.

A total of 4,123,569 feed intake visits were recorded using automatic feed stations (RIC Feed-Weigh Trough, Hokofarm Group BV, Marknesse, The Netherlands) on all animals with GEM system measures. Feed intake was estimated as the total feed consumed per animal from both GEM systems and automatic feed stations each calendar day. Feed intake records were quality controlled by using a feeding rate metric (i.e., weight of feed consumed divided by the duration of visit) with the top and bottom 0.5% removed from the analysis (Kelly et al., 2020). Top and bottom 1% feed intake values based on the weight of feed consumed daily were also removed. To ensure all feed intake data directly related to the same period as GEM system measurements, only feed intake records recorded when the animal also had access to the GEM system were retained.

Trait definitions

Each individual GEM CH_4 and CO_2 emission spot measure is reported as grams per day per spot measure, resulting in animals potentially having multiple CH_4 and CO_2 grams per day values. Nine different trait definitions for CH_4 and CO_2 were generated in the present study with the simplest consisting of all the individual spot CH_4 measures. As the length of the test period varied per cohort, the opportunity for a different number of emission spot measures varied per animal. Seven time period definitions were constructed for both CH_4 and CO_2 using the following fixed time periods where the individual spot measures were averaged within each; 3-h, 6-h, 12-h, 1-d, 5-d, 10-d, and 15-d which were collectively referred to as multi-hour or multi-day averaged traits (Supplementary Table S3 and Figure S2). For DMI, feed consumed was summed in 3-h, 6-h, 12-h, and 1-d periods and averaged across days in the 5-d, 10-d, and 15-d periods. Feed intake duration varied largely (average = 166 s, minimum = 12 s, and maximum = 1,181 s). Additionally, a DMI trait for DMI consumed in the time periods prior to the GEM system measurement was also derived for the 3-,6-, and 12-h preceding periods (DMI_{prior}). The DMI_{prior} correlation analysis was used to assess whether CH_4 output may be more influenced by feed intake in the period prior to CH_4 measurement. Lastly, a single full test average per animal trait definition was used where all GEM system CH_4 and CO_2 spot measures and separately daily DMI throughout the test were averaged (Supplementary Figure S2). All nine GEM trait definitions were reported in grams per day (Supplementary Table S3 and Figure S2). As a result, each of the 1,473 animals had at least one phenotype for all nine traits for GEM system measurements for CH_4 and CO_2 separately.

Statistical analyses

(Co)variance component estimation.

Additional edits for parameter estimation included the removal of 13 animals with missing sires and a further 297 animals whose sires did not have a minimum of three progeny per cohort, along with the removal of eight animals that visited the GEM systems on less than four individual days across the test period (Supplementary Figure S1). In total, 318 animals did not meet the inclusion criterion for parameter estimation. After these edits, GEM emission measurements and feed intake records were available on 1,155 animals of which 611 were steers, 421 were heifers and 123 were young bulls. Genetic parameters were estimated for all nine GEM trait definitions (CH_4 and CO_2 separately) and eight DMI definitions using univariate animal models in DMU (Madsen and Jensen, 2013) and included repeated records for all traits with the exception of the full test average trait. Relationships among animals were accounted for in the mixed models using the numerator relationship matrix constructed using five generations, where available; the pedigree file consisted of 14,288 animals. Three statistical models were used to estimate genetic parameters for CH_4, CO_2, and DMI:

(1) Full test average model:

$$y = X\mathbf{b} + Z\mathbf{a} + \mathbf{e}$$

where y is the average phenotype across the duration of the test; $\boldsymbol{X}$ is the appropriate incidence matrix linking effects to the relevant animals; **b** is a vector of fixed effects which included the fixed class effects of contemporary group and the fixed regressions of breed composition, age and heterosis; **a** is a vector of random additive genetic effects with incidence matrix $\boldsymbol{Z}$, and **e** is a vector of random residual values. Contemporary group included cohort number (number assigned to a group of animals within a pen that were grouped according to their sex, live weight, breed, and type composition, i.e., suckler-bred beef, beef-sired animals from the dairy herds and dairy bred animals) and GEM system number. Breed composition represented the proportion of each breed present in the animal, with 14 breeds included (Angus, Aubrac, Belgian Blue, Charolais, Friesian, Hereford, Holstein, Jersey, Piedmontese, Parthenaise, Saler, Shorthorn, Simmental, and Other). Due to the nature of data collection, animals attended only one GEM system, resulting in one phenotype per full test average trait.

(2) Multi-day average repeated model:

$$y = X\mathbf{b} + Z\mathbf{a} + P\mathbf{u} + \mathbf{e}$$

where y is the average phenotype across 1, 5, 10, and 15 d of test, $\boldsymbol{X}$ is the appropriate incidence matrix linking effects to the relevant animals, **b** is a vector of fixed effects similar to the full test average model; **a** is a vector of random additive genetic effects with incidence matrix $\boldsymbol{Z}$; **u** is a vector of random within multi-day period permanent environmental effects, with incidence matrix $\boldsymbol{P}$ and **e** is a vector of random residual values. Contemporary groups for each multi-day (1-d, 5-d, 10-d, and 15-d) averaged phenotypes included the time period (day(s) of the test) across which records were averaged, cohort number, and GEM system number.

(3) Hourly averaged repeated model:

$$y = X\mathbf{b} + Z\mathbf{a} + W\mathbf{v} + P\mathbf{u} + \mathbf{e}$$

where y is the average phenotypes across 3, 6, and 12 h, X is the appropriate incidence matrix linking effects to the relevant animals, **b** is a vector of fixed effects, respectively, similar to those present in the multi-day average repeated model above; **a** is a vector of random additive genetic effects with incidence matrix Z, **v** is a vector of random within-day, across time (3-h, 6-h, and 12-h periods) effects, with incidence matrix W; **u** is a vector of random within-day permanent environmental effects, with incidence matrix P and **e** is a vector of random residual values. For the hourly averaged phenotypes, contemporary group definition included cohort number, GEM system number, and the time-of-day period (3, 6, or 12-h period in which the measurement occurred) and observation date.

For the analysis of the spot measures, a fixed effect representing time of day was also added to the **b** vector of this model (3). Six classes were used for time of day, with each day split into six defined 4-h periods. Contemporary group included observation date, cohort number, and GEM system number.

Genetic covariances between each of the nine CH_4 trait definitions, the nine CO_2 trait definitions, and the eight DMI trait definitions were estimated using a series of bivariate analyses using the model fitted in the univariate analyses. In addition, bivariate analysis between the 3, 6, and 12-h averaged CH_4 traits and the DMI estimate from the preceding time period, i.e., a 3-h averaged CH_4 measurement was correlated with the DMI in the 3-h period prior to the CH_4 measurement (DMI_{prior}). A bivariate analysis between the spot measure CH_4 and 1-d average DMI was also conducted.

EBV estimation and validation

EBV and their associated accuracies for CH_4 were calculated using the genetic parameter estimates calculated in DMU and the larger dataset of 1,473 animals. These quality control edits applied to the larger dataset of 1,473 animals, are more representative of normal data editing practise applied in routine genetic evaluations. EBV were computed using MiX99 software (MiX99 Development Team, 2017) using the models from the univariate analyses. Following the addition of the breed covariate solutions to assess stability of EBV across trait definitions, Pearson correlation coefficients were estimated between the EBV across each of the different CH_4 trait definitions (i.e., spot measure CH_4 and 3-h CH_4, spot measure CH_4 and 6-h CH_4, etc.) for the 1,473 phenotyped animals. EBV were validated using two approaches, the first approach involved the computation of phenotypes adjusted for fixed effects followed by the regression of the adjusted phenotypes (AP) on the respective EBV of the animal. The second approach also involved the use of linear regression using the method as described by Legarra and Reverter, (2018) and Macedo et al. (2020) which utilizes EBV from partial and whole datasets and their respective exact accuracies.

(1)Adjusted phenotype validation.

AP for each animal were calculated using MiX99 for all 1,473 animals. Phenotypes were adjusted for contemporary group, age, and heterosis while the random genetic, random permanent environment, breed, and residual error remained in the AP. The adjustment process, as defined by VanRaden and Wiggans, (1991), ensures that the AP values reflect the true genetic differences among animals, with minimal influence of other non-genetic factors. To assess the accuracy of the EBV, four validation subpopulations were derived where each validation subpopulation represented approximately one-quarter of the full dataset. Whole contemporary groups were masked in the validation evaluations rather than individual animals within a contemporary group; the number of animals per validation subpopulation was 361, 305, 424, and 383. Four genetic evaluations were undertaken using the model already described with the phenotypes of the validation population masked. Prediction success for each validation animal was computed as (a) the bias or regression slope of the average AP on the parental average EBV from the evaluation excluding that individual's phenotype, and (b) the correlation between average AP and parental average EBV. For each trait definition, the regression slope and correlation, herein referred to as AP-on-EBV validation, were computed between the corresponding AP and the parent average EBV. A weighted average across each of the four replicates was calculated for the regression slope and correlation, along with standard deviation for each metric across replicates as a measure of robustness. Additionally, the correlation was standardized by the square root of the heritability of each trait to enable comparison across trait and trait definitions (Legarra and Reverter, 2018).

(2) Legarra and reverter validation.

The validation followed a linear regression approach as described by Legarra and Reverter, (2018) and Macedo et al., (2020) using two sets of EBV: a 'whole' dataset of EBV computed from all 1,473 phenotypes, and a 'partial' dataset of EBV computed from the four validation genetic evaluations (as previously described), and herein referred to as EBV-on-EBV validation. All EBV were adjusted to a common base (sires with progeny in more than one validation cohort). Prediction success from this method was measured from a linear regression of the whole evaluation EBV run on each partial evaluation EBV (parental average EBV) and included: (a) level bias was computed as the average difference between whole and partial genetic merit, a value of 0 is the ideal indicating no bias, a value < 0 indicates over prediction of average validation EBV and a value > 0 suggests under prediction; (b) dispersion bias computed as the slope of a linear regression of EBV from the whole dataset on those from the partial data, where a value of 1 is the expected, a value < 1 suggests over prediction and a value > 1 suggests under prediction; and (c) the ratio of the partial evaluation accuracies on whole evaluation accuracies calculated as the covariance of the partial EBV to whole EBV, divided by variance of whole EBV. All validation metrics were then averaged across the four replicates and the standard deviation of these metrics was also calculated as a measure of robustness.

Results

Individual CH_4 spot measures ranged from 52 to 524 g/d, with an average full test CH_4 estimate of 242.4 g/d (Supplementary Table S4). The CO_2 spot measures ranged from 4,867 to 14,794 g/d with an average full test CO_2 estimate of 9,504.7g/d, while the 1-d average DMI had a mean of 12.3 kg

of dry matter per day and ranged from 5.0 to 17.5 kg/d in the full test average DMI (Supplementary Table S4).

(Co)variance components

The estimated additive genetic standard deviation was relatively consistent for all nine CH_4 trait definitions (mean = 22.15 g/d, min. = 20.62 g/d, max. = 23.24 g/d). However, as the duration of the time period considered increased from individual spot measures to full test average, the residual standard deviation reduced (mean = 39.38 g/d, min. = 20.11 g/d, max. = 60.03 g/d) resulting in higher heritability estimates as the period over which the measures were averaged lengthened (Table 1). This was reflected in the coefficient of residual variation (CV_e) for CH_4 ranging from 8.3% to 24.4% with the spot measure trait exhibiting the largest environmental variation. The heritability for CH_4 ranged from 0.09 ± 0.03 for the spot measure trait to 0.43 ± 0.11 for full test average trait (Table 1), with the lowest standard error (0.03) observed in the spot measure trait definition. For all CH_4 traits, as the heritability estimate increased, so too did the standard error. The coefficient of genetic variation (CV_g) for CH_4 ranged from 8.4% to 9.4% across trait definitions with the 3-h CH_4 trait definition exhibiting the largest genetic variability.

The genetic standard deviation for CO_2 was largest (578.2 g/d) for the 6-h average CO_2 trait, followed by the spot measure CO_2 (572.2 g/d). The CV_g of CO_2 was consistent across all traits ranging from 5.50% to 5.98%, with a mean CV_g of 5.67%. Heritability estimates for the CO_2 traits increased as the average time period increased, with estimates ranging from 0.17 ± 0.04 for the spot measure trait to 0.50 ± 0.11 for the full test average trait. Heritability estimates for DMI increased as the time period considered increased with estimates ranging from 0.03 ± 0.01 (3-h average) to 0.55 ± 0.12 for the full test average DMI trait (Table 1).

Repeatability ranged from 0.27 for spot measures of CH_4 to 0.71 for the 15-d average CH_4 trait (Table 1). Similarly, the repeatability of CO_2 was 0.31 for spot measures and 0.77 for the 15-d average. Repeatability of DMI also had a similar trend; 3-h DMI had a repeatability of 0.07 and 15-d average DMI had a repeatability of 0.81(Table 1).

Genetic correlations

Genetic correlations between CH_4 and DMI ranged from moderate to strong (Table 2). The genetic correlation calculated between an individual CH_4 spot measure and 1-d average DMI trait had the strongest genetic correlation of 0.72 ± 0.06. Moderate genetic correlations between CH4 and DMI were observed in all multi-day periods, ranging from 0.38 ± 0.16 in the 15-d average period to 0.49 ± 0.15 in the full test average period (Table 2). The weakest correlation observed in the multi-hour traits was between 3-h average CH_4 and 3-h DMI_{prior} (0.25 ± 0.19), albeit not significant; the 6-h CH_4 period yielded a correlation of 0.41 ± 0.15 with 6-h DMI_{prior}, whereas the strongest correlation was observed between 12-h CH_4 and 12-h DMI_{prior} (0.45 ± 0.15).

Carbon dioxide and DMI were strongly correlated across all trait definitions (Table 2) with correlations ranging from 0.78 ± 0.08 for full test average to 0.89 ± 0.03 for the 3-h average. Spot measure CO_2 and DMI had a correlation of 0.87 ± 0.03. A moderate correlation of 0.62 ± 0.12 was observed between spot measures of CH_4 and spot measures of CO_2, with all CH_4 trait definitions also yielding a strong correlation ranging from 0.60 to 0.63.

Estimated breeding values

The standard deviation of the EBV for CH_4 ranged from 10.91 to 15.83 g/d depending on the CH_4 trait definition. Correlations between the resulting EBV for all CH_4 trait definitions from all phenotyped animals (n = 1,473) were near unity between the individual spot measures, 3-h, 6-h, 12-h,

Table 1. Genetic and residual standard deviation (σ), heritability (h^2) with standard error (SE) and repeatability (t) in parenthesis of enteric methane (CH_4), carbon dioxide (CO_2), and dry matter intake (DMI) based on 1,155 animals.

	Number of records	Average number of records per animal	CH_4 (g/d)				CO_2 (g/d)				DMI (kg/d)			
			σ_g	σ_e	h^2 (SE)	t	σ_g	σ_e	h^2 (SE)	t	σ_g	σ_e	h^2 (SE)	t
Spot measures	186,131	156.1	20.6	60.0	0.09 (0.03)	0.27	572.2	1137.6	0.17 (0.04)	0.31	—	—	—	—
3-h average	183,409	150.9	23.2	53.0	0.12 (0.03)	0.35	566.4	977.8	0.20 (0.05)	0.41	0.1	0.9	0.03 (0.01)	0.07
6-h average	166,120	135.7	22.8	54.4	0.12 (0.03)	0.33	578.2	999.4	0.20 (0.04)	0.40	0.3	1.0	0.06 (0.02)	0.10
12-h average	106,714	87.1	22.0	47.7	0.13 (0.04)	0.39	532.7	903.5	0.19 (0.05)	0.44	0.5	1.2	0.12 (0.03)	0.21
1-d average	59,489	51.5	22.2	43.3	0.17 (0.05)	0.36	530.5	790.3	0.24 (0.06)	0.47	1.0	1.4	0.28 (0.07)	0.45
5-d average	13,256	11.5	22.4	27.6	0.28 (0.07)	0.57	537.1	520.6	0.35 (0.08)	0.67	1.0	0.8	0.43 (0.10)	0.72
10-d average	6,999	6.1	22.1	23.4	0.31 (0.08)	0.65	531.3	444.8	0.38 (0.09)	0.73	1.0	0.7	0.45 (0.10)	0.77
15-d average	4,852	4.2	22.4	20.1	0.36 (0.09)	0.71	539.4	394.9	0.42 (0.10)	0.77	1.0	0.6	0.49 (0.11)	0.81
Full test average	1,155	1	21.6	24.8	0.43 (0.11)	—	531.6	528.2	0.50 (0.11)	—	1.0	0.9	0.55 (0.12)	-

1-d average, and 5-d average CH_4 traits (Table 3). However, the weakest correlation of 0.837 was different from one (P-value < 0.05) and was observed between the 10-d average CH_4 and the full test average CH_4 trait definition (Table 3). Similar results were observed between EBV for all CH_4 trait definitions adjusted for breed effects. Exact accuracies estimated in MiX99 as part of the EBV validation for two CH_4 traits (spot measure CH_4 and full test average CH_4) are in Figure 1 and were grouped by the number of GEM system observations per animal. As shown in Figure 1, three distinct outliers where spot measure exact accuracy was < 0.50 and full test average exact accuracy was < 0.65 were identified; all three animals had less than 10 GEM system observations in the test period and were in two separate contemporary groups. Animals with less than 10 visits to the GEM system, of which there were six in this study, had an exact accuracy average for spot measures of CH_4 of 0.485 and exact accuracy average for full test average CH_4 of 0.652 for the full test average CH_4 definition. In contrast, animals with more than 10 GEM system visits had an average exact accuracy for spot measures CH_4 of 0.619 and 0.657 for full test average CH_4.

Table 2. Genetic correlations (r_g) and standard error (SE) between enteric methane (CH_4) and corresponding dry matter intake (DMI), and carbon dioxide (CO_2) and corresponding dry matter intake averaged across varying time periods

	Trait description	DMI
		r_g (SE)
CH_4	Spot measure [1]	0.72 (0.06)
	3-h average	0.52 (0.17)
	6-h average	0.44 (0.15)
	12-h average	0.46 (0.15)
	1-d average	0.48 (0.14)
	5-d average	0.45 (0.15)
	10-d average	0.43 (0.16)
	15-d average	0.43 (0.16)
	Full test average	0.49 (0.15)
CO_2	Spot measure [1]	0.87 (0.03)
	3-h average	0.89 (0.08)
	6-h average	0.82 (0.07)
	12-h average	0.80 (0.07)
	1-d average	0.80 (0.07)
	5-d average	0.78 (0.07)
	10-d average	0.76 (0.08)
	15-d average	0.78 (0.07)
	Full test average	0.78 (0.08)

[1]Genetic correlation with 1-d average dry matter intake (DMI).

(1) AP-on-EBV validation

Table 4 shows the validation results for all CH_4 traits across both the adjusted phenotype validation and the linear regression validation. The correlation between EBV and corresponding AP ranged from 0.33 to 0.37 but did not differ from each other (P-value > 0.05). Following adjustment of the correlations to reflect heritability of the trait, the spot measure trait definition yielded the highest mean adjusted correlation between the EBV and corresponding AP (when adjusted for the heritability [Legarra and Reverter, 2018]) of 1.14 with a range of 0.87 to 1.43, where one is the desired value. The 3-h, 6-h, and 12-h also yielded strong adjusted correlations between EBV and corresponding AP of 0.95, 0.96, and 0.92, respectively, with a reduction in correlation for every increase in averaging period thereafter, with the full test average definition yielding the weakest correlation of 0.56. Standard deviation of correlation across replicates ranged from 0.05 in 15-d average CH_4 to 0.07 for both 6-h average and 12-h average CH_4. Results for the slope of the regression between EBV and corresponding AP suggest underprediction of the parental average EBV in all CH_4 trait definitions with the exception of the full test average which was overpredicted (1.16; Table 4). The slope closest to 1, suggesting no over or underprediction of the EBV from the AP, was observed in the spot measure CH_4 trait (0.98) which was different (P-value < 0.05) from all other definitions, with the exception of the 3-h average CH_4. Standard deviation of the slope across replicates ranged from 0.22 in 15-d average CH_4 to 0.28 in full test average CH_4.

(2) EBV-on-EBV validation

Level bias results indicate underprediction of EBV for all trait definitions (Table 4). The spot measure CH_4 trait definition was the least underpredicted (–0.45 g/d), with the full test average CH_4 trait indicating substantial underprediction (–0.81 g/d). Both spot measure CH_4 and full test average CH_4 were different from each other (P-value < 0.05) and different from zero (P-value < 0.05). Standard deviation for

Table 3. Pearson correlation coefficients between estimated breeding values (EBV) of varying enteric methane (CH_4) trait definitions and summary statistics for phenotyped animals

	Spot measure	3-h average	6-h average	12-h average	1-d average	5-d average	10-d average	15-d average	Full test average
3-h average	0.994	—	—	—	—	—	—	—	—
6-h average	0.991	0.995	—	—	—	—	—	—	—
12-h average	0.990	0.990	0.996	—	—	—	—	—	—
1-d average	0.988	0.983	0.986	0.990	—	—	—	—	—
5-d average	0.981	0.975	0.978	0.983	0.993	—	—	—	—
10-d average	0.970	0.963	0.966	0.970	0.981	0.995	—	—	—
15-d average	0.974	0.968	0.972	0.977	0.988	0.991	0.986	—	—
Full test average	0.850	0.846	0.846	0.848	0.852	0.846	0.837	0.843	—

All values were different from 1 (P-value < 0.05).

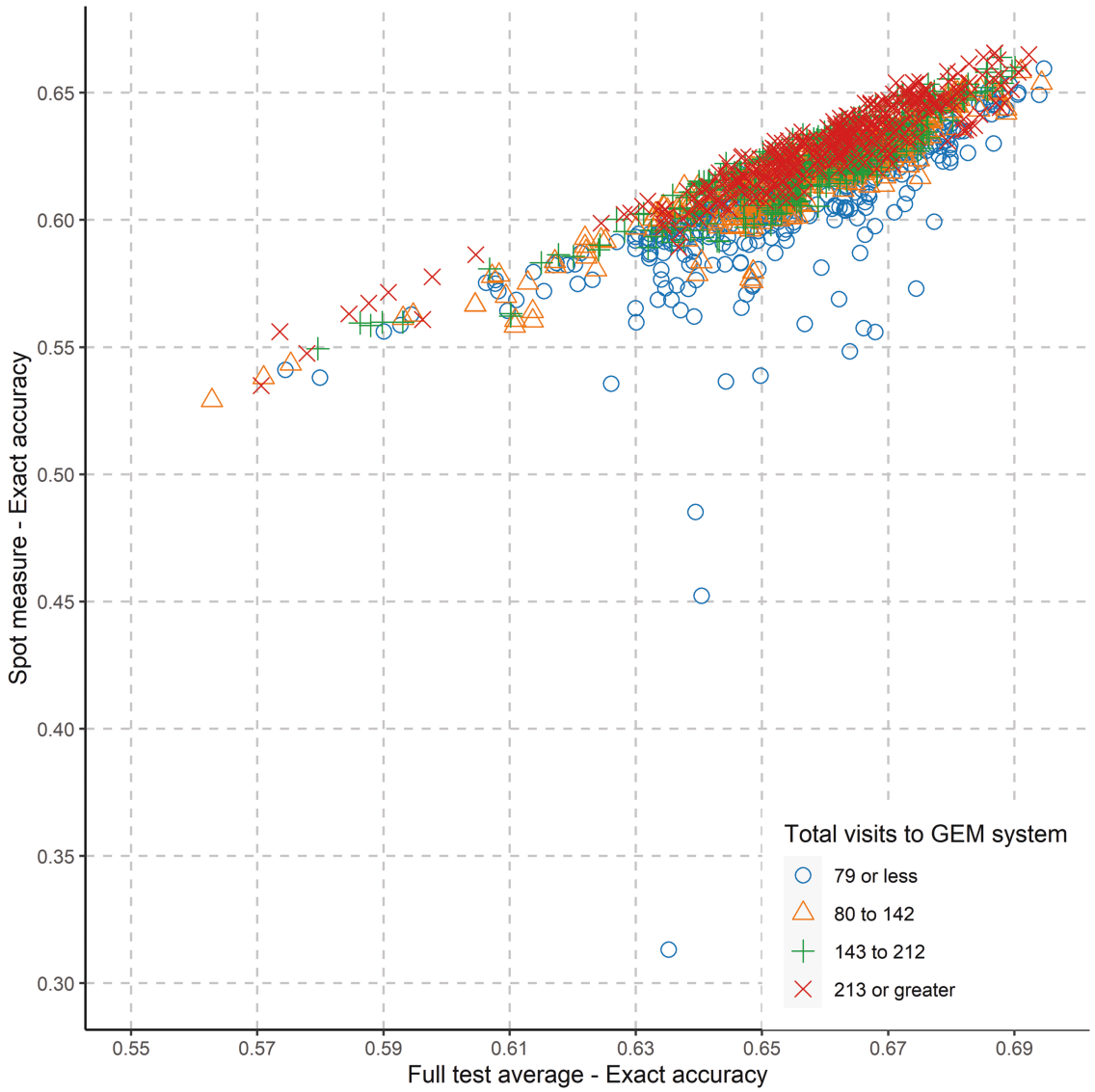

Figure 1. Scatter plot with exact accuracies from the full evaluation for spot measure methane and full test average methane by total number of visits to the GreenFeed Emission Monitoring (GEM) system.

Table 4. Mean and standard deviation of validation results from adjusted phenotype (AP-on-EBV) validation and the legarra and reverter (EBV-on-EBV) validation of enteric methane (CH_4) traits

	AP-on-EBV Validation			EBV-on-EBV Validation		
	Correlation	Adjusted Correlation	Slope	Level bias	Dispersion bias	Ratio accuracy
Spot measure	0.34 ± 0.06	1.14 ± 0.20	0.98 ± 0.23	−0.45 ± 2.54	1.17 ± 0.23	0.38 ± 0.05
3-h average	0.33 ± 0.06	0.95 ± 0.18	0.96 ± 0.23	−0.57 ± 2.89	1.09 ± 0.22	0.34 ± 0.06
6-h average	0.33 ± 0.07	0.96 ± 0.20	0.93 ± 0.23	−0.62 ± 2.19	1.03 ± 0.22	0.31 ± 0.06
12-h average	0.33 ± 0.07	0.92 ± 0.19	0.92 ± 0.23	−0.56 ± 2.45	1.00 ± 0.22	0.30 ± 0.05
1-d average	0.33 ± 0.06	0.80 ± 0.16	0.93 ± 0.25	−0.52 ± 2.30	1.07 ± 0.19	0.34 ± 0.05
5-d average	0.33 ± 0.06	0.62 ± 0.11	0.94 ± 0.24	−0.67 ± 2.66	1.07 ± 0.16	0.35 ± 0.04
10-d average	0.33 ± 0.05	0.60 ± 0.10	0.94 ± 0.24	−0.74 ± 2.68	1.06 ± 0.15	0.36 ± 0.05
15-d average	0.34 ± 0.06	0.56 ± 0.10	0.93 ± 0.22	−0.65 ± 3.40	1.05 ± 0.18	0.35 ± 0.04
Full test average	0.37 ± 0.06	0.56 ± 0.09	1.16 ± 0.28	−0.81 ± 4.95	0.93 ± 0.19	0.28 ± 0.03

Correlation, correlation between the adjusted phenotype and parental average estimated breeding value (EBV); Adjusted correlation, correlation divided by $\sqrt{h^2}$ to express the correlation relative to an expectation of 1; Slope, slope of a linear regression between adjusted phenotype and parental average EBV; level bias, difference between whole and partial EBV after adjusting to a common base; dispersion bias, slope of a linear regression of EBV from the whole dataset on those from the partial data; ratio accuracy, ratio of the partial evaluation accuracies on whole evaluation accuracies. AP, adjusted phenotypes.

level bias across replicates ranged from 2.19 g/d in the 6-h average CH_4 to 4.95 g/d in the full test average CH_4. The dispersion bias validation metric varied from 0.93 (overprediction of parental average EBV) for the full test average CH_4 trait definition to 1.17 (underprediction of parental average EBV) in the spot measure CH_4 trait definition. Dispersion bias for spot measure CH_4 was different from all other trait definitions (P-value < 0.05) and different from the expectation of one (P-value < 0.05). Dispersion bias results for the multi-day average traits yielded similar results (1.05 to 1.07), were not significantly different from each other (P-value > 0.05) but were different from the expectation of one (P-value < 0.05). The trait definition with least bias when measured on dispersion bias was the 12-h average CH_4 trait (1.00), with both the full test average CH_4 trait and 1-d average CH_4 trait performing equally relative to the expectation of one. Standard deviation of dispersion bias across replicates ranged from 0.15 in 10-d average CH_4 to 0.23 in spot measure CH_4. Ratio accuracy, which was the ratio of the partial evaluation accuracies to whole evaluation accuracies, with a desired value of 1, ranged from 0.28 to 0.38, with higher ratio accuracies observed in shorter averaging periods (Table 4). The highest ratio accuracy was observed in the spot measure CH_4 trait (0.38) and was different from all other trait definitions (P-value < 0.05) with the lowest ratio accuracy observed in the full test average CH_4 trait (0.28). Standard deviation of ratio accuracy ranged from 0.03 in full test average CH_4 to 0.06 in both 3-h average and 6-h average CH_4.

Discussion

Knowledge of the genetic and residual variance components is necessary to generate genetic evaluations for CH_4. Heritability estimates for CH_4, CO_2, and DMI observed in the present study are similar to existing estimates from cattle (Crowley et al., 2010; Donoghue et al., 2016; Hayes et al., 2016; Manzanilla-Pech et al., 2016; van Engelen et al., 2018; Breider et al., 2019; van Breukelen et al., 2022). The present study demonstrates that CH_4 emissions are under moderate genetic control and exhibit genetic variation irrespective of the trait definition, thereby suggesting it is possible to select animals for reduced daily CH_4 emissions.

Reducing methane emissions through genetics

Genetic variation, intensity of selection, accuracy of identifying genetically divergent animals, and generation interval are the integral components of genetic gain (Rendel and Robertson, 1950). Houle (1992) argued that the CV_g is potentially more informative than the heritability to quantify the capacity for genetic change; because it is unitless, the CV_g also facilitates comparison of the genetic variability across traits (and across studies with different sample population means). The CV_g for CH_4 of between 8.4% and 9.4% in the present study is similar, if not higher, than reported for traits such as average daily gain in beef (7.8%, Crowley et al., 2010) or milk production in dairy cows (6.2%; Berry et al., 2003) both of which are well documented to have benefited greatly from breeding programs. Using the (within breed) mean genetic standard deviation of 22.1 g/d for CH_4, the expected mean difference, within breed, in CH_4 for the bottom 10% emitters genetically relative to the population average is 38.76 g/d. Focusing just on a 100-d finishing period, this equates to 3.88 kg CH_4 translating to 3,876 tons CH_4 per 1 million animals, just over their 100-d finishing period. How knowledge on whether EBV for CH_4 emissions for finishing cattle fed indoors on a high input feeding system translates to CH_4 emissions earlier in life, possibly when the animal is grazing, is not yet known.

Heritability is not explicitly a direct component of the breeder's equation (Rendel and Robertson, 1950) but it does; however, impact the accuracy of selection. For traits well recorded in some jurisdictions like growth rate, carcass merit, or reproductive performance, the vast quantity of available phenotypic data mitigates any low heritability (e.g., reproductive performance; Berry, 2018). Heritability is an important statistic when developing a breeding program for traits that are resource-intensive to measure, as is the case for CH_4 (and DMI). Based on the spot measure CH_4 trait with the estimated variance components in the present study (heritability of 0.09 and repeatability of 0.27), the accuracy of selection for a sire (ignoring parental contributions and any genomic information) with 1, 5, 10, and 20 progeny would be 0.15, 0.32, 0.43, and 0.56, respectively; should the CH_4 be measured on the selection candidate itself, then the accuracy of selection from a test with 10 observations would be 0.51. Genetic evaluations for beef cattle globally are transitioning to genomic evaluations (Berry et al., 2016). Assuming 1,000 effective chromosomal segments and that single nucleotide polymorphisms could explain 80% of the genetic variance, based on the heritability (repeatability) of 0.09 (0.27) for spot measures of CH_4, a calibration population with CH_4 phenotypes on 7,390 cattle would be required to generate genomic predictions with an accuracy of 0.70; a calibration population size of 32,767 cattle with CH_4 phenotypes would be required to achieve a desirable accuracy of 0.90. In contrast, assuming a heritability of 0.43 for a full test average CH_4, a reference population with CH_4 phenotypes on just 19,949 cattle would be required to generate genomic predictions with an accuracy of 0.90.

Heritability estimates for all CH_4 trait definitions in the present study were moderate and similar to existing heritability estimates for CH_4 in cattle. Previously reported heritability estimates for CH_4 in cattle have ranged from 0.11 ± 0.02 (Netherlands; van Engelen et al., 2018) to 0.45 ± 0.11 (United Kingdom; Breider et al., 2019) with the difference in estimates attributable, in part, to differences in trait definitions, measurement method, length of test period and the population the heritability was derived from. While few studies have estimated heritability for CH_4 from beef populations, estimates from beef populations to date have been derived from respiration chamber measurements on Angus cattle (Donoghue et al., 2016, 2020; Hayes et al., 2016; Manzanilla-Pech et al., 2016) and, to the best of our knowledge, no estimates using GEM systems in beef have been previously reported. The increase in heritability as the number of spot measures and test length contributing to the individual animal phenotype increased is consistent with expectations (Berry et al., 2017) as the random variability contributing to the individual measures is expected to be evened out.

While CH_4 and nitrous oxide are two potent greenhouse gas emissions from livestock, CO_2 remains a significant contributing factor to greenhouse gas emission levels. Despite this, limited research to date has been documented on the contribution of genetic variability to phenotypic differences in CO_2

of cattle. Heritability estimates for CO_2 emissions traits in the present study (0.17 to 0.50) were comparable with those previously estimated by Donoghue et al. (2020; 0.53 ± 0.17) in Australian Angus beef cattle albeit with different measurement methods. Van Breukelen et al. (2022) also determined CO_2 heritability using sniffers in a population of Dutch dairy cows and reported similar heritability estimates for daily and weekly means with estimates ranging from 0.16 ± 0.02 to 0.34 ± 0.03 and heritability estimates increasing in longer averaging periods. The CV_g of CO_2 was lower than CH_4, with the maximum CV_g of CO_2 of 5.98% in the 6-h average, with spot measure CO_2 having a CV_g of 5.94%. While CV_g of CO_2 is lower than CH_4, it is comparable with the 6.2% CV_g observed in milk production of dairy cows (Berry et al., 2003) suggesting genetic gain is achievable.

The DMI_{prior} correlation analysis highlighted stronger correlations where CH_4 and DMI were recorded concurrently, suggesting that it is best to collect both phenotypes contemporaneously or as closely as possible. Due to the extensive grazing nature of Irish production systems, DMI recording at pasture is not a viable option due to the intensive and invasive nature of data recording (Mayes et al., 1986). The strong correlation between CH_4 with DMI confirms the potential use of CH_4 as proxy for DMI in pasture-based situations and CH_4 could be recorded using pasture-based GEM systems (Donoghue et al., 2020). As CO_2 is also collected by the GEM system and has stronger correlations with DMI in all time periods, CO_2 also offers another proxy measure for DMI, where feed intake data collection may not be possible. Whether these correlations hold in grazing situations needs to be investigated.

Practical applications

Given the societal pressure to reduce CH_4 emissions from the agricultural sector, it is likely that the collection of CH_4 phenotypic data will continue in order to facilitate the development of accurate genetic evaluations; however, the quality control applied to the data needs further exploration. Spot measure-based CH_4 evaluations facilitate a data structure that may be representative of commercial farm and feedlot settings, with different test lengths as well as accommodating the inclusion of data from animals that do not regularly frequent the GEM. EBV accuracy was impacted by GEM visit frequency where animals with poor visitation to GEM systems had low spot measure CH_4 accuracy. In comparison, the accuracy of the low-frequency visitation animals in the full test average CH_4 accuracy was greater than in spot measure CH_4 as the averaging approach essentially treated these animals as having the same volume of data as high GEM frequency visitor animals. Additionally, spot measure evaluation of CH_4 was the only approach investigated which facilitated time of day inclusion to address the diurnal pattern of CH_4 production. The diurnal pattern of CH_4 has been well documented (Gao et al., 2011; Basarab et al., 2013; Brask et al., 2015; Hammond et al., 2015; Bell et al., 2018) but, to the best of our knowledge, research does not currently exist on how best to consider or model the time of the day when the measurement happened.

Two validation methods were utilized in this study; AP-on-EBV validation focuses on cross-validation, whereas EBV-on-EBV validation focuses on stability metrics from parental average EBV from partial evaluations to full evaluation EBV. Level bias, by definition, is the difference in means of true breeding value and EBV whereas dispersion bias is defined as the slope of the regression of true breeding value on EBV (Legarra and Reverter, 2018). Ratio accuracy is a measure of the inverse increase in reliabilities from selected to whole (Macedo et al., 2020). In real-life datasets, the expectation of zero for level bias, one for dispersion bias, and ratio accuracy, are rarely achieved (Legarra and Reverter, 2018).

Due to some minor disagreement between validation metrics across methods, there is difficulty in interpreting the validation results to select the best trait. There were significant differences between spot measure CH_4 and full test average CH_4 in all validation metrics, except correlation in AP-on-EBV validation. As yet, the gold standard phenotype for comparison for validation from the GEM systems is unknown. While full test average CH_4 had the highest heritability in this study, the overprediction suggested by validation alongside the heritability estimate suggests a creep of environmental effects into the genetic effects. The simpler statistical model used for the full test average CH_4 has several limitations; it does not allow for GEM system effects where animals may attend more than one GEM system, differences in individual animal visitation patterns across test or variation in time of day of visit to the GEM system to be captured and it would need adaptation to a repeatability model where animals have multiple measurement periods throughout their life periods not evaluated in the current study. While consideration must also be given to multi-hour and multi-day averaged traits, the opportunities, and difficulties of these must be analyzed. Multi-hour averaged traits present an opportunity to capture time of day within the contemporary group; however, contemporary group size is reduced as a result. Conventional genetic evaluations tend to omit small contemporary groups from genetic evaluations, potentially resulting in biased sire EBV (Vasconcelos et al., 2008). Multi-day traits also provide the opportunity to utilize a higher heritability trait with larger contemporary groups; however, multi-day traits do not allow for time-of-day inclusion in genetic evaluation—thus missing out on the ability to capture diurnal effect. In addition, the genetic correlation reduction with the multi-day traits between CH_4 and DMI would reduce the effectiveness of DMI as a predictor trait.

Setting a lower limit of 10 d with GEM system records for inclusion resulted in only 1% of animals being lost from the analysis; however, animals with poor, infrequent, inconsistent visitation patterns pose a difficulty for full test average CH_4 evaluations and have been well documented (Waghorn et al., 2016; Manafiazar et al., 2017). An analysis of the number of animals who have GEM system measurements in all six classes of time of day, as included in the spot measure CH_4 model, indicated that 99% of animals had visits in all six periods (0 to 3 a.m., 4 to 7 a.m., 8 to 11 a.m., 12 to 3 p.m., 4 to 7 p.m., and 8 to 11 p.m.) across the test period; however importantly, the animals in this study were indoors and near the GEM system, at all times. Visitation frequency in grass-based studies has been much lower (1.6 visits/d; dairy heifers, United Kingdom [Hammond et al., 2015]). Poor visitation patterns can result in biased measurements when averaging across test periods, due to a lack of visitation during peaks of diurnal variation (Hammond et al., 2015). While the use of repeated records in genetic evaluations has been well documented in relation to milk traits for dairy cows (Swalve, 2000; Jensen, 2001) and behavioral traits (König et

al., 2006), little research is available on repeated record analysis of CH_4 traits to date. As shown by the outliers in Figure 1., a recommendation of a minimum of 10 spot measure GEM system measurements could be applied to ensure an exact accuracy of 50% is achieved for phenotyped animals for spot measure CH_4. While the phenotyping of additional animals (n = 12,818) is required for a calibration population to achieve 0.90 accuracy in genomic evaluations when utilizing the spot measure CH_4 trait instead of full test average CH_4 trait, repeated record analysis in the spot measure CH_4 trait allows for more precision around adjustments for temporary environmental effects (Jensen, 2001) which facilitates the capture of diurnal effects and inter-day effects for CH_4. From a CH_4 genetic evaluation perspective, the spot measures CH_4 trait can be assessed using a repeated records model that incorporates spot measures, without the requirement for data averaging.

Conclusion

In this study, we have shown CH_4, CO_2, and DMI trait definitions to be moderately heritable traits and similar to estimates of the same from other beef populations. Considerable genetic variation exists in all CH_4 trait definitions, suggesting that breeding for reduced CH_4 is possible. Strong genetic correlations were observed between CH_4 and DMI as well as between CO_2 and DMI, suggesting that selection on GEM system measurements alone will have a direct impact on DMI and vice versa, which has a practical application in settings where either CH_4 and CO_2 or DMI may be recorded, but not all. This analysis in this study establishes methodology for developing EBV for CH_4 traits. Despite the lack of a clear consensus across the validation metrics for nine alternative definitions of CH_4 EBV in this study, for implementation of a national genetic evaluation, Irish Cattle Breeding Federation have initially opted for a spot measure of CH_4 trait based on the validation results and ability to capture diurnal effect in the analysis.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

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Conflict of Interest Statement

The authors have no conflict of interest to declare.

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