# Meta-analysis of heritability estimates for methane emission indicator traits in cattle and sheep

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## Summary

Genetic selection is a very promising alternative to breed lower-methane emitter animals and its success will depend on the heritability ($h^2$) of the indicator traits included in the breeding programs. In the last decade, a considerable number of genetic parameter studies in various sheep and cattle populations have been reported in the literature. In order to summarize these results, a comprehensive literature review identified 60 $h^2$ estimates across 18 scientific papers published between 2011 and 2017. A meta-analysis using a random-effects model and different scenarios (based on indicator traits grouping and data included in the analyses) was performed. Our findings confirmed that methane emission indicator traits in cattle and sheep are under moderate genetic control ($h^2$ estimates ranged from 0.14 to 0.26). It seems that methane intensity and residual methane traits and direct measures of methane emission have homogeneous estimates of $h^2$ across the analysed studies, contrarily to methane production and methane yield traits and indirect measures of methane emission based on prediction equations, which displayed significant heterogeneity across studies. This might have practical implications when deciding which kind and which traits to use in selection programs, especially when international collaboration might be involved. More investigation in this area is warranted.

*Keywords: beef cattle, dairy cattle, methane intensity, genetic parameters, random-effects model*

## Introduction

Enteric methane ($CH_4$) produced by ruminants (primarily sheep and cattle) contributes substantially to the total greenhouse gases (GHG) produced in the world (Herrero *et al*., 2011) and is considered a key player in the aggravation of climate change consequences. There are various strategies to mitigate $CH_4$ production by ruminants (Knapp *et al*., 2014) and genetic selection for lowering methane production by the host animal is expected to outstand in this regard, as improvements are cumulative and permanent over generations. Reliable heritability ($h^2$) estimates are essential to improve the prediction of breeding values for methane emission, which require large across-generation datasets. However, especially for hard or expensive-to-measure traits such as $CH_4$ emission, the number of records per population might be limited. Furthermore, over the last decade a number of methods have been developed and adapted to directly measure or predict $CH_4$ emission from individual

animals (de Haas *et al*., 2017; Negussie *et al*, 2017). Consequently, more recently, various studies reporting $h^2$ estimates for a variety of methane production indicator traits have been published (e.g., Pickering *et al*., 2015; de Haas *et al*., 2016, Table S1). However, a considerable variability among $h^2$ estimates has been observed, which highlights the need for a quantitative synthesis of previous findings in order to provide summary estimates for the development of more precise breeding objectives. This can be achieved through a statistical method known as meta-analysis (Sutton *et al*., 2000), which takes into account the variability among studies.

One of the foremost decisions to be made when conducting a meta-analysis is whether to use a fixed-effects or a random-effects model (Lean *et al*., 2009). Random-effects models have an underlying assumption that a distribution of effects exists and the variance representing the amount of heterogeneity among different studies is tested. Hence, this model has been proposed as a more conservative method of meta-analysis that yields results that can be generalized (as discussed by Akanno *et al*., 2013; and, Lean *et al*., 2009). Therefore, this study aimed to integrate published $h^2$ estimates for methane emission traits in beef and dairy cattle, and in sheep using a meta-analysis approach based on a random-effects model.

## Materials and methods

### Literature search and description of indicator traits of methane emission

A systematic literature search of electronic databases was performed to identify all scientific papers reporting $h^2$ estimates for $CH_4$ emission indicator traits. A total of 18 peer-reviewed papers with full description of methods and published between 2011 and 2017 were reviewed. In the case where estimates from the same population were reported in different publications, only the most recent was included in the analysis. There are various traits used as indicators of $CH_4$ emissions in livestock species and researchers have used different definitions and names/abbreviations for the traits. For this study, $CH_4$ indicator traits were categorized in four main categories: 1) methane intensity (MI), defined as methane production rate per unit of product (i.e., g of $CH_4$ per kg/L of milk produced per day or kg of carcass); 2) methane yield (MY), defined as methane production rate per kg of dry matter intake (g $CH_4$/kg of DMI); 3) methane production (MP), defined as methane production rate per time unit (e.g., g/day) and residual methane (RM) traits, which were computed as actual minus expected methane production. In some cases, $CH_4$ production was calculated using prediction equations based on milk fatty acids composition, feed intake, body weight, body condition score, diet composition and others.

### Statistical analyses

In order to understand the nature of variability in the studies, it is important to distinguish between different sources of heterogeneity. Important factors were recorded such as publication year, number of records, species/production purposes (i.e., dairy and beef cattle or sheep), breed, methane emission indicator trait, unit of measurement, measurement procedure (i.e., direct measurement or prediction equations), duration of measurement, variance component estimation method and statistical model. The standard errors associated with $h^2$ estimates were used in the meta-analysis to weight each estimate from the various studies by the amount of information used in each study. For some published estimates no standard errors were reported and, therefore, approximate standard error estimates were

obtained using the combined variance method proposed by Sutton *et al*., (2000).

In the study by Kandel *et al*., (2012), dual-purpose animals were grouped as dairy cattle. The meta-analyses were performed on the basis of a random-effects model (Borenstein *et al*., 2009), in which the parameter estimates for all traits were analysed assuming independence and normality. The analyses performed here were performed following Oliveira *et al*. (2017). In brief, the *metafor* package (Viechtbauer, 2010) available in the R software (R Core Team 2016) was used to fit the following random-effects model for each trait:

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Where  is the published parameter estimate in the $j^{th}$ article,  is the weighted population parameter mean,  is the among-study component of the deviation from the mean, assumed as , where  is the variance representing the amount of heterogeneity among studies, and,  is the within-study component due to sampling error in the parameter estimate in the $j^{th}$ article. The $I^2$ index (Higgins *et al*. 2003) and the Q statistics (Cochran, 1954) were used to quantify the degree of heterogeneity among studies. In general, $I^2$ values estimated of magnitude 25%, 50% and 75% can be considered as low, moderate and high heterogeneity respectively (Higgins *et al*., 2003). The 95% lower and upper limits for each estimate were also calculated.  Four meta-analysis scenarios were investigated: 1) combining sheep and cattle data and the four trait categories (and all $h^2$ estimates together); 2) using only estimates from cattle studies; 3) using only sheep studies; and, 4) using only cattle data and grouping traits based on assessment method (i.e., directly measured or calculated based on prediction equations).

## Results and discussion

The substantial increase in the number of papers reporting $h^2$ estimates for methane emission traits from 2011 to 2017 indicates the importance given to this trait more recently, which has also become possible due to great technological advancements in recording equipment and greater support from research funding agencies. A total of 60 $h^2$ estimates for various traits indicator of methane emission in cattle and sheep were included in this meta-analysis. A summary of the study and traits is presented as Supplementary material (Table S1). In brief there were 16, 36 and eight beef cattle, dairy cattle and sheep estimates, respectively. From those estimates, 33 were calculated based on direct measures of $CH_4$, while 27 were based on prediction equations. The majority of $h^2$ estimates were derived using restricted maximum likelihood (REML) methods. Unfortunately, due to the limited number of estimates available per group (e.g., breed, country, measurement methods), it was not possible to appropriately estimate the significance of these factors.

Heritability estimates with their respective 95% CI, $I^2$ index and the Q test for heterogeneity are shown in Table 1. There were significant differences (*p-value* < 0.05) among published estimates of $h^2$ for indicator traits of methane emission. The $h^2$ estimates for the different group of traits were moderate and ranged from 0.14 to 0.26 among all four scenarios. This indicates that methane production is under additive genetic control and satisfactory genetic gains are expected if these traits are included in sheep and cattle breeding objectives. The significant heterogeneity observed ($I^2 > 50\%$ and Q *p-value* < 0.05) for some scenarios (Table 1) highlights the existence of significant variation among $h^2$ estimates from different studies. It is worth of note that for MP and MY there was significant variation among $h^2$ estimates from different studies, but this was not the case for MI and RM, for which $h^2$ estimates were not significantly different across studies. It is also interesting to notice that the $h^2$ estimates for direct measures of methane emission did not show significant variation

across studies, but the $h^2$ estimates for indirect measures based on prediction equations were significantly different across studies.

Since meta-analysis brings together published parameter estimates provided by studies based on different populations, with different sample sizes and considering distinct effects in the model, it is expected that the true parameter may vary from study to study. However, a random effect model, as used in this study, accounts for the existence of other sources of variation besides random error.

*Table 1. Heritability ($h^2$) ($\pm$ SE) estimated from meta-analysis using random-effects model, 95% confidence interval (95% CI), and $I^2$ index and Q statistics to test the heterogeneity for direct $h^2$ estimates in each group of traits (MI: methane intensity, MP: methane production, MY: methane yield, and RM: residual methane).*

| Scenario | Trait | $h^2$ | 95% CI | Test of heterogeneity | | |
|---|---|---|---|---|---|---|
| | | | | $I^2$ (%) | Q | *p-value* |
| Cattle + sheep data | MI | 0.19 ± 0.02 | 0.15 – 0.23 | 5.65 | 2.91 | 0.71 |
| | MP | 0.24 ± 0.02 | 0.20 – 0.27 | 81.74 | 84.35 | < 0.0001 |
| | MY | 0.21 ± 0.03 | 0.14 – 0.26 | 86.44 | 178.65 | < 0.0001 |
| | RM | 0.17 ± 0.03 | 0.12 – 0.22 | 0.00 | 0.38 | 0.98 |
| | ALL | 0.22 ± 0.01 | 0.19 – 0.24 | 83.53 | 281.22 | < 0.0001 |
| Only cattle data | MI | 0.19 ± 0.02 | 0.15 – 0.23 | 5.65 | 2.91 | 0.7135 |
| | MP | 0.25 ± 0.02 | 0.22 – 0.29 | 75.52 | 53.39 | 0.0026 |
| | MY | 0.23 ± 0.03 | 0.16 – 0.29 | 88.02 | 148.07 | < 0.0001 |
| | RM | 0.17 ± 0.03 | 0.12 – 0.22 | 0.00 | 0.3852 | 0.9837 |
| | ALL | 0.23 ± 0.01 | 0.21 – 0.26 | 82.99 | 223.82 | <0.0001 |
| Only sheep data | ALL | 0.14 ± 0.02 | 0.10 – 0.18 | 42.5 | 11.58 | 0.12 |
| Only cattle data | DIR | 0.21 ± 0.01 | 0.18 – 0.23 | 0.00 | 15.15 | 0.91 |
| | PRED | 0.26 ± 0.02 | 0.21 – 0.30 | 93.37 | 200.78 | < 0.0001 |

*DIR: direct measured traits, PRED: traits calculated based on prediction equations; ALL: all traits considered together.*

## Conclusions

Our meta-analysis using a random-effects model indicated that methane emission indicator traits in cattle and sheep are under moderate genetic control and will serve as a basis for comparing genetic parameter estimates for these traits in the future. It seems that methane intensity and residual methane traits and direct measures of methane emission have homogeneous estimates of $h^2$ across the analysed studies, contrarily to methane production and methane yield traits and indirect measures of methane emission based on prediction equations, which displayed significant heterogeneity across studies. This might have practical implications when deciding which kind and which traits to use in selection programs, especially when international collaboration might be involved. More investigation in this area is warranted.

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Table S1. Publications, number of records (*N*), livestock breed group (**Dairy**: dairy cattle, **Beef**: beef cattle, **DP**: dual-purpose cattle, breed, trait measurement unit (**Unit**), measurement method (**Measure**, where Prediction: estimates based on prediction equations; and, Direct: direct measurements).

| Publication | N | Group | Breed | Unit | Measure | h² (± SE) |
|---|---|---|---|---|---|---|
| de Haas *et al.* (2011) | 665 | Dairy | Holstein | g/day | Prediction | 0.35 ± 0.12 |
| Patiño *et al.* (2011) | 105 | Sheep | DP | g/kg of DMI | Direct | 0.30 ± 0.26 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.17 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.15 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.26 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.22 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.07 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.36 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.35 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.52 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.52 ± 0.11 |
| Kandel *et al.* (2012) | 11,999 | DP | Belgian Blue | g/day | Prediction | 0.37 ± 0.11 |
| Patiño *et al.* (2013) | 5,236 | Sheep | Dual-purpose | g/Kg of DMI | Direct | 0.13 ± 0.03 |

| Publication | N | Group | Breed | Unit | Measure | h² (± SE) |
|---|---|---|---|---|---|---|
| Patiño *et al.* (2013) | 5,235 | Sheep | Dual- purpose | g/day | Direct | 0.29 ± 0.05 |
| Robinson *et al.* (2014) | 2,455 | Sheep | | mg/h | Direct | 0.12 ± 0.05 |
| Robinson *et al.* (2014) | 2,455 | Sheep | | mg/h | Direct | 0.11 ± 0.05 |
| Visker *et al.* (2014) | 1,838 | Dairy | Holstein | g/kg of DMI | Prediction | 0.12 ± 0.03 |

*Table S1. Cont.*

| Publication | N | Group | Breed | Unit | Measure | h² (± SE) |
|---|---|---|---|---|---|---|
| Visker *et al.* (2014) | 1,898 | Dairy | Holstein | g/kg of DMI | Prediction | 0.20 ± 0.03 |
| Visker *et al.* (2014) | 1,898 | Dairy | Holstein | g/kg of DMI | Prediction | 0.44 ± 0.02 |
| Lassen *et al.* (2015) | 3,121 | Dairy | Holstein | ppm | Direct | 0.16 ± 0.04 |
| Lassen *et al.* (2015) | 1,745 | Dairy | Holstein | g/day | Direct | 0.21 ± 0.06 |
| Lassen *et al.* (2015) | 1,745 | Dairy | Holstein | g/L of milk | Direct | 0.21 ± 0.06 |
| van Engelen *et al.* (2015) | 1,905 | Dairy | Holstein | g/ kg of DMI | Prediction | 0.12 ± 0.03 |
| van Engelen *et al.* (2015) | 1,905 | Dairy | Holstein | g/ kg of DMI | Prediction | 0.20 ± 0.05 |
| van Engelen *et al.* (2015) | 1,905 | Dairy | Holstein | g/ kg of DMI | Prediction | 0.44 ± 0.07 |
| Pickering *et al.* (2015) | 274,211 | Dairy | | g/day | Prediction | 0.13 ± 0.04 |
| Pickering *et al.* (2015) | 1,308 | Dairy | | mg/Kg | Direct | 0.05 ± 0.07 |
| Sobrinho *et al.* (2015) | 955 | Beef | Nellore | g/day | Prediction | 0.47 ± 0.07 |
| Sobrinho *et al.* (2015) | 955 | Beef | Nellore | g/day | Prediction | 0.32 ± 0.07 |
| Yin *et al.* (2015) | 7,804 | Dairy | Brown Swiss | Mcal/day | Prediction | 0.31 ± 0.06 |
| Yin *et al.* (2015) | 7,781 | Dairy | Brown Swiss | g/day | Prediction | 0.25 ± 0.06 |
| Arthur *et al.* (2016) | 1,043 | Beef | Angus | g/day | Direct | 0.24 ± 0.06 |
| Arthur *et al.* (2016) | 1,043 | Beef | Angus | g/ kg of DMI | Direct | 0.22 ± 0.06 |
| Arthur *et al.* (2016) | 1,043 | Beef | Angus | g/day | Direct | 0.18 ± 0.06 |
| Arthur *et al.* (2016) | 1,043 | Beef | Angus | g/day | Direct | 0.27 ± 0.07 |
| Arthur *et al.* (2016) | 1,043 | Beef | Angus | g/ kg of DMI | Direct | 0.22 ± 0.06 |
| Arthur *et al.* (2016) | 1,043 | Beef | Angus | g/day | Direct | 0.19 ± 0.06 |
| Hayes *et al.* (2016) | 1,020 | Beef | Angus | g/ kg of DMI | Direct | 0.28 ± 0.06 |
| Hayes *et al.* (2016) | 1,020 | Beef | Angus | g/day | Direct | 0.20 ± 0.05 |
| Hayes *et al.* (2016) | 747 | Beef | Angus | g/day | Direct | 0.18 ± 0.05 |
| Kandel *et al.* (2016) | 567,526 | Dairy | Holstein | g/day | Prediction | 0.24 ± 0.01 |
| Kandel *et al.* (2016) | 567,526 | Dairy | Holstein | g/kg of milk | Prediction | 0.18 ± 0.02 |
| Lassen *et al.* (2016) | 339 | Dairy | Holstein | g/day | Direct | 0.25 ± 0.16 |
| Lassen *et al.* (2016) | 339 | Dairy | Holstein | g/L of milk | Direct | 0.20 ± 0.16 |
| Lassen *et al.* (2016) | 339 | Dairy | Holstein | ppm | Direct | 0.16 ± 0.15 |
| Lassen *et al.* (2016) | 339 | Dairy | Holstein | g/day | Direct | 0.24 ± 0.15 |
| Lassen *et al.* (2016) | 339 | Dairy | Holstein | g/L of milk | Direct | 0.26 ± 0.14 |
| Lassen *et al.* (2016) | 339 | Dairy | Holstein | ppm | Direct | 0.09 ± 0.11 |
| Vanrobays *et al.* (2016) | 241,236 | Dairy | Holstein | g/day | Prediction | 0.25 ± 0.01 |
| Pech *et al.* (2016) | 1,020 | Beef | Angus | g/day | Direct | 0.30 ± 0.06 |
| Pech *et al.* (2016) | 1,020 | Beef | Angus | g/kg of DMI | Direct | 0.20 ± 0.05 |
| Pech *et al.* (2016) | 1,020 | Beef | Angus | g/kg weight | Direct | 0.25 ± 0.06 |
| Pech *et al.* (2016) | 1,020 | Beef | Angus | g/day | Prediction | 0.19 ± 0.05 |
| Pech *et al.* (2016) | 1,020 | Beef | Angus | g/day | Prediction | 0.15 ± 0.05 |
| Pech *et al.* (2016) | 205 | Dairy | Holstein | g/day | Direct | 0.23 ± 0.23 |
| Pech *et al.* (2016) | 205 | Dairy | Holstein | g/kg of DMI | Direct | 0.30 ± 0.23 |
| Pech *et al.* (2016) | 205 | Dairy | Holstein | g/kg of milk | Direct | 0.42 ± 0.23 |

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|---|---|---|---|---|---|---|
| Paganoni *et al.* (2017) | 2,677 | Sheep | Merino | g/day | Direct | 0.11 ± 0.03 |
| Paganoni *et al.* (2017) | 959 | Sheep | Merino | g/day | Direct | 0.14 ± 0.05 |
| Paganoni *et al.* (2017) | 438 | Sheep | Merino | g/day | Direct | 0.10 ± 0.06 |