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# Genetic variance and covariance components for carbon dioxide production and postweaning traits in Angus cattle

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## Abstract

This experiment investigated phenotypic and genetic relationships between carbon dioxide production, methane emission, feed intake, and postweaning traits in Angus cattle. Respiration chamber data on 1096 young bulls and heifers from 2 performance recording research herds of Angus cattle were analyzed to provide phenotypic and genetic parameters for carbon dioxide production rate (**CPR**; *n* = 425, mean 3,010 ± SD 589 g/d) and methane production rate (**MPR**; *n* = 1,096, mean 132.8 ± SD 25.2 g/d) and their relationships with dry matter intake (**DMI**; *n* = 1,096, mean 6.15 ± SD 1.33 kg/d), body weight (**BW**) and body composition traits. Heritability estimates were moderate to high for CPR (0.53 [SE 0.17]), MPR (0.31 [SE 0.07]), DMI (0.49 [SE 0.08]), yearling BW (0.46 [SE 0.08]), and scanned rib fat depth (0.42 [SE 0.07]). There was a strong phenotypic (0.83 [SE 0.02]) and genetic (0.75 [SE 0.10]) correlation between CPR and MPR. The correlations obtained for DMI with CPR and with MPR were high, both phenotypically ($r_p$) and genetically ($r_g$) ($r_p$: 0.85 [SE 0.01] and 0.71 [SE 0.02]; $r_g$ (0.95 [SE 0.03] and 0.83 [SE 0.05], respectively). Yearling BW was strongly correlated phenotypically ($r_p \geq 0.60$) and genetically ($r_g > 0.80$) with CPR, MPR, and DMI, whereas scanned rib fat was weakly correlated phenotypically ($r_p < 0.20$) and genetically ($r_g \leq 0.20$) with CPR, MPR, and DMI. The strong correlation between both CPR and MPR with DMI confirms their potential use as proxies for DMI in situations where direct DMI recording is not possible such as on pasture.

**Key words:** carbon dioxide, cattle, methane, growth, genetics

## Introduction

Methane is a greenhouse gas (**GHG**) produced by ruminants, and it is estimated that ruminants contribute 80% of global livestock emissions mostly through the production of methane (Gerber et al., 2013). Thus, much attention has been focused on reducing methane production in domesticated ruminants, such as sheep and cattle in an effort to reduce GHG emissions. This has resulted in refinement and development of technologies for the measurement of methane production rate (**MPR**), with most of these technologies having the capability to measure production of other gases simultaneously, including carbon dioxide production rate (**CPR**).

The MPR and CPR of cattle and sheep are both positively correlated phenotypically with feed intake (Pelchen and Peters 1998;

**Abbreviations**

| | |
|---|---|
| BW | body weight |
| BWT | birth weight |
| CM | carbon dioxide to methane ratio |
| CPR | carbon dioxide production rate |
| CY | carbon dioxide yield |
| DM | dry matter |
| DMI | dry matter intake |
| EMA | eye muscle area |
| FWT | final weight |
| GHG | greenhouse gas |
| IMF | intramuscular fat |
| NSW | New South Wales |
| MPR | methane production rate |
| MY | methane yield |
| P8FAT | P8 rump fat thickness |
| RCP | residual carbon dioxide production |
| RIBFAT | rib fat thickness |
| RMP | residual methane production |
| $r_g$ | genetic correlation |
| $r_p$ | phenotypic correlation |
| TWT | test period weight |
| WWT | weaning weight |
| YWT | yearling weight |

Charmley et al., 2016), leading to the possibility of using gas emissions information to estimate feed intake. In the past, the availability of appropriate and accurate measurement technologies for these emissions from free-ranging cattle and sheep were limited, but this is no longer the case. This has revived interest in the heritability of these gases and their phenotypic and genetic relationships with DMI and other production traits. Heritability estimates for MPR have been reported for sheep by Pinares-Patino et al. (2013) and Robinson et al. (2014); for beef cattle by Donoghue et al. (2016) and for dairy cattle by Lassen and Løvendahl (2016). Information on genetic parameters for CPR is limited to only the report by Jonker et al. (2018) in sheep.

The objective of this study was to provide phenotypic and genetic variance and covariance estimates for carbon dioxide emission by Angus cattle and to examine its relationships with MPR, DMI, and production traits.

## Materials and Methods

### Animal management and emissions measurement

The project was approved by the New South Wales (**NSW**) Department of Primary Industries and the University of New England Animal Ethics Committees. All animals in the project were managed according to the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC, 2013). The animals used in this study were from 2 fully pedigreed, performance-recording herds of registered Angus cattle at the NSW Department of Primary Industries, Agricultural Research Centre at Trangie in Australia. The cattle were born in 2009, 2011, 2012, and 2013, and were raised as calves by their dams on pasture until weaning at ~8 mo of age. The weaned bulls and heifers remained on pasture throughout their lives except for the period of gas emission measurement. Details on the composition of pasture species and supplementary feeding strategies have been previously reported by Donoghue et al. (2016). The weight of cattle was recorded at birth, weaning, yearling age, and close to 600 d of age, at which time body composition measurements were also taken by real-time ultrasound imaging.

Carbon dioxide production and methane production were measured in respiration chambers over 2 consecutive 24-h periods. Animals to be measured for emissions were first prepared at the research center at Trangie. Within each herd and sex, cohorts of up to 40 cattle in 4 groups of 10 were formed and prepared for measurement. Progeny of individual sires were stratified across groups and cohorts. The cohort of up to 40 animals were weighed and then fed in their groups of 10 an amount calculated, using the Australian feeding standards formulae (SCA, 2000) to provide 1.2 times their estimated energy requirement for maintenance. The test ration was a commercial alfalfa and oaten hay chaff purchased from the same supplier over the duration of the project (Manuka "Blue Ribbon" chaff; Manuka Chaff Pty. Ltd., Quirindi, NSW, Australia). The ration contained 88% dry matter (**DM**), 14% crude protein (DM basis), 67% DM-digestibility and metabolizable energy content of 9 MJ/kg DM (NSW Department of Primary Industries Feed Quality Service, Wagga Wagga, NSW, Australia). After 10 d, the animals were weighed again, with this weight used as their test period weight (**TWT**). The animals were then transported (~ 470 km) to the emissions testing facility at the University of New England, Armidale, NSW, Australia. The cattle were kept in their groups of 10 in external holding yards and fed the same amount of chaff ration for a minimum of 4 d. Then the first of the 4 groups was moved into the animal house and each animal fed in an individual pen (1.8 m × 3 m) for 2 d at 1.2 times estimated maintenance based on the TWT of the animal. Details on the design of the respiration chambers and emissions measurement protocols have been published earlier by Herd et al. (2014) and Donoghue et al. (2016).

### Traits studied

The definitions of the traits studied are provided in Table 1. Of the 1,096 animals with MPR data, 39% had CPR measured as well. The animals which had both MPR and CPR data were from the 2012- and 2013-born groups. Average daily DMI during the carbon dioxide/methane measurement period were used to calculate carbon dioxide yield (**CY**; CPR per unit DMI), methane yield (**MY**; MPR per unit DMI), and carbon dioxide to methane ratio (**CM**; g CPR per g MPR). Residual carbon dioxide production (**RCP**) and residual methane production (**RMP**) were defined to target carbon dioxide production or methane production independent of feed intake. The residuals obtained from the simple regression of CPR or MPR on DMI with cohort fitted as class effect were used as RCP or RMP. The $R^2$ for the regression of CPR on DMI was 0.91 and MPR on DMI was 0.86. A residual production trait is therefore a measure of actual trait (e.g., CPR) minus expected trait.

Growth traits recorded included BW at birth (**BWT**), weaning (**WWT**), yearling (**YWT**), and final BW (**FWT**), which were measured at birth and at mean age (± SD) of 231 ± 23 d, 423 ± 28 d, and 606 ± 71 d, respectively. Body composition traits, rib fat (**RIBFAT**) and P8 rump fat (**P8FAT**) thickness, eye muscle area (**EMA**), and intramuscular fat percentage (**IMF**) were measured by accredited real-time ultrasound scanners at a mean (± SD) age of 563 ± 94 d. Growth and body composition measurements were available on 1,532 animals, who were the progeny of 75 sires (average 20 progeny per sire, range 1 to 38), though not all animals had all traits recorded. Editing of records included removal of animals with incomplete pedigrees, missing birth date, large feed refusals and trait measurements >4 SDs from the contemporary group mean. The total number of animals for each trait, after editing of the original records is presented in Table 2.

**Table 1.** Definition of traits

| Trait name | Abbreviation | Unit | Definition |
|---|---|---|---|
| Test period weight | TWT | kg | Weight at time of emissions test |
| Dry matter intake | DMI | kg/d | Dry matter intake during the emission test |
| Carbon dioxide production rate | CPR | g/d | Carbon dioxide produced |
| Methane production rate | MPR | g/d | Methane produced |
| Carbon dioxide yield | CY | g/kg | CPR per unit DMI (CPR/DMI) |
| Carbon dioxide to methane ratio | CM | | Ratio of carbon dioxide produced to methane produced |
| Residual carbon dioxide production | RCP | g/d | CPR net of expected CPR (expCPR) from the DMI, with expCPR obtained by regression of CPR on DMI |
| Residual methane production | RMP | g/d | MPR net of expected MPR (expMPR) from the DMI, with expMPR obtained by regression of MPR on DMI |
| Birth weight | BWT | kg | Weight at birth |
| Weaning weight | WWT | kg | Weight at weaning (~200 d of age) |
| Yearling weight | YWT | kg | Weight at yearling age (~400 d of age) |
| Final weight | FWT | kg | Weight close to maturity (~600 d of age) |
| Rib fat thickness | RIBFAT | mm | Subcutaneous 12/13 rib fat depth measured by ultrasound scanning |
| P8 rump fat thickness | P8FAT | mm | Subcutaneous rump fat depth measured by ultrasound scanning |
| Eye muscle area | EMA | $cm^2$ | Cross-sectional area of the *M. longissimus dorsi* between the 12th and 13th ribs measured by ultrasound scanning |
| Intramuscular fat | IMF | % | Intramuscular fat measured by ultrasound scanning |

## Statistical analyses

Variance and covariance components were estimated with an animal model using ASReml (Gilmour et al., 2014). Preliminary analyses were conducted to evaluate appropriate models for each trait. The random genetic effects (direct, maternal, direct-maternal, and maternal permanent environment) were sequentially added to the basic model for each trait. Log-likelihood values were examined, and additional genetic effects were retained for the trait only when addition of the effect improved the fit of the model to the data. The standard model used for the final analyses included the fixed effect of contemporary group, random direct genetic effects, and residual effects. Contemporary group included cohort, methane measurement group, and management group. Additional fixed effects and covariates were added to the standard model where these variables were significant ($P < 0.05$) for a particular trait. The standard model was used for RCP and RMP, while for BWT, age of dam (in years) was added to the model as a linear covariate, and for FWT a linear covariate for age of animal (in d) was included in the model. For the remaining traits (TWT, DMI, CPR, MPR, CY, MY, WWT, YWT, RIBFAT, P8FAT, EMA, and IMF) age of animal as well as age of dam were added to the model as linear covariates. For the traits of BWT, WWT, YWT, and FWT, maternal genetic and maternal permanent environmental effects were also included in the model, with the direct-maternal relationship fixed at zero. Pedigree records for all animals with records and 2 further generations of ancestors were used. Univariate analyses were undertaken for all traits to obtain genetic parameters, and bivariate analyses of all trait combinations were conducted to obtain phenotypic and genetic correlations among traits.

**Table 2.** Descriptive statistics for carbon dioxide and methane production, feed intake, growth, and body composition traits measured on Angus cattle

| Trait | No. of records | Average (SD) | Minimum | Maximum |
|---|---|---|---|---|
| TWT, kg | 1,096 | 365 (96) | 156 | 640 |
| DMI, kg/d | 1,096 | 6.15 (1.33) | 3.59 | 9.42 |
| CPR, g/d | 425 | 3010 (589) | 2059 | 4973 |
| MPR, g/d | 1,096 | 132.8 (25.2) | 78.9 | 251.0 |
| CY, g/kg DMI | 425 | 579 (43) | 434 | 846 |
| CM | 425 | 26.6 (2.6) | 21.2 | 39.8 |
| RCP, g/d | 425 | 0 (181) | –654 | 1,036 |
| RMP, g/d | 1,096 | 0 (9.7) | –39.6 | 64.1 |
| BWT, kg | 1,532 | 34 (4.8) | 19 | 50 |
| WWT, kg | 1,517 | 241 (37) | 110 | 355 |
| YWT, kg | 1,437 | 368 (54) | 172 | 592 |
| FWT, kg | 1,210 | 457 (63) | 265 | 652 |
| RIBFAT, mm | 1,252 | 4.4 (2.6) | 1 | 18 |
| P8FAT, mm | 1,252 | 6.1 (3.6) | 1 | 32 |
| EMA, $cm^2$ | 1,252 | 61.9 (8.5) | 35 | 96 |
| IMF, % | 1,233 | 4.2 (1.5) | 1.5 | 8.1 |

TWT = test period weight; CPR = carbon dioxide production rate; MPR = methane production rate; CY = carbon dioxide yield; CM = carbon dioxide production to methane production ratio; RCP = residual carbon dioxide production; RMP = residual methane production; BWT = birth weight; WWT = weaning weight; YWT = yearling weight; FWT = final weight; RIBFAT = rib fat thickness; P8FAT = P8 rump fat thickness; EMA = eye muscle area; IMF = intramuscular fat.

## Results and Discussion

Descriptive statistics of the traits studied are presented in Table 2. This study and the genetic parameters for methane study ($n$ = 1,471) reported by Donoghue et al. (2016) are from the same emissions project; however, in this study ($n$ = 1,517), data from additional animals have been included. In spite of these differences in the number of animals, the level of variation in BW and ultrasound fat scan traits are similar in both reports. The large amount of variation observed for both TWT and age of emissions measurement was due to the older age at measurement of the animals born in 2009. The carbon dioxide traits exhibited substantial phenotypic variation even after

adjustment of CPR for DMI (to generate CY and the RCP). The CV for the carbon dioxide traits was 19.6%, 7.4%, and 9.8% for CPR, CY, and CM, respectively.

Genetic parameter estimates for emissions and production traits are presented in Table 3. Estimates of heritability for CY were low (<0.2), whereas those for DMI, CPR, CM, YWT, FWT, RIBFAT, and P8Fat were moderate to high (>0.4). The remaining traits, including MPR, RMP, and RCP, had moderate (0.2 to 0.4) heritability. These results indicate that the emissions traits are heritable.

Methane is a by-product of microbial fermentation of plant material in the rumen. It is known that MPR is driven by hydrogen dynamics in the rumen (Janssen, 2010), but the mechanisms by which the host (the ruminant, as opposed to the microorganisms) exercises control of rumen function are not yet fully understood. For example, in sheep, differences between host in rumen volume and the outflow rate of the digesta through the rumen have been shown to have a significant effect on MY (Okine et al., 1989; Goopy et al., 2014; Bond et al., 2019). Carbon dioxide on the other hand is largely a by-product of the process of oxidation of energy substances in the animal and the carbon dioxide produced is then exhaled. The measurement of gaseous emissions in ruminants has been increasingly studied since the 1960s; however, it is only in recent years that large numbers of animals have been measured in an effort to explore genetic improvement strategies to reduce GHG emissions. Hence, most of the research has been on ruminants reporting genetic and phenotypic parameters for methane traits. The heritability estimate for MPR obtained in this study is similar to the moderate heritability estimates reported for sheep (Pinares-Patino et al., 2013) and for cattle (de Hass et al., 2011; Donoghue et al., 2016; Hayes et al., 2016). In a study in sheep, Jonkers et al. (2018) reported a heritability estimate for CPR of 0.34 for lambs assessed in respiration chambers, 0.16 for lambs assessed in portable accumulation chambers, and 0.27 for ewes assessed in portable accumulation chambers. These heritability estimates in sheep are lower than the 0.53 reported in the current study. The authors are not aware of any other published heritability estimates for CPR in cattle or sheep.

The moderate to large heritability estimates for DMI are similar to that reported in the review by Berry and Crowley (2013). Genetic parameters for growth and body composition traits obtained in this study are similar to those published for Australian Angus cattle by Jeyaruban and Johnston (2013), except for WWT and YWT where estimates from the current study were higher but still within the range published in the literature for beef cattle (Koots et al., 1994).

Phenotypic and genetic correlations among the carbon dioxide and methane emission traits are reported in Table 4. The phenotypic association of CPR with DMI, MPR, and RCP were positive and strong ($r_p$ > 0.6), indicating that phenotypically, animals with higher CPR also had higher DMI, MPR, and RCP. Other recent studies have reported positive and strong phenotypic correlation between CPR and MPR in beef heifers ($r_p$ > 0.8; Renand et al., 2019) and in lambs ($r_p$ > 0.7; Jonker et al., 2018). In the current study, it is worth noting that CPR had a stronger correlation coefficient with DMI than does MPR (CPR $r_p$ 0.85; MPR $r_p$ 0.71). It is already known that animals in respiration chambers are unable to achieve the higher levels of DMI expected from ad libitum feeding in productions systems (Bickell et al., 2014; Herd et al., 2016). In this study, the cattle were not fed ad libitum but at 1.2 times their expected maintenance energy requirements, thus raising the issue of whether similar results will be obtained where cattle were fed ad libitum. In a project where Angus cattle were fed ad libitum and CPR and MPR measured using GreenFeed Emission Monitors (**GEM**; C-Lock Inc., Rapid City, SD), Bird-Gardiner et al. (2017) reported the phenotypic correlations between MPR and DMI as 0.75 for heifers on a roughage diet and 0.62 for steers on a grain-based diet. Using data collected on the same cattle as Bird-Gardiner et al. (2017), Arthur et al. (2018) reported phenotypic correlations between CPR and DMI as 0.84 and 0.83 for the heifers and steers, respectively. In general, the phenotypic correlations among CPR, MPR, and DMI from the cited GEM ad libitum fed studies where the cattle were in their production environment are similar to those in the current respiration chamber study where the cattle were fed a restricted diet.

The genetic correlations among carbon dioxide and methane traits were similar in nature (positive or negative coefficient) to the phenotypic correlations. However, the genetic correlations were higher in magnitude than their equivalent phenotypic correlations. Similarly, a high positive genetic correlation (0.84) between CPR and MPR was reported by Jonker et al. (2018) in lambs. In the current study, the genetic correlation (0.95) between CPR and DMI which was close to unity raises the

**Table 3.** Genetic parameters[1] (SE) for carbon dioxide and methane production, feed intake, growth, and body composition traits in Angus cattle

| Trait | $\sigma^2_d$ | $\sigma^2_m$ | $\sigma^2_c$ | $\sigma^2_p$ | $h^2_d$ | $h^2_m$ | $c^2$ |
|---|---|---|---|---|---|---|---|
| DMI | 0.087 (0.017) | — | — | 0.178 (0.009) | 0.49 (0.08) | — | — |
| CPR | 18,879 (7,210) | — | — | 35,836 (3,059) | 0.53 (0.17) | — | — |
| MPR | 52.7 (12.3) | — | — | 168.2 (8.2) | 0.31 (0.07) | — | — |
| CY | 66.5 (63.3) | — | — | 596.1 (44.1) | 0.11 (0.10) | — | — |
| CM | 1.22 (0.41) | — | — | 2.31 (0.19) | 0.53 (0.15) | — | — |
| RCP | 3,250 (1,835) | — | — | 13,304 (1,015) | 0.24 (0.13) | — | — |
| RMP | 18.8 (5.1) | — | — | 85.7 (4.0) | 0.22 (0.06) | — | — |
| BWT | 6.42 (1.57) | 3.16 (1.07) | 0.53 (0.87) | 18.36 (0.83) | 0.35 (0.08) | 0.17 (0.06) | 0.03 (0.05) |
| WWT | 174.5 (48.5) | 76.8 (34.9) | 99.5 (33.9) | 666.3 (28.4) | 0.26 (0.07) | 0.12 (0.05) | 0.15 (0.05) |
| YWT | 449.4 (90.3) | 56.8 (44.8) | 25.3 (46.0) | 981.6 (45.4) | 0.46 (0.08) | 0.06 (0.05) | 0.03 (0.05) |
| FWT | 725.8 (128.3) | — | — | 1,463.7 (71.8) | 0.50 (0.07) | — | — |
| RIBFAT | 1.02 (0.19) | — | — | 2.41 (0.11) | 0.42 (0.07) | — | — |
| P8FAT | 2.42 (0.44) | — | — | 5.57 (0.26) | 0.43 (0.07) | — | — |
| EMA | 8.85 (2.04) | — | — | 30.54 (1.34) | 0.29 (0.06) | — | — |
| IMF | 0.218 (0.048) | — | — | 0.651 (0.029) | 0.33 (0.07) | — | — |

[1]Parameter symbols $\sigma^2$ and $h^2$ denote variance and heritability, respectively; and subscripts *d*, *m*, and *c* denote direct, maternal, and permanent environmental, respectively.

**Table 4.** Genetic (above diagonal) and phenotypic (below diagonal) correlations (±SE) among feed intake and emissions traits

| Trait | DMI | CPR | MPR | CY | CM | RCP | RMP |
|---|---|---|---|---|---|---|---|
| DMI | | 0.95 (0.03) | 0.83 (0.05) | –0.37 (0.28) | –0.34 (0.19) | 0.57 (0.25) | 0.008 (0.17) |
| CPR | 0.85 (0.01) | | 0.75 (0.10) | 0.34 (0.42) | –0.12 (0.25) | 0.89 (0.11) | 0.15 (0.23) |
| MPR | 0.71 (0.02) | 0.83 (0.02) | | –0.12 (0.34) | –0.74 (0.11) | 0.44 (0.25) | 0.56 (0.12) |
| CY | –0.44 (0.05) | 0.26 (0.05) | –0.12 (0.06) | | 0.33 (0.35) | 0.77 (0.19) | 0.10 (0.38) |
| CM | –0.37 (0.05) | –0.03 (0.06) | –0.75 (0.02) | 0.44 (0.04) | | 0.09 (0.31) | –0.92 (0.08) |
| RCP | 0.12 (0.06) | 0.68 (0.03) | 0.36 (0.05) | 0.87 (0.01) | 0.31 (0.05) | | 0.22 (0.26) |
| RMP | –0.01 (0.03) | 0.33 (0.05) | 0.70 (0.02) | 0.48 (0.04) | –0.81 (0.02) | 0.52 (0.04) | |

CPR = carbon dioxide production rate; MPR = methane production rate; CY = carbon dioxide yield; CM = carbon dioxide production to methane production ratio; RCP = residual carbon dioxide production; RMP = residual methane production.

**Table 5.** Phenotypic correlations (±SE) between feed intake and emissions traits, and growth and body composition traits

| Trait | DMI | CPR | MPR | CY | CM | RCP | RMP |
|---|---|---|---|---|---|---|---|
| BWT | 0.37 (0.04) | 0.24 (0.07) | 0.23 (0.04) | 0.01 (0.06) | 0.0006 (0.07) | 0.13 (0.06) | –0.03 (0.04) |
| WWT | 0.70 (0.03) | 0.67 (0.03) | 0.52 (0.03) | –0.21 (0.06) | –0.18 (0.06) | 0.19 (0.06) | 0.05 (0.04) |
| YWT | 0.79 (0.02) | 0.73 (0.04) | 0.60 (0.03) | –0.16 (0.07) | –0.21 (0.07) | 0.27 (0.06) | 0.08 (0.04) |
| FWT | 0.76 (0.02) | 0.73 (0.03) | 0.56 (0.02) | –0.09 (0.07) | –0.33 (0.06) | 0.33 (0.06) | 0.08 (0.04) |
| RIBFAT | 0.18 (0.04) | 0.009 (0.06) | 0.10 (0.04) | –0.10 (0.07) | 0.02 (0.06) | –0.09 (0.06) | –0.04 (0.04) |
| P8FAT | 0.18 (0.04) | –0.01 (0.07) | 0.12 (0.04) | –0.12 (0.07) | 0.03 (0.07) | –0.11 (0.07) | –0.004 (0.04) |
| EMA | 0.42 (0.03) | 0.31 (0.06) | 0.28 (0.03) | 0.07 (0.07) | –0.12 (0.06) | 0.21 (0.06) | 0.003 (0.03) |
| IMF | 0.19 (0.04) | –0.02 (0.06) | 0.15 (0.04) | –0.18 (0.06) | –0.05 (0.06) | –0.14 (0.06) | 0.03 (0.04) |

**Table 6.** Genetic correlations (±SE) between feed intake and emissions traits, and growth and body composition traits

| Trait[1] | DMI | CPR | MPR | CY | CM | RCP | RMP |
|---|---|---|---|---|---|---|---|
| $BWT_d$ | 0.51 (0.14) | 0.28 (0.24) | 0.28 (0.17) | 0.25 (0.41) | –0.13 (0.23) | 0.21 (0.31) | –0.11 (0.20) |
| $BWT_m$ | 0.18 (0.16) | 0.08 (0.32) | 0.45 (0.22) | –0.76 (0.49) | –0.80 (0.36) | –0.26 (0.39) | 0.29 (0.26) |
| $WWT_d$ | 0.85 (0.06) | 0.91 (0.08) | 0.82 (0.09) | 0.09 (0.37) | –0.16 (0.24) | 0.66 (0.28) | 0.36 (0.20) |
| WWTm | 0.41 (0.12) | 0.82 (0.49) | 0.37 (0.18) | –0.80 (0.49) | –0.58 (0.35) | 0.10 (0.48) | –0.23 (0.28) |
| $YWT_d$ | 0.94 (0.03) | 0.85 (0.08) | 0.83 (0.07) | –0.18 (0.37) | –0.23 (0.21) | 0.53 (0.24) | 0.26 (0.18) |
| $YWT_m$ | 0.11 (0.14) | 0.58 (0.30) | 0.01 (0.26) | –0.40 (0.80) | –0.21 (0.47) | 0.29 (0.57) | –0.39 (0.38) |
| FWT | 0.92 (0.04) | 0.96 (0.06) | 0.76 (0.07) | –0.08 (0.34) | –0.39 (0.16) | 0.71 (0.22) | 0.15 (0.16) |
| RIBFAT | 0.20 (0.13) | –0.16 (0.19) | 0.11 (0.15) | –0.93 (0.55) | 0.16 (0.19) | –0.65 (0.27) | –0.07 (0.16) |
| P8FAT | 0.18 (0.13) | –0.15 (0.19) | 0.08 (0.14) | –0.76 (0.38) | 0.18 (0.19) | –0.69 (0.28) | –0.09 (0.16) |
| EMA | 0.56 (0.11) | 0.47 (0.20) | 0.41 (0.15) | –0.36 (0.43) | –0.31 (0.20) | 0.10 (0.30) | –0.05 (0.18) |
| IMF | 0.27 (0.14) | –0.15 (0.21) | 0.35 (0.15) | –0.99 (0.42) | –0.01 (0.21) | –0.59 (0.25) | 0.21 (0.17) |

[1]For BWT, WWT and YWT the subscripts d and m denote direct and maternal, respectively.

possibility of using CPR for genetic improvement in situations where DMI could not be measured, such as on pasture.

Phenotypic and genetic correlations between the emissions traits and growth and body composition traits are presented in Tables 5 and 6, respectively. The weaning/postweaning body weight traits (WWT, YWT, and FWT) were phenotypically and genetically correlated with DMI and the emissions traits (CPR and MPR), with the direct genetic correlations ($r$ = 0.76 to 0.96) being higher than the phenotypic ($r$ = 0.52 to 0.79) correlations. As expected, these results are similar to those reported by Donoghue et al (2016), which used much of the same data but without CPR information. In general, the correlations between CPR and the weaning/postweaning bodyweight traits were higher than those with MPR. Similarly strong phenotypic ($r$ = 0.79) and genetic ($r$ = 0.96) correlations between CPR and BW of lambs were reported by Jonker et al. (2018). The magnitude of phenotypic correlation coefficients between DMI and the body size traits (BWT, WWT, YWT, FWY, and EMA) were similar to those for CPR and the body size traits. A similar pattern was observed for their respective genetic correlation coefficients. Given the strong phenotypic as well as genetic correlation between DMI and CPR, the pattern of their observed correlation with body size traits was not unexpected. In general, the fatness traits (RIBFAT, P8FAT, and IMF) were weakly correlated phenotypically and genetically with both DMI and CPR. The genetic correlations between the fatness traits and the DMI-adjusted CPR traits (CY and RCP) were negative and strong, indicating that animals who genetically emit less CPR per unit DMI have the propensity to convert the extra feed energy absorbed into body tissue rather than to emit it as expired carbon dioxide. It should be noted that the standard errors of the correlation coefficients for CY and RCP were high, likely due to the low number of animals with CPR records. Further research is required to confirm this.

The results of this study show that genetic variation in carbon dioxide and methane production is present in this beef cattle population, and that there is an opportunity to use these emission traits not only to reduce GHG emissions but also to estimate DMI where direct measurement of DMI is not possible.

The latter should be developed further for the estimation of DMI at pasture, given that the enabling technologies (emissions monitoring equipment) capable of being deployed in the animal's production setting (e.g., GEM) are currently available.

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## Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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