Genomic prediction of methane emissions in Danish Holstein using single step and multi-trait prediction models

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Abstract

Enteric methane emissions from ruminants are a major contributor to global greenhouse gas emissions and pose a significant challenge to the sustainability of livestock production. To mitigate these emissions, breeding strategies have been mentioned as a promising tool, but prediction accuracies of methane emission traits are still limited by the size of datasets with records. Hence, using methane concentrations (MeC) in Danish Holstein cows as target trait, this study evaluated the predictive performance of pedigree-based BLUP (pBLUP) and single-step genomic BLUP (ssGBLUP) in univariate and multi-trait models, the latter including milk production traits. Previously, both ssGBLUP as well as multi-trait models have been shown to enhance prediction accuracies. The dataset included 1,744 primiparous (PP) and 2,989 multiparous (MP) cows from 15 Danish dairy farms, with over 600,000 daily records of MeC, fat yield (FY), and energy-corrected milk yield (ECM). Methane concentrations were measured using sniffers, and milk production data was acquired from milking robots and national milk recording data. At first, a pedigree-based variance component estimation revealed heritabilities between 0.17 (SE=0.03) for MeC in PP and MP cows to 0.38 (SE=0.06) for ECM in PP cows. Similarly, repeatabilities ranged from 0.32 (MeC, SE=0.01) to 0.81 (ECM, SE=0.01). Genetic correlations between MeC and production traits were positive but unfavorable, i.e., in a range from 0.15 (SE=0.13) between MeC and ECM in PP cows to 0.41 (SE=0.09) between MeC and ECM in MP cows, indicating a genetic antagonism between reducing emissions and maintaining milk yield. Prediction accuracies were generally higher for ssGBLUP compared to pBLUP models (up to 61.90% increase), and for MP cows compared to PP cows. Multi-trait models outperformed univariate models, particularly when phenotypic data for FY and ECM were available in both the reference and validation populations. The highest accuracy for MeC prediction in PP cows was 0.38 (ssGBLUP), while MP cows reached up to 0.51, both for the multi-trait model including both, ECM and FY. While incorporating FY and ECM improved MeC prediction, the unfavorable genetic correlations highlight the risk of compromising milk production when selecting for reduced emissions. Therefore, future breeding strategies should aim to expand methane phenotyping, develop methane traits independent of milk production, and implement multi-trait selection indices that balance environmental and economic goals. This study demonstrates the potential of multi-trait genomic prediction to enhance the genetic evaluation of methane emissions and supports its integration into sustainable dairy cattle breeding programs.

Key words: methane concentrations, single-step genomic prediction, multi-trait genomic prediction, predictor traits

Introduction

Methane is a potent greenhouse gas (GHG) with a global warming potential approximately 28 times greater than that of carbon dioxide (IPCC, 2024). At this, a significant proportion of anthropogenic methane emissions originates from enteric fermentation in ruminants, where microbial digestion of fiber in the rumen produces methane as a by-product (Knapp et al., 2014). Effective and sustainable mitigation strategies have thereby become imperative, given the fact that the European Union has committed to reducing GHG emissions by 55% by 2030 and achieving climate neutrality by 2050 (European Commission, 2019). Among the various approaches to reduce enteric methane emissions, such as feed additives and improved management practices, genetic selection offers a particularly promising long-term solution. This is, because unlike management-based strategies, genetic improvement can lead to cumulative and permanent reductions in methane emissions across generations (Knapp et al., 2014; Manzanilla-Pech et al., 2022a). However, the success of breeding programs targeting methane emissions depends on the availability of reliable phenotypic data for large populations of genotyped animals. Recent advances in phenotyping technologies have enabled the development of non-invasive, high-throughput methods for measuring methane emissions. Here, the sniffer method has gained popularity world-wide and measures methane concentrations (MeC) in the breath of cattle during routine milking or feeding (Garnsworthy et al., 2019; Lassen and Difford, 2020). This approach facilitates large-scale data collection at relatively low cost and has been shown to result in heritable phenotypes, with heritability estimates of MeC around 0.14 (e.g., Manzanilla-Pech et al., 2020). Despite these advances, accuracies of genomic prediction for methane emissions that are sufficiently high to enable genetic progress, remains limited, primarily due to the relatively small datasets. Different strategies to improve prediction accuracies of genomic evaluations, e.g., simultaneously exploiting genotypic, phenotypic and pedigree information, as in single step genomic prediction (Christensen and Lund, 2010), or by applying indirect information from correlated predictor traits, as in multi-trait prediction, have been proposed. Multi-trait genomic prediction methods are thereby exploiting genomic information from predictor traits that are highly correlated with the target trait and have earlier been shown to outperform univariate prediction methods (Calus and Veerkamp, 2011).

The objective of this study was to evaluate the predictive ability of pBLUP and ssGBLUP as well as univariate and multi-trait models to estimate genetic breeding values (GEBV) for MeC. Fat yield (FY) and energy corrected milk yield (ECM) were included as predictor traits in multi-trait models, since they were previously shown to be genetically correlated with methane emissions (Lassen and Difford, 2019). Moreover, these traits are directly recorded on the large scale, as they are part of the national milk recording scheme (Danish Cattle Database (SEGES, Skejby, Denmark)). To account for physiological differences between growing and mature animals, presumably leading to a different covariance structure between the applied traits, analyses were conducted separately for primiparous (PP) and multiparous (MP) cows.

Materials and Methods

Data collection

The dataset used in this study comprised daily records from 1,744 PP and 2,989 MP Danish Holstein cows, housed on 15 commercial dairy farms in Denmark. In total, 182,288 (PP) and 424,888 (MP) daily records were available for MeC, ECM and FY, collected between March 2021 and December 2024. Additional animal-level information, including pedigree, genotypic data, days in milk (DIM; 0–365 days), week in milk (WIM), parity, and age at first calving (AFC), was retrieved from the Danish Cattle Database (SEGES Innovation, Skejby, Denmark). The pedigree was pruned using the DMU trace software (Madsen, 2012) to include only animals with records and their ancestors born after 1970, resulting in a final pedigree of 47,383 animals. Genotypic data were provided by Nordic Cattle Genetic Evaluation (Skejby, Denmark). Most animals were genotyped using the Illumina BovineSNP50 BeadChip or imputed from lower-density panels. Imputation was performed by SEGES Innovation as part of routine evaluations resulting in a total of 46,342 single nucleotide polymorphisms available for the analysis. The majority, i.e. 97.31% of PP cows were genotyped, whereas the genotyping rate was lower for MP cows (73.00%).

Methane concentration measurements

Methane concentrations were recorded every second during the cows` visits to the automatic milking system (AMS) using sniffers, i.e., nondispersive infrared sensors (Guardian NG, Edinburgh Sensors, Livingston, UK) that were installed in the AMS feed bins and had a measurement range of 0–10 000 ppm for MeC. Since the sniffers themselves did not record animal identification numbers, which, however, are required to extract the abovementioned additional information about the cows from the Danish Cattle Database, a matching filter approach (Milkevych et al., 2022) was applied to link each measurement to the corresponding cow. Next, we applied a method to correct for background gas concentrations, head-lifting and diurnal variation, as described in detail in Løvendahl et al. (2024). For each visit, the mean MeC was calculated and then averaged across all visits per day to calculate daily MeC records, that are applied in this study.

Milk production traits

Daily milk yields (MY) were calculated from AMS data by using all milkings within the previous 96 hours, following ICAR standards (ICAR, 2023). Moreover, milk component data, i.e., fat percentage (FPCT) and protein percentage (PPCT), from monthly milk recordings were obtained from the Danish Cattle Database and linearly interpolated between two consecutive milk component recordings to generate daily values in alignment with the daily methane records. Next, daily FY and protein yield (PY) were computed by multiplying MY with FPCT and PPCT, respectively, in order to calculate ECM as $\text{ECM (kg)} = 0.25 * \text{MY (kg)} + 12.2 * \text{FY (kg)} + 7.7 * \text{PY (kg)}$, using the formula from Sjaunja et al. (1991).

Variance components and GEBV estimation

At first, variance components for MeC, ECM, and FY were estimated using the AI-REML algorithm implemented in the DMU software (Version 6, Release 5.4; Madsen and Jensen, 2014), thereby applying the following linear mixed model

$$y = X\beta + Za + Wpe + Ie.$$

Here, y is the vector of phenotypic observations for MeC, ECM, or FY. The vector β includes the overall mean and fixed effects, i.e., the WIM, as well as the AFC for PP cows (20–30 months), and parity (2nd to 8th parity) for MP cows. Moreover, a combined fixed effect of herd-year-season × AMS × sniffer box (HYS × AMS × sniffer) was included for MeC, while for ECM and FY, only HYS was modeled as a fixed effect. The corresponding incidence matrix that links the trait records to the fixed effect was denoted with X, and the terms a and pe are the random additive genetic as well as the permanent environmental effect with their corresponding matrices Z and W. The residual was denoted with e. It was assumed that these three terms follow a normal distribution with $a \sim N(0, A\sigma_a^2)$, $pe \sim N(0, I\sigma_{pe}^2)$, and $e \sim N(0, I\sigma_e^2)$, where A is the pedigree-based relationship matrix and I an identity matrix. Conversely, the additive genetic, permanent environmental and residual variance were denoted with σ_a^2, σ_{pe}^2, and σ_e^2. The heritability was calculated as $h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2)$, and the repeatability as $t = (\sigma_a^2 + \sigma_{pe}^2)/(\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2)$. Genetic and phenotypic correlations were estimated from multi-trait analyses for MeC, ECM, and FY.

Table 1 Overview over the different scenarios performed per method (pBLUP, ssGBLUP).

Traits included in GEBV estimation	Type of analysis	Scenario name	Information included in	
			validation population	reference population
MeC	Univariate	1	-	MeC
MeC-FY	Bivariate	2a	FY	MeC, FY
		2b	-	
MeC-ECM	Bivariate	3a	ECM	MeC, ECM
		3b	-	
MeC-ECM-FY	Trivariate	4a	ECM, FY	MeC, ECM, FY
		4b	-	

GEBV: genomic EBV, pBLUP: pedigree-based BLUP, ssGBLUP: single-step genomic BLUP, MeC: methane concentrations, ECM: energy corrected milk, FY: fat yield

Next, different pBLUP and ssGBLUP methods, divided into seven univariate and multi-trait scenarios, were applied to estimate GEBV for MeC. An overview of the different scenarios can be taken from Table 1.

Briefly, the basic scenario, i.e., scenario 1, was a simple univariate scenario where phenotypes were only available for animals in the reference population. Multi-trait scenarios included FY, ECM, or both as predictor traits, each with two sub-scenarios: one where predictor trait phenotypes were available in both reference and validation populations, and one where they were restricted to the reference population. All scenarios were applied separately to PP and MP cows. GEBVs for MeC were estimated using DMU, applying the same fixed and random effects as in the variance component estimation. For ssGBLUP, the inverse of the H matrix was computed following Aguilar et al. (2010) and Christensen and Lund (2010):

$$\boldsymbol{H}^{-1} = \boldsymbol{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & (\omega\boldsymbol{G} + (1-\omega)\boldsymbol{A}_{22})^{-1} - \boldsymbol{A}_{22}^{-1} \end{bmatrix}$$

where $\boldsymbol{G}$ is the genomic relationship matrix (VanRaden, 2008), computed using the invgmatrix software (Su and Madsen, 2011), $\boldsymbol{A}_{22}$ is the pedigree relationship matrix for genotyped animals, and $\omega = 0.8$ is the weight assigned to the genomic information.

Cross-validation groups

A 10-fold cross-validation strategy was used to assess the prediction accuracy of each scenario. Validation groups were constructed by sire using stratified random sampling to ensure balanced representation of paternal half-sibs. Sires were ranked by the number of genotyped daughters with MeC records, and one sire from each group of ten was randomly assigned to one of the ten folds. For each fold, MeC phenotypes were excluded from the validation group, and GEBVs were predicted using the remaining data as the reference population.

Accuracy calculation

Prediction accuracies were obtained following the approach of Manzanilla-Pech et al. (2020). At first, adjusted phenotypes for MeC were computed as the sum of the estimated genetic and permanent environmental effects from the full dataset, providing a single phenotype per animal. Then, accuracies for cross-validation group were calculated as the correlation between the adjusted phenotype and the GEBV for MeC divided by the following formula adapted from Mrode (2013) computed to calculate the accuracy for repeated records.

$$\text{Accuracy} = \frac{r}{\sqrt{\frac{nh^2}{\sqrt{1+(n-1)t}}}}$$

Here, the correlation between the adjusted phenotype and GEBV is denoted with r. The average amount of repeated records for each animal, specified per cross-validation group, is defined as n, and h^2 (t) is the heritability (repeatability) of MeC, taken from the variance component estimation (Table 2). Then, the accuracy for each scenario was calculated as the average of all cross-validation groups, and corresponding standard errors were obtained by dividing the standard deviation of accuracies across cross-validation groups by the square root of the number of validation groups, i.e., 10.

Results & Discussion

The estimation of variance components revealed moderate heritability estimates for MeC, FY, and ECM. Specifically, the heritability for MeC was estimated at 0.17 (SE=0.03) in both PP and MP cows. In contrast, ECM in PP cows exhibited the highest heritability at 0.38 (SE=0.06). These findings are consistent with previously reported estimates in the literature, such as heritabilities ranging from 0.26 to 0.37 for ECM (Li et al., 2018) and 0.14 for MeC (Manzanilla-Pech et al. 2020). Moreover, ECM in PP cows showed the highest repeatability with 0.81 (SE=0.01), while MeC was found to have low repeatability in both PP and MP cows, i.e., 0.32 (SE=0.01). Genetic correlations between MeC and production traits were moderate to weak and varied by parity. In MP cows, the genetic correlation between MeC and ECM was 0.41 (SE=0.09), and 0.37 (SE=0.09) between MeC and FY. In PP cows, these correlations were lower and accompanied by larger standard errors: 0.15 (SE=0.13) for MeC and ECM, and 0.18 (SE=0.13) for MeC and FY. Importantly, these positive genetic correlations are considered unfavorable, as they suggest that selection for increased milk production may inadvertently lead to higher methane emissions. A similar structure has been reported in previous studies, including a genetic correlation of 0.35 between MeC and ECM (Manzanilla-Pech et al., 2022b) and a correlation of 0.27 between GEBV for MeC and FY (Lopez-Paredes et al., 2020). A detailed summary of the estimated genetic parameters is provided in Table 2.

Table 2 Genetic parameters for methane concentrations (MeC), energy corrected milk (ECM) and fat yield (FY). Shown are the heritabilities (h^2), repeatabilities (t), and the genetic correlation (r_g) with MeC together with the corresponding standard errors in parentheses.

Trait	Primiparous			Multiparous		
	h^2	t	r_g with MeC	h^2	t	r_g with MeC
MeC	0.17 (0.03)	0.32 (0.01)		0.17 (0.02)	0.32 (0.01)	
ECM	0.38 (0.06)	0.81 (0.01)	0.15 (0.13)	0.24 (0.03)	0.74 (0.01)	0.41 (0.09)
FY	0.31 (0.06)	0.74 (0.01)	0.18 (0.13)	0.20 (0.03)	0.65 (0.01)	0.37 (0.09)

Regarding the different prediction scenarios, accuracies were generally higher for ssGBLUP than pBLUP models and for MP compared with PP cows. For PP cows, the increase from pBLUP to ssGBLUP was largest, i.e., 61.90% for the univariate scenario. Two scenarios resulted in a decrease in accuracies between pBLUP and ssGBLUP, i.e., -4.55% for scenario 3a in MP cows and -3.58% for scenario 3b in PP cows (Table 3). However, the observed difference was only small and might be owed to the generally rather small dataset. Moreover, we found an increase in accuracy from univariate to multi-trait models, but only when phenotypic information on predictor traits was available for the animals in the validation population. For PP cows, the highest accuracy of 0.38 was found for the ssGBLUP scenarios 4a (SE=0.03), 4b and 2b (SE=0.05, respectively), whereas the lowest accuracy was observed for the pBLUP scenario 1 (0.21, SE=0.04). In MP cows, prediction accuracies ranged from 0.31 (SE=0.04) in pBLUP scenario 2b to a maximum of 0.51 (SE=0.03) in ssGBLUP scenario 4a. A comprehensive overview of.

Table 3 Overview over the different pBLUP and ssGBLUP scenarios` accuracies (Acc), corresponding standard errors (SE, in parentheses), and difference between pBLUP and ssGBLUP (in %).

Traits included in GEBV estimation	Scenario	pBLUP		ssGBLUP			
		PP	MP	PP		MP	
		Acc (SE)	Acc (SE)	Acc (SE)	Difference to pBLUP (in%)	Acc (SE)	Difference to pBLUP (in%)
MeC	1	0.21 (0.04)	0.35 (0.02)	0.34 (0.03)	61.90	0.43 (0.03)	22.86
MeC-FY	2a	0.27 (0.03)	0.43 (0.04)	0.37 (0.03)	37.04	0.49 (0.04)	13.95
	2b	0.28 (0.05)	0.31 (0.04)	0.38 (0.05)	35.71	0.42 (0.03)	35.48
MeC-ECM	3a	0.24 (0.03)	0.44 (0.04)	0.36 (0.03)	50.00	0.42 (0.05)	-4.55
	3b	0.28 (0.05)	0.33 (0.04)	0.27 (0.04)	-3.58	0.41 (0.04)	24.24
MeC-ECM-FY	4a	0.28 (0.03)	0.44 (0.04)	0.38 (0.03)	35.71	0.51 (0.03)	15.91
	4b	0.28 (0.05)	0.33 (0.04)	0.38 (0.05)	35.71	0.43 (0.03)	13.16

GEBV: genomic EBV, pBLUP: pedigree-based BLUP, ssGBLUP: single-step genomic BLUP, MeC: methane concentrations, ECM: energy corrected milk, FY: fat yield, PP: primiparous, MP: multiparous

prediction accuracies across all scenarios is presented in Table 3

As anticipated based on previous results in dairy cattle (Hayes and Goddard, 2008; VanRaden et al., 2009), the accuracies of GEBV obtained using ssGBLUP were consistently higher than those obtained using pBLUP. This trend was observed across all scenarios and parities. Furthermore, multi-trait prediction scenarios yielded mostly higher GEBV accuracies compared to the univariate scenarios, which is in alignment with e.g. Tsuruta et al. (2011) for linear type traits. Notably, the improvement in prediction accuracy was most pronounced when phenotypic information for the predictor traits, ECM and FY, was available in both the reference and validation populations. This observation is consistent with the results of Pszczola et al. (2013), who reported enhanced prediction accuracy for dry matter intake when information on predictor traits was included in both populations. It is important to emphasize that the gain in GEBV accuracy for the goal trait in multi-trait genomic prediction depends on the extent of genetic correlations between the goal and predictor traits. Additionally, as noted by Jia and Jannink (2012), the relative heritability of the goal trait compared to the predictor traits also influences the extent of accuracy improvement. Specifically, the benefit of multi-trait prediction is more substantial when the goal trait has a lower heritability, as the contribution of genetically correlated traits becomes more impactful. Interestingly, both PP and MP cows exhibited increased prediction accuracies when FY and ECM were included in the genomic prediction models, despite the relatively low and imprecise genetic correlations between MeC and the predictor traits in PP cows. This may be explained by the larger difference in heritability between MeC and the predictor traits in PP cows, which could enhance the relative contribution of the predictor traits to the accuracy of MeC predictions.

Conclusions

In conclusion, using ECM and FY records can improve accuracy of MeC breeding values, especially for individuals without MeC records. However, it is important to keep in mind that the genetic correlations between MeC and both FY and ECM are unfavorable, indicating that selection for reduced methane emissions may reduce genetic progress in milk production. Since multi-trait prediction models are designed to exploit, but not to disentangle genetic correlations, selection based on these models may lead to genetic gains in MeC at the expense of economically important traits such as milk yield. Hence, further efforts are urgently needed to record methane emissions in more animals; to develop methane emission traits that are genetically independent from economically important, correlated traits like FY or ECM; and to design a multi-trait selection index including all economically important.

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