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Estimates of genetic parameters for rumination time, feed efficiency, and methane production traits in first lactation Holstein cows

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ABSTRACT

The large-scale recording of traits such as feed efficiency and methane emissions for use in genetic improvement programs is complex, costly, and time-consuming. Therefore, heritable traits that can be continuously recorded in dairy herds and are correlated to feed efficiency and methane emission traits could provide useful information for genetic evaluation. Rumination time has been suggested to be associated with feed efficiency, methane production (methane emission in g/day), and production traits at the phenotypic level. Therefore, the objective of this study was to investigate the genetic relationships among rumination time, feed efficiency, methane and production traits using 7,358 records from 656 first lactation Holstein cows. The estimated heritabilities were moderate for rumination time (0.45 ± 0.14), methane production (0.36 ± 0.12), milk yield (0.40 ± 0.08), fat yield (0.29 ± 0.06), protein yield (0.32 ± 0.07), and energy corrected milk (0.28 ± 0.07), while low and non-significant for feed efficiency (0.15 ± 0.07), which was defined as the residual of the multiple linear regression of DMI on ECM and MBW. A favorable negative genetic correlation was estimated between rumination time and methane production (−0.53 ± 0.24), while a positive favorable correlation was estimated between rumination time and energy corrected milk (0.49 ± 0.11). The estimated genetic correlation of rumination time with feed efficiency (−0.01 ± 0.17) was not significantly different from zero but showed a trend of a low correlation with dry matter intake (0.21 ± 0.13, $P = 0.11$). These results indicate that rumination time is genetically associated with methane production and milk production traits, but high standard errors indicate that further analyses should be conducted to verify these findings when more data for rumination time, methane production and feed efficiency become available.

Key Words: rumination time, methane production, feed efficiency, heritability

INTRODUCTION

Livestock is responsible for 6% of anthropogenic greenhouse gas (**GHG**) emissions (Gerber et al., 2013). Methane (**CH_4**) expelled in ruminant eructation is a major contributor to these emissions and has an estimated lifetime of approximately 10 years in the atmosphere (Beauchemin et al., 2020). Beyond the environmental sustainability burden, enteric CH_4 emissions also represent an inefficient conversion of dietary energy (2 to 12% loss), which has negative implications for both animal productivity and farm profitability (de Haas et al., 2011; Richardson et al., 2020). Thus, there is a need to decrease CH_4 emissions of the dairy sector so that an increase in efficiency and sustainability can be attained. In addition to reducing CH_4 emissions, the improvement of feed efficiency (**FE**) would also contribute to increase the sustainability and efficiency of the dairy industry (Houlahan et al., 2021). However, measuring FE and CH_4 is time-consuming and expensive, and several studies have proposed the use of indicator traits such as rumination time (**RT**) for FE and CH_4 (Byskov et al., 2017; Zetouni et al., 2018; Beauchemin et al., 2020).

Rumination is essential in the regulation of both ingestion and digestion of feed. To degrade the fiber of vegetal feed and reduce feed particle size, ruminants initially chew their feed, and after it is swallowed for the first time, the feed bolus goes through a cyclical process of regurgitation, mastication, and re-swallowing (Beauchemin, 2018). This recurring process increases the surface area available for fermentation by the ru-

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men microbiota and subsequently increases the passage rate in the reticulorumen, allowing for faster digestion and absorption of nutrients (Kennedy, 1985). Further, rumination increases saliva production, improving rumen functionality as it inhibits the excessive decrease of ruminal pH, which could lead to illnesses, weight loss, and reduced milk production (Mertens, 1997). Different environmental events in the life of ruminants may have an impact on rumination. For example, the occurrence of stressful events such as diseases (Hansen et al., 2003; Antanaitis et al., 2019) and heat stress (Müschner-Siemens et al., 2020) might negatively affect rumination, affecting animal welfare and productivity. Also, dietary, and nutritional factors such as digestibility of the feed, fiber intake, and forage quality may increase or decrease rumination (Welch and Smith, 1970; White et al., 2017).

Before the commercialization of rumination collars, the most common method to assess RT was visual observation of the animal, where RT was measured directly (Krause et al., 1998; Couderc et al., 2006), by video (Lindström et al., 2001), or both (Kononoff et al., 2003). Today, RT can be monitored by an electronic system developed for the automated recording of RT in cattle (e.g., Allflex SCR, Hi Tag, SCR Engineers Ltd., Netanya, Israel). This system was previously validated (Schirmann et al., 2009) and used in the evaluation of RT and its association with milk production (phenotypic correlation [r_p] = 0.37; Kaufman et al., 2018), FE ($r_p = -0.11$; Byskov et al., 2017), methane emission (**ME**) ($r_p = -0.08$; Zetouni et al., 2018), and estrus (−20min /day before estrus; Reith and Hoy, 2012).

While the physiology of RT has been thoroughly studied, its underlying genetics are not well understood when compared with other traits such as milk production. Few studies have estimated genetic parameters for RT, or its genetic relationships with FE, production, or ME traits (Byskov et al., 2017; Moretti et al., 2018). Furthermore, as quantitative traits, FE and ME are also partially regulated by genetics (Williams et al., 2011; Tempelman et al., 2015; Miglior et al., 2017). Consequently, genetic relationships between RT and these other relatively novel traits must be present and quantified to assess RTs potential value as an associated trait.

The objective of this study was to estimate genetic parameters for RT and genetic correlations among RT, FE, methane production (CH_4 emission in g/day; **MeP**), and milk production traits in first lactation Holstein cows.

MATERIALS AND METHODS

Ethics and Animal Care

This study was approved by the University of Guelph Animal Care Committee (AUP 3503; AUP 4445).

Data and Quality Control

The data used in this study was provided by the Resilient Dairy Genome Project (http://www.resilientdairy.ca/; (van Staaveren et al., 2023). The initial data set consisted of 656 cows and comprised 7,358 records for milk (**MILK**), fat (**FAT**), and protein (**PRT**) yields; 25,219 records for body weight (**BW**), 31,535 records for dry matter intake (**DMI**), 2,229 records for MeP, and 1,907 records for RT. All 656 first-lactation Holstein cows used in the study were raised in the same research herd (Ontario Dairy Research Centre, Elora, ON, Canada). The pedigree included information up to 10 generations back from the phenotyped animals, resulting in a file containing 7,761 animals, with 1,925 unique sires and 5,467 unique dams. Cows with records had their first calving between January 2012 and October 2021 and cows older than 30 mo of age at first calving were excluded from the analyses.

Only records between 110 and 210 d in milk (**DIM**) were used for all traits since animals were measured for RT and MeP within this interval. Each trait was assessed individually for normality and outliers, and records outside the range of 3 standard deviations from the mean were removed. Traits measured more than once per week (i.e., BW, DMI, RT, and MeP) needed a minimum of 2 records per week of lactation to be considered in the analysis, where the week of lactation was defined based on the milk collection day. Finally, all traits were averaged to obtain weekly means. Therefore, cows evaluated for RT and MeP would only have one record (weekly average) for these traits in any given week of lactation between 110 and 210 DIM. For the remaining traits, cows had from one to 15 records (weekly averages) in the same interval (110 - 210 DIM).

Phenotype Collection

Energy Corrected Milk. Milk samples were collected weekly, weighed, and analyzed by Lactanet (Guelph, ON, Canada) for MILK, FAT and PRT in kilograms. Energy corrected milk (**ECM**) was calculated based on the equation by Sjaunja et al. (1990):

$$\text{ECM} = (0.25 \text{ x MILK}) + (12.2 \text{ x FAT}) + (7.7 \text{ x PRT})$$

where MILK, FAT and PRT represent kilograms of milk, fat, and protein, respectively. The measurements of these traits were considered representative of the whole week in which they were taken and, therefore, used in lieu of the weekly averages for MILK, FAT, PRT, and ECM, respectively.

Dry Matter Intake. Feed intake was recorded as described by Seymour et al. (2019), where samples of the offered total mixed ration (**TMR**) were collected 3 times per week, combined and analyzed for dry matter content in forced-air drying ovens following the National Forage Testing Association guidelines (Undersander et al., 1993). The daily DMI values were calculated as the product between TMR intake in kilograms and the calculated dry matter percentage in the diet. The daily TMR intake was calculated as the difference between offered and remaining feed for each day.

Metabolic body weight. The methodology used for recording BW was described previously (Seymour et al., 2020). Briefly, BW was recorded twice per week with a conventional scale; after measuring and collecting BW records, metabolic body weight (**MBW**) was calculated as $BW^{0.75}$.

Methane. Before collecting CH_4 measurements, cows were housed in a free-stall barn where they were fed, milked, and managed the same way as the rest of the milking herd. Between 110 to 210 DIM in their first lactation, cows were moved from the free-stall to a separate tie-stall wing of the farm for a period of 7 d to evaluate their MeP. Animals were moved in groups of 2 to 4 and brought into the tie-stall area 3 d before the testing week to allow for acclimatization to their new environment, which included the use of the GreenFeed machine (GreenFeed; C-Lock Inc., Rapid City, SD).

The GreenFeed machine consists of a mobile feeding station that uses airflow, integration of gas concentration measurements, temperature, humidity, and recognition of muzzle position to measure CH_4 and carbon dioxide CO_2 fluxes throughout each testing period (Huhtanen et al., 2015). Each animal visit is determined based on RFID infrared sensors, and all data is automatically recorded. The estimates of daily MeP are provided by measuring gas concentration and airflow. In this study, the airflow rate was 20 to 40 L/s, where the air was filtered, quantified, and sub-sampled for the analysis of concentrations of CH_4 and CO_2 by 2 embedded non-dispersive infrared sensors. This filter was cleaned once per week in our study. The analyzers were calibrated weekly, around milking time (i.e., 5:30am and 5:30pm), when the cows were not in proximity of the device, with a zero gas (pure N_2) and a span gas containing 5,000 ppm of CO_2 and 500 ppm of CH_4 per liter, respectively. Records from each visit were averaged to obtain daily MeP for 5 d.

During the week in the tie-stall area, cows were fed *ad libitum*. Once the adaptation period was concluded, MeP was measured 4 times per day (from Monday to Friday) at 8:00am, 12:00pm, 4:00pm, and 8:00pm from February 2017 to September 2020, and 3 times per day at 8:00am, 12:00pm and 4:00pm after September 2020. The change from 4 to 3 daily measurements occurred due to the difficulty of staffing the 8:00 p.m. measurement and the results from Kamalanathan et al. (2023), which showed that the 8:00 p.m. measurement had the same mean as the following 8:00 a.m. measurement and the same variance as the previous measurement at 4 p.m. These 2 measurements (before and after the 8 p.m. measurement) captured the variation in mean and variance of the 8 p.m. measurement, and it was therefore removed. Each measurement took approximately 10 to 12 min, where 10 min of data collection was considered the minimum for a sample to be complete. During methane collection, feed pellets were provided to the cows so they would keep their heads inside the machine. The machine was adjusted so that each cow could receive approximately 30 feed drops (23 s apart from each other) of 30g high-fat and 90% dry matter pellets per visit. The pellets were not considered in the final calculation of dry matter intake, because the individual pellet consumption was not recorded. However, this is not expected to impact the results, as the pellets should represent a maximum of 15% of the daily DMI in the week of the test and several repeated weeks of recorded DMI were used in the analyses for each cow.

Feed Efficiency. Feed efficiency (FE) in this study was defined by the residual of the multiple linear regression of DMI on ECM and MBW (Koch et al., 1963). The estimated intercept and regression coefficients for ECM and MBW were 4.76, 0.223 and 0.069, respectively.

Rumination Time. Measuring of RT occurred simultaneously to CH_4, where cows between 110 and 210 DIM had RT collected for a week. From March 2017 to February 2022, daily RT was measured by electronic loggers (Allflex SCR, Hi Tag, SCR Engineers Ltd., Netanya, Israel) located in the neck identification collars. Complete device description and accuracy validation were reported in a previous study (Schirmann et al., 2009). In summary, the built-in microphone and acoustic microprocessor are used to filter sounds of regurgitation and mastication that occur during rumination. Acoustic data are filtered on a 2-min resolution and summarized into 2-h periods. Data are transferred to the database by infrared readers located in the barn. The provided software outputs a 24-h average RT as well as information for each of the 12 intervals of 2 h. The collar's built-in algorithm requires a training period for adaptation to the animal and for identifying rumination and ingestion. In this study, a period of 7 d was used before the cows were relocated to the tie-stall. To avoid the use of data created by equipment or human error, rumination records for the cows were only used if all 12 measurements in a day were obtained and if the sum of these measurements was larger than zero before removing outliers 3 or more standard deviations from the mean.

Variance Component Estimation

(Co)variance components were estimated by pairwise bivariate analyses between all traits using the average information restricted maximum likelihood algorithm implemented in ASReml version 4.2 (Gilmour et al., 2015). Homogenous residual variances were assumed for all analyses. Then average estimates over all bivariate analyses for genetic, residual and permanent environment variances, and heritability estimates were obtained.

A single-record animal model was used to evaluate RT and MeP, while a repeatability animal model was used to evaluate ECM, MBW, DMI, MILK, FAT, PRT, and FE. A random regression model was not used because of the limitations imposed by the current sample size.

The single-record animal model used for RT and MeP was as follows:

$$\mathrm{y_{ijkl} = \mu + CA_i + DM_j + YSM_k + a_i + e_{ijkl},}$$

where y_{ijkl} represents measurements of the traits of the lth animal; μ is the overall mean of the trait; CA_i is the fixed effect of the ith class of age at calving in months (3 levels: younger than 24; between 24 and 25; older than 25 mo of age); DM_j is the fixed effect of the jth class of days in milk (3 levels: less than 135; between 135 and 145; more than 145 DIM); YSM_k is the fixed effect of the kth year and season of the week of methane collection (11 levels: from March 2017 to March 2022, where season 1 was defined as September to February and season 2 as March to August); a_i is the random additive genetic effect of the lth cow with $a \sim N\left(0, \mathbf{A}\sigma_a^2\right)$, where $\mathbf{A}$ is an additive genetic relationship matrix and σ_a^2 is the additive genetic variance; e_{ijkl} is the random residual error term with $e \sim N\left(0, \mathbf{I}\sigma_e^2\right)$, where $\mathbf{I}$ is the identity matrix and σ_e^2 is the variance of the residual error.

The repeatability animal model used for ECM, MBW, DMI, MILK, FAT, PRT, and FE was as follows:

$$\mathrm{y_{ijklm} = \mu + AC_i + WL_j + YS_k + a_i + pe_l + e_{ijklm},}$$

where y_{ijklm} represents measurements of the traits and the mth record of the lth animal; μ is the overall mean of the trait; AC_i is the fixed effect of the ith class of age at calving in months (4 levels: 23 mo or younger; between 24 and 25 mo; between 25 and 27 mo; older than 27 mo of age); WL_j is the fixed effect of the jth week of lactation (15 levels: 16 to 30 weeks); YS_k is the fixed effect of the kth year and season of calving (40 levels: winter 2011 to winter 2021); a_i is the random additive genetic effect of the lth cow with $a \sim N\left(0, \mathbf{A}\sigma_a^2\right)$, where $\mathbf{A}$ is an additive genetic relationship matrix and σ_a^2 is the additive genetic variance; pe_l is the random permanent environmental effect of the lth cow, with $pe \sim N\left(0, \mathbf{I}\sigma_{pe}^2\right)$, where σ_{pe}^2 is the permanent environmental variance; and e_{ijklm} is the random residual error term with $e \sim N\left(0, \mathbf{I}\sigma_e^2\right)$, where σ_e^2 is the variance of the residual error. $\mathbf{I}$ is the identity matrix.

Permanent environmental effects between traits with repeated records were assumed to be possibly correlated with covariance equal to σ_{pe}.

The idea was to use all the information available for ECM, MBW, DMI, MILK, FAT, PRT, and FE (i.e., traits with repeated records), while fitting a simple repeatability model to achieve better estimates for these traits and aid the analyses involving RT and MeP. However, when doing this, a genetic correlation of 1.0 between the repeated records for ECM, MBW, DMI, FAT, PRT, and FE was assumed and, consequently, a constant genetic correlation of these traits with MeP and RT over the range of DIM in the study. In this case, a tradeoff between having more information for ECM, MBW, DMI, FAT, PRT, and FE in the analyses and an assumption of genetic correlation of 1 was made; we assumed that the short range of DIM (110 - 210 DIM) minimized the impact of this approach. A significance level of 5% was assumed for all statistical tests, while, where noted, a trend was assumed for a significance level of 10%.

RESULTS AND DISCUSSION

The number of records and animals used in the final analyses as well as the descriptive statistics for each trait are reported in Table 1. Average estimates over all bivariate analyses for genetic, residual, and permanent environment variances are shown in Table 2, while average heritability estimates, genetic, and phenotypic correlations are shown in Table 3. Rumination time had a moderately high heritability (0.45 ± 0.14), negative genetic correlations with MeP (−0.53 ± 0.24), and MBW (−0.24 ± 0.13), and positive genetic correlations with all other traits except FE (estimated genetic cor-

Table 1 Number of records, number of animals with records, mean, standard deviation (SD), minimum, maximum, and coefficient of variation (CV) for production, efficiency, methane production, and rumination time traits in first-lactation Holstein cows

Trait	Records	Animals	Mean (SD)	Min	Max	CV (%)
ECM	6,812	650	31.20 (4.14)	15.31	44.24	13.29
MBW	5,305	476	127.85 (7.45)	106.40	150.14	5.83
DMI	5,024	491	20.62 (3.08)	6.20	31.11	14.95
FE	3,050	461	0.00 (2.85)	−14.85	7.76	NA
MILK	6,892	650	31.42(4.63)	17.50	45.50	14.75
FAT	6,841	650	1.25 (0.20)	0.51	1.97	16.03
PRT	6,847	650	1.05 (0.14)	0.50	1.60	13.90
MeP	451	451	491.70 (80.61)	263.80	708.60	16.39
RT	363	363	451.14 (49.03)	316.80	580.80	10.86

Traits: ECM = energy corrected milk in kg/day; MBW = metabolic body weight in kg$^{0.75}$; DMI = dry matter intake in kg/day; FE = feed efficiency (residual of the linear regression of DMI on ECM and MBW) in kg/day; MILK = Milk yield in kg/day; FAT = fat yield in kg/day; PRT = protein yield in kg/day; MeP = methane production in g/day; RT = rumination time in min/day.

relation between RT and FE was not statistically different from zero). Methane production had an estimated heritability of 0.36 ± 0.12, was genetically correlated to all production traits, FE (0.63 ± 0.17), and negatively correlated to RT (−0.53 ± 0.24). As defined in this study, FE was highly genetically correlated to DMI (0.93 ± 0.04). Phenotypic correlations followed a similar pattern observed for genetic correlations (Table 3).

The association of automatically recorded RT with production, reproduction, and health status of dairy cows has been evaluated previously (e.g., Kaufman et al., 2018; Reith and Hoy, 2012; Soriani et al., 2012). Understanding whether there is a genetic relationship between RT and novel sustainability traits may inform if there is potential value to add RT into breeding programs. In this study, we found a moderate to high heritability of RT, suggesting potential for genetic selection. Moreover, RT was correlated to CH_4 emissions, DMI, and milk production traits, but uncorrelated to FE in mid-first lactation cows. Further research with larger and more comprehensive data sets may offer more insight into the complex relationships between these traits, however our study provides an initial probe into these associations.

Descriptive Statistics

Records for the traits assessed in this study were as expected for cows of comparable status, age, and lactation. The average RT in this study (451.10 ± 49.03 min / day) is within the expected range (400 to 600 min / day) for Holstein cows, and comparable to values in studies on cows of similar age and lactation stage (487.3 ± 108.9 in Moretti et al., 2018 and 473.00 ± 80.00 in López-Paredes et al., 2020). A lower RT in young first lactation cows could be caused by lower feed intake levels, smaller rumen size and activity (Ducharme, 1990; Niehaus, 2009). In addition, environmental disturbances are more relevant for primiparous cows when compared with multiparous cows (Soriani et al., 2012), which might lead to interruptions in their rumination and consequently to a shorter average rumination time

Table 2 Average estimates and SE (between brackets) for genetic, residual, and permanent environment variance for production, efficiency, methane production, and rumination time traits in first-lactation Holstein cows over all bivariate analyses

Trait	Genetic Variance	Residual Variance	Permanent Environment Variance
ECM	5.56 (1.38)	5.17 (0.09)	6.84 (1.04)
MBW	23.30 (6.98)	3.38 (0.07)	25.52 (5.19)
DMI	2.14 (0.66)	4.49 (0.09)	2.64 (0.51)
FE	1.13 (0.53)	4.31 (0.12)	2.25 (0.45)
MILK	9.38 (2.03)	4.56 (0.08)	8.19 (1.41)
FAT	0.01 (0.003)	0.02 (0.0003)	0.01 (0.002)
PRT	0.01 (0.001)	0.01 (0.0001)	0.01 (0.001)
MeP	1,964.31 (615.42)	2,819.62 (480.97)	—
RT	1,192.85 (378.23)	1,227.81 (286.65)	—

Traits: ECM = energy corrected milk in kg/day; MBW = metabolic body weight in kg$^{0.75}$; DMI = dry matter intake in kg/day; FE = feed efficiency (residual of the linear regression of DMI on ECM and MBW) in kg/day; MILK = Milk yield in kg/day; FAT = fat yield in kg/day; PRT = protein yield in kg/day; MeP = methane production in g/day; RT = rumination time in min/day.

in younger animals. Similarly, values for MeP (Zetouni et al., 2018; Manzanilla-Pech et al., 2021; Richardson et al., 2021), FE and production traits (ECM, MBW, MILK, FAT, PRT) (Jamrozik et al., 2017; Andreen et al., 2020; Kappes et al., 2022) were also consistent with those in the literature.

Heritabilities

Our results showed heritability estimates ranging from 0.15 ± 0.07 for FE to 0.45 ± 0.14 for RT, with an estimate of 0.36 ± 0.12 for MeP.

Heritability for RT was moderately high (0.45 ± 0.14) and slightly higher compared with previously reported heritability estimates (0.33 ± 0.16, 0.34 ± 0.05, 0.17 ± 0.06) (Byskov et al., 2017; Moretti et al., 2018; López-Paredes et al., 2020), respectively. Byskov et al. (2017) obtained their estimate (0.33 ± 0.16) with a smaller sample size and averaged RT over weeks, Moretti et al. (2018) had double the animals compared with our study and averaged RT over lactation stages (0.34 ± 0.05). This could potentially explain the comparatively higher standard error in the current study and in Byskov et al. (2017) when compared with Moretti et al. (2018). In addition, we only measured RT in one herd whereas López-Paredes et al., (2020) estimated a heritability of 0.17 ± 0.06 from 775 cows across 8 herds. A standard trait definition and a larger sample size with data collected from multiple herds, would provide more reliable estimates; our results, however, provide additional evidence for heritable variance in RT.

The estimated heritability for MeP was moderate (0.36 ± 0.12) in the current study. Literature values for MeP heritability range from 0.03 to 0.45 (de Haas et al., 2011; Pickering et al., 2015; Breider et al., 2019; Manzanilla-Pech et al., 2021) depending on trait definitions, measurement protocols and populations included. Using an international database that comprises data collected from 6 countries (including a portion of the Canadian data in the current study) and different technologies (e.g., GreenFeed, Sniffers, SF6), heritability for MeP was estimated at 0.21 ± 0.04 (Manzanilla-Pech et al., 2021). However, using only GreenFeed data from multiple countries, heritability for MeP was estimated at 0.31 ± 0.15 (Manzanilla-Pech et al., 2021), which is more similar to our current results.

Feed efficiency had an estimated heritability comparable to that reported by Lu et al. (2018) (0.16 ± 0.02), who used similar statistical approaches and a linear regression of DMI on its energy sinks (i.e., ECM and MBW) to define FE. As another example of similar results obtained from the same methodology, the regression coefficients for ECM and MBW (0.223 and 0.069) are within the range of coefficients reported by Tempelman et al. (2015) using data from different countries and herds. In contrast, studies that defined feed efficiency by genetically adjusting DMI for the energy sinks reported smaller estimates for the heritability of feed efficiency, but similar regression coefficients for ECM and MBW (Jamrozik et al., 2017; Jamrozik and Kistemaker, 2020)

Finally, estimated heritabilities for DMI, MBW, MILK, FAT, PRT and ECM of (0.23, 0.43, 0.40, 0.29, 0.32, and 0.28, respectively) were all within the expected literature range (Oliveira Junior et al., 2021)

Genetic Correlations

With RT as a heritable trait, it is further important to understand its genetic correlations to other traits. The estimated genetic correlation between RT and MeP (−0.53 ± 0.24) indicates that animals with longer RT emit less CH_4. Our estimate is more extreme than the point estimate of −0.43 ± 0.35 reported by

Table 3 Genetic correlation (above diagonal), heritability[1] (diagonal), and phenotypic correlation (below diagonal) for production, efficiency, methane production, and rumination time traits in first-lactation Holstein cows

	ECM	MBW	DMI	FE	MILK	FAT	PRT	MeP	RT
ECM	0.28 (0.07)	−0.04 (0.21)	0.57 (0.16)	0.20 (0.26)	0.74 (0.07)	0.87 (0.04)	0.89 (0.03)	0.74 (0.13)	0.49 (0.11)
MBW	−0.03 (0.04)	0.43 (0.11)	0.37 (0.21)	0.34 (0.28)	−0.10 (0.19)	−0.05 (0.20)	0.07 (0.20)	0.68 (0.10)	−0.24 (0.13)
DMI	0.34 (0.03)	0.21 (0.04)	0.23 (0.07)	0.93 (0.04)	0.51 (0.15)	0.39 (0.18)	0.65 (0.15)	0.83 (0.11)	0.21 (0.13)
FE	0.05 (0.03)	0.07 (0.04)	0.94 (0.004)	0.15 (0.07)	0.16 (0.24)	0.10 (0.25)	0.33 (0.23)	0.63 (0.17)	−0.01 (0.17)
MILK	0.83 (0.01)	−0.09 (0.05)	0.31 (0.03)	0.06 (0,04)	0.40 (0.08)	0.33 (0.14)	0.80 (0.05)	0.33 (0.12)	0.52 (0.12)
FAT	0.91 (0.01)	−0.02 (0.04)	0.29 (0.03)	0.02 (0.03)	0.55 (0.02)	0.29 (0.06)	0.61 (0.10)	0.89 (0.12)	0.36 (0.11)
PRT	0.90 (0.01)	0.01 (0.04)	0.35 (0.03)	0.08 (0.03)	0.88 (0.01)	0.67 (0.02)	0.32 (0.07)	0.55 (0.14)	0.54 (0.11)
MeP	0.37 (0.06)	0.45 (0.07)	0.46 (0.05)	0.26 (0.08)	0.18 (0.06)	0.41 (0.05)	0.23 (0.06)	0.36 (0.12)	−0.53 (0.24)
RT	0.25 (0.07)	−0.17 (0.08)	0.20 (0.07)	0.08 (0.09)	0.30 (0.07)	0.16 (0.07)	0.29 (0.07)	−0.09 (0.06)	0.45 (0.14)

Traits: ECM = energy corrected milk in kg/day; MBW = metabolic body weight in $kg^{0.75}$; DMI = dry matter intake in kg/day; FE = feed efficiency (residual of the linear regression of DMI on ECM and MBW) in kg/day; MILK = Milk yield in kg/day; FAT = fat yield in kg/day; PRT = protein yield in kg/day; MeP = methane production in g/day; RT = rumination time in min/day. The value in brackets is the SE associated with the estimate.

[1] Average estimate and SE over all bivariate analyses.

López-Paredes et al., (2020), estimated from a larger number of animals (n = 1,501) across multiple farms. Our results are also more extreme than the small non-significant genetic correlation (−0.08 ± 0.06) reported by Zetouni et al. (2018), who used a slightly smaller number of animals (n = 343) from one research farm. Both groups of authors used similar trait definitions and collection methods for RT and MeP as in the present study, however they also included animals in second and third parity, whereas we did not. Factors such as age, parity, diet, feed intake, digesta turnover, and ruminal fermentation may influence RT and MeP (Moe and Tyrrell, 1979; Mertens, 1997; Mendes et al., 2012). All these factors can influence the ratio of acetate and propionate, 2 volatile fatty acids in the rumen that are transformed into CH_4 and fat, respectively (Hassanat et al., 2013). Despite the difference in estimated correlations between the studies, they indicate a potential negative genetic correlation between RT and MeP.

Rumination time has also been suggested as a potential indicator for traits related to feed efficiency (Byskov et al., 2017). Byskov et al. (2017) estimated negative genetic correlation between RT and RFI (−0.34 ± 0.12) and a small non-significant genetic correlation with DMI (−0.09 ± 0.12) at a similar lactation stage as that used in our study, indicating that RFI and RT seem to be associated. In the current study, there were no genetic correlations between RT and FE (−0.01 ± 0.17) and only a trend for a low genetic correlation between RT and DMI (0.21 ± 0.13, $P = 0.11$). These results must be further verified once more phenotypic records are available.

In the current study, genetic correlations between RT and ECM (0.49 ± 0.11), FAT (0.36 ± 0.11), and PRT (0.54 ± 0.11) were high, indicating that RT is genetically associated with milk production traits. In the process of milk protein biosynthesis, dietary crude protein is initially degraded in the rumen and then utilized to synthesize microbial protein (Larson, 1965). This microbial protein is digested into amino acids and absorbed in the intestine (Larson, 1965), then directed to the liver and then to the mammary gland for the synthesis of milk protein (Larson, 1965; Xue et al., 2020). Therefore, a longer period of rumination could be associated with a higher availability of protein, based on the higher degradation of the dietary protein.

The estimated genetic correlations between RT and ECM (0.49 ± 0.11), and MILK (0.52 ± 0.12) were high, but comparable to the estimate of 0.41 ± 0.75 between RT and MILK by López-Paredes et al. (2020), while differing considerably from the −0.03 (ECM) and 0.12 (MILK) correlation estimates by Byskov et al. (2017) and Moretti et al. (2018), respectively. In the current study, higher milk production was also positively genetically correlated to higher levels of feed intake (ECM and DMI genetic correlation of 0.57 ± 0.16, and MILK and DMI correlation of 0.51 ± 0.15). These results together suggest that, genetically, animals that ruminate for longer periods of time produce more milk and may tend to have a higher dry matter intake.

The MBW of an animal was associated with their DMI and RT, and this relationship is complex. The estimated trend for a genetic correlation between MBW and DMI (0.37 ± 0.21, $P < 0.10$) indicated that heavier animals tended to eat more than lighter animals. Despite this positive correlation, the relationship between MBW and DMI is not isometric, meaning increases in MBW are not at the same scale as increases in DMI (Weckerly, 2013). Instead, MBW and DMI scale allometrically, therefore on a per kilo basis of MBW, DMI in lighter animals can be greater than the DMI of heavier animals (Weckerly, 2013). In this context, the RT of lighter animals could be longer in comparison to heavier animals as seen in the trend for a negative correlation between RT and MBW (−0.24 ± 0.13, $P < 0.10$). Weckerly et al. (2013) suggested that lighter animals break down feed particles more quickly than heavier animals because they chew more thoroughly (longer RT), resulting in a quicker rumen turnover. In our study, the negative correlation between MBW and RT also indicated that lighter animals spent more time ruminating than heavier animals. Van Soest (1994) found that smaller ruminants needed to compensate for their reduced gastrointestinal capacity, relative to their MBW, and this could be achieved by faster digestion or ruminal passage rate. Therefore, a longer period of rumination could be expected and would be plausible for lighter animals.

Overall, the genetic correlations in our study indicate that RT is negatively correlated to MeP and positively correlated to milk production traits. With regards to the correlation between RT and FE and DMI, results indicate no genetic correlation with FE and a trend of low correlation with DMI. Additional studies will be necessary to validate these findings as the amount of data for these traits increases, however the initial indications observed in this study are promising.

Phenotypic Correlations

Phenotypic correlations between RT and the traits included in this study generally followed trends observed in the genetic correlations, although in some cases the phenotypic correlations were not as pronounced (e.g., RT and MILK, FAT, and PRT). In these cases, the genetic correlations were close to twice as high as the phenotypic correlations. Phenotypic correlations for RT and other traits in dairy cattle have been more widely explored in comparison to genetic correlations. Phenotypic correlations between RT and DMI have been previously reported (e.g., Watt et al., 2015; Schirmann et al., 2012) where cows with higher intake tended to ruminate for longer periods of time; this is also in line with our results. Additionally, RT has been used to estimate individual cow variation in feeding behavior and intake but seems to be a poor indicator of DMI when used as a daily summarized trait (Schirmann et al., 2012).

One of the main differences between our results and the current literature regarding RT is the phenotypic correlation between RT and milk production traits. Moretti et al., (2018) estimated negative correlations between RT and milk (−0.14 ± 0.03), fat (−0.09 ± 0.03) and protein (−0.09 ± 0.06) yields at 151–300 DIM, whereas we estimated positive correlations for RT and MILK (0.30 ± 0.07), ECM (0.25 ± 0.07), FAT (0.16 ± 0.07), and PRT (0.29 ± 0.07) at 110–210 DIM. Differences in phenotypic correlations between studies could be due to the stage of lactation analyzed (Houlahan et al., 2022; Manzanilla-Pech et al., 2022), as the relationship between traits has been shown to be dynamic over the lactation. Such differences could be further explored with the use of random regression models if a full lactation of records is available. Studies estimating correlations between RT and other traits have often concentrated on the transition period (Kaufman et al., 2018) or the dry period (Schirmann et al., 2012), with limited research available for the whole lactation (Moretti et al., 2018; Zetouni et al., 2018). Animals in the current study were in their mid-lactation stage (110–210 DIM) and were neither at the peak of lactation, or in negative energy balance, nor affected by events such as calving or estrus. Thus, the mid-lactation stage could potentially represent the relationships among RT, MeP, FE and milk production traits with fewer confounding physiological effects.

CONCLUSIONS

The objectives of this study were to estimate the heritability of RT measured by automated sensors and its genetic correlations with MeP, FE, and milk production traits. Rumination time had a moderately high heritability, was negatively genetically correlated to MeP, positively genetically correlated to MILK, FAT and PRT, ECM, and was genetically uncorrelated to DMI and FE. These results suggest that rumination time could be used to indicate animals of lower MeP and higher milk production traits. Additional studies with larger data sets will be necessary to validate these findings.

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