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## Between-cow variation in the components of feed efficiency

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### ABSTRACT

A meta-analysis based on an individual-cow data set was conducted to investigate between-cow variations in the components and measurements of feed efficiency (FE) and to explore the associations among these components. Data were taken from 31 chamber studies, consisting of a total of 841 cow/period observations. The experimental diets were based on grass or corn silages, fresh grass, or a mixture of fresh grass and straw, with cereal grains or by-products as energy supplements, and soybean or canola meal as protein supplements. The average forage-to-concentrate ratio across all diets on a dry matter basis was 56:44. Variance component and repeatability estimates of FE measurements and components were determined using diet, period, and cow within experiment as random effects in mixed procedures of SAS (SAS Institute Inc., Cary, NC). The between-cow coefficient of variation (CV) in gross energy intake (GE; CV = 0.10) and milk energy ( $E_l$ ) output as a proportion of GE ( $E_l/GE$ ; CV = 0.084) were the largest among all component traits. Similarly, the highest repeatability estimates ( $\geq 0.50$ ) were observed for these 2 components. However, the between-cow CV in digestibility (DE/GE), metabolizability [metabolizable energy (ME)/GE], methane yield ( $CH_4E/GE$ ), proportional urinary energy output (UE/GE), and heat production (HP/GE), as well as the efficiency of ME use for lactation ( $k_l$ ), were rather small. The least repeatable component of FE was UE/GE. For FE measurements, the between-cow CV in residual energy-corrected milk (RECM) was larger than for residual feed intake (RFI), suggesting a greater possibility for genetic gain in RECM than in RFI. A high DE/GE was associated with increased  $CH_4E/GE$  ( $r = 0.24$ ), HP/GE ( $r = 0.12$ ), ME/GE ( $r = 0.91$ ), energy balance as a proportion of GE (EB/GE;  $r = 0.35$ ), and  $k_l$  ( $r = 0.10$ ). However, no correlation between DE/GE and GE

intake or UE/GE was observed. Increased proportional milk energy adjusted to zero energy balance ( $E_{l(0)}/GE$ ) was associated with increases in DE/GE, ME/GE, EB/GE, and  $k_l$  but decreases in UE/GE,  $CH_4E/GE$ , and HP/GE, with no effect on GE intake. In conclusion, several mechanisms are involved in the observed differences in FE among dairy cows, and reducing  $CH_4E$  yield ( $CH_4E/GE$ ) may inadvertently result in reduced GE digestibility. However, the selection of dairy cows with improved energy utilization efficiencies offers an effective approach to lower enteric  $CH_4$  emissions.

**Key words:** variation, energy, residual feed intake, residual energy-corrected milk

### INTRODUCTION

Improved feed efficiency (FE) of the modern dairy cow is the result of high milk yield-oriented breeding programs, together with proper feeding and management of cows over the past decades. This enhanced FE is predominantly driven by dilution of maintenance requirement (Bauman et al., 1985), whereby a greater proportion of feed energy intake is used for milk production instead of maintenance as production and feed intake increase. Currently, elite dairy cows produce milk and meat, which is energetically equivalent to more than 4× their maintenance requirements (VandeHaar and St-Pierre, 2006). However, by the time they attain about 5× maintenance, marginal increases in efficiency begin to plateau (VandeHaar et al., 2016) because of depressed energy digestibility associated with a high ruminal rate of passage at high intake levels (NRC, 2001; Huhtanen et al., 2009). Therefore, further selection for higher milk production alone will no longer lead to substantial increases in FE. It is well known that selection programs with milk production as a sole trait have negatively affected health and reproductive performance (De Vries et al., 1999; Collard et al., 2000). For instance, the fertility of Holstein-Friesian dairy cows in the United States declined steadily from 1960 and reached a nadir in 2000. Although remedial actions have been taken and fertility has begun to im-

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prove since the year 2000, it will take 2 to 3 decades to return the population to the fertility levels they had some 50 years ago (Rogers and Cooper, 2011). In addition, selection exclusively on genetic merit for milk yield has resulted in larger cows together with greater maintenance costs per unit of metabolic BW (Agnew and Yan, 2000; Hansen, 2000), which partly offset the benefits of increased production. Thus, future increases in FE should not rely only on increasing production but must also focus on alternative approaches.

Previous studies have reported considerable between-animal variation in FE (Coleman et al., 2010; Arndt et al., 2015). This variation is mostly linked to differences in dietary energy losses [fecal, methane (CH<sub>4</sub>), and urinary], heat production (HP), and energy retention (VandeHaar, 2016). On this premise, a holistic approach to improving the FE of individual cows is to consider it in the framework of classical dietary energy partitioning, which follows from the second law of thermodynamics. In simple terms, this law states that no transformation of energy into useful work is completely efficient, and the inefficiencies are lost as heat. Gross energy (GE) is the total chemical energy contained in a feed; some of which is lost as the chemical energy in feces, gases, and urine, and some are lost as the heat associated with the metabolic work of fermenting, digesting, and processing nutrients. The remaining energy is known as net energy, which is the actual energy utilized for maintenance and for production (lactation, body tissue accretion, and conceptus). Measuring the between-animal variability at each step of energy metabolism may provide the basis for future efforts to enhance FE. Because animal variation is possibly under genetic control, selective breeding for animals that partition less energy to feces, CH<sub>4</sub>, urine, maintenance, HP, or accreted body tissues could both increase the proportion of GE available for milk production and improve FE.

Our understanding of the relationships among the components involved in the observed between-animal variation of FE is essential for the future development of effective selection strategies for this trait. Hence, the objectives of our study were to evaluate between-cow variation in the components of FE and to assess the relationships among these components using a data set from chamber studies with a meta-analytical approach. Our companion paper (Guinguina et al., 2020) focuses on the effects of these components on FE.

## MATERIALS AND METHODS

### *Animals, Feeding, and Data Recording*

Data used were collected from 31 individual studies conducted using a continuous design (9 studies)

and changeover design (Latin square or switchback). The majority of these studies have been published in peer-reviewed scientific journals, and their references are presented in the supplemental data file (<https://doi.org/10.3168/jds.2020-18257>). A total of 841 cow/period observations from 4 dairy breeds (609 Holstein-Friesian, 171 Nordic Red, 32 Jersey, and 29 Holstein-Friesian × Jersey) were included in the complete data set. The cow per period observations were considered as experimental units. Cows in our study were from 3 research herds from the UK (20 studies, 97 diets, and 534 observations), Denmark (9 studies, 35 diets, and 171 observations), and Finland (2 studies, 3 diets, and 136 observations). The research herds were located at Agri-Food and Biosciences institute–AFBI (Hillsborough, UK), the Danish Cattle Research Centre (AU Foulum, Denmark), and Natural Resources Institute Finland (LUKE; Jokioinen, Finland). A total of 100 cows used in the EU project RUMINOMICS (<http://www.ruminomics.eu>) were from the Finnish herd and were part of our data set. The minimum requirement for a study to be included in the meta-analysis was that feed intake, BW, milk production data, diet digestibility, and gas consumption and production data were available.

The data set was collated to cover a wide range of dietary compositions from studies that investigated feeding level, forage type, proportion of concentrate supplementation, concentrate energy or carbohydrate sources, fat and protein supplementation, CH<sub>4</sub> mitigation strategies, forage maturity at harvest, and silage fermentation quality. Cows were offered forage-only diets (n = 44) or forages with a proportion of concentrates (n = 797) varying from 130 to 820 g/kg of DM. The diets were offered as TMR or concentrates, and forages were fed separately to fulfill specific aims within individual experiments. The mean forage-to-concentrate ratio of the diets was 56:44 on DM basis. Except for 4 studies in which animals were fed restrictively, cows had ad libitum access to experimental diets. Diets containing less than 250 g/kg DM proportion of forage were deleted from the data set so that only diets within the normal range as fed to dairy cows were included. The forages offered included grass silage (649), mixture of grass silage and corn silage (n = 112), fresh grass (n = 25), mixture of fresh grass and straw (n = 4), corn silage (n = 8), and mixture of corn and grass-clover silages (n = 43). Grass silages were produced from primary growth, primary regrowth, and secondary regrowth material, and were either wilted or unwilted before ensiling with or without application of silage additives. The concentrates used in each of the studies included cereal grains (barley, wheat, or corn), agro-industrial by-products (molassed or unmolassed sugar beet pulp,

citrus pulp, or molasses), protein supplements (soybean meal, canola expeller, or meal), oil supplements, and mineral-vitamin supplements.

Experiments constituted digestibility trials where animals spent part of the experimental period in open-circuit indirect calorimeter chambers. Feed intake was recorded manually as the difference between feed offered and refusals. Before measurements in the respiration chambers, the cows were adapted to their experimental diets for at least 14 to 21 d in a loose-housing barn (in tiestalls for Danish studies). They were then transferred to individual tiestalls (Finnish and UK studies) for a period of 5 to 8 d, where measurements of total feed intake and the total collection of feces and urine were made during the final 3 to 6 d (Danish and UK studies). Immediately after digestibility measurements, cows were housed in calorimeter chambers for 3 to 5 d with measurements of gaseous exchanges ( $\text{CH}_4$ ,  $\text{CO}_2$ , and  $\text{O}_2$ ) taking place during the final 2 to 5 d (for Danish and UK studies). In the case of Finnish studies, digestibility and gaseous exchanges were measured simultaneously in calorimeter chambers.

### Calculations

Only studies including digestibility data were used in the final analysis. When either GE or OM digestibility (**DE/GE** and **OMD**, respectively) were not reported, they were estimated using prediction equations derived from the present data set with a mixed model regression analysis, as follows:

$$\begin{aligned} \text{DE/GE (kJ/MJ)} = & -13.6 \pm 12.66 \\ & + 1.00 \pm 0.018 \times \text{OMD} \end{aligned} \quad [1]$$

[adjusted root mean square error (**RMSE**) = 5.63; n = 136];

$$\begin{aligned} \text{OMD (g/kg of DM)} = & 42.0 \pm 11.23 + 0.96 \pm 0.016 \\ & \times \text{DE/GE (kJ/MJ)} \end{aligned} \quad [2]$$

(adjusted RMSE = 5.40; n = 136). The RMSE was adjusted for random experiment, diet within experiment, and period within experiment effects.

Heat production (MJ/d) was calculated from volumes of  $\text{O}_2$  consumption (L/d),  $\text{CO}_2$  production (L/d),  $\text{CH}_4$  production (L/d), and urinary nitrogen excretion (UN, g/d), according to Brouwer (1965):

$$\begin{aligned} \text{HP} = & 0.01618 \times \text{O}_2 + 0.00502 \times \text{CO}_2 - 0.00599 \\ & \times \text{UN} - 0.00217 \times \text{CH}_4 \end{aligned} \quad [3]$$

When the UN (g/d) was not reported (n = 705), it was calculated as follows:

$$\begin{aligned} \text{UN} = & \text{N intake} - \text{Fecal N} - \text{Milk N} \\ & - \text{Scurf N} - \text{Retained N}, \end{aligned} \quad [4]$$

where scurf N was calculated according to NRC (2001), N retention was estimated from the calculated energy balance (**EB**) by assuming that BW gain corresponds to EB of 34 MJ/kg and BW loss to 28 MJ/kg, and that BW change represents 25.2 g of N/kg (MAFF, 1975).

Energy balance (MJ/d) was calculated for each cow using the following equation:

$$\text{EB} = \text{ME intake} - \text{HP} - \text{E}_1, \quad [5]$$

where  $\text{E}_1$  is milk energy output (MJ/d).

When ME intake (MJ/d) was not reported (n = 65), it was calculated as follows:

$$\text{ME intake} = \text{DE intake} - \text{CH}_4\text{E} - \text{UE}, \quad [6]$$

where **UE** is urinary energy output. Methane energy (**CH<sub>4</sub>E**, MJ/d) was calculated using the factor 0.05524 MJ/g of  $\text{CH}_4$  proposed by Kriss (1930).

When UE was not reported, it was calculated using prediction equations derived from the current data set with a mixed model regression analysis, as follows:

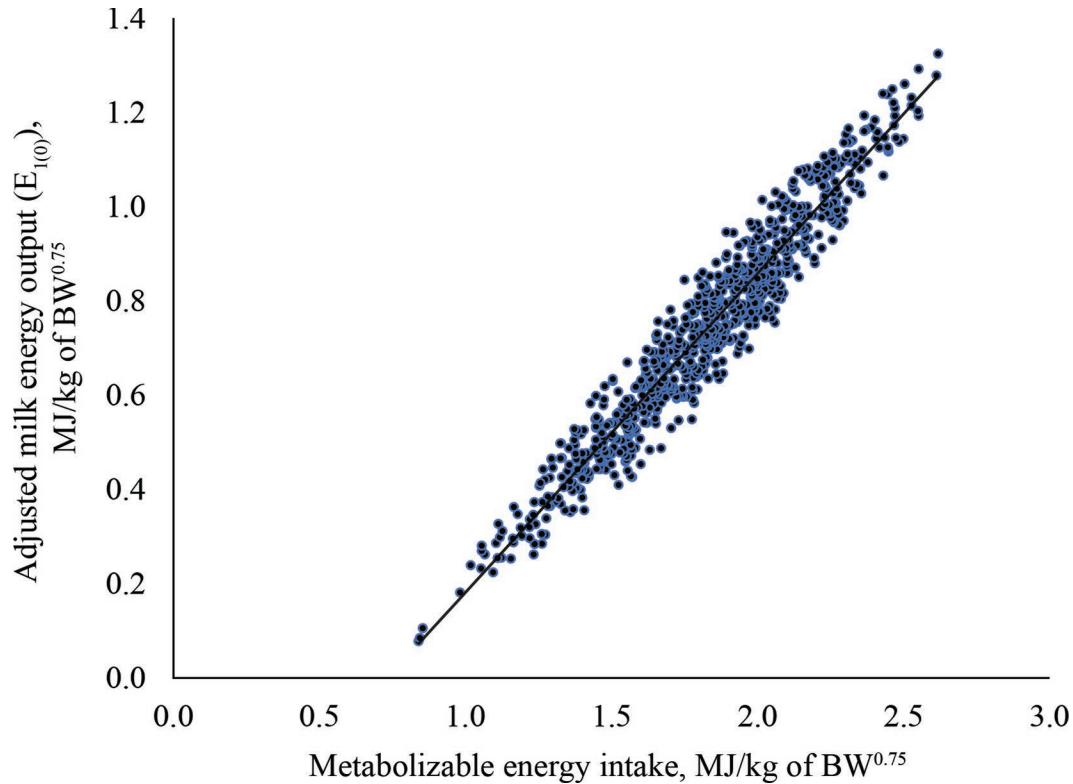
$$\begin{aligned} \text{UE (MJ/d)} = & -3.6 \pm 1.88 + 0.37 \pm 0.052 \\ & \times \text{DMI (kg/d)} + 0.006 \pm 0.0014 \times \text{forage proportion} \\ & \text{(g/kg of DM)} + 0.03 \pm 0.008 \times \text{CP (g/kg of DM)} \end{aligned} \quad [7]$$

(adjusted RMSE = 3.34; n = 624). The RMSE was adjusted for random experiment, diet within experiment, and period within experiment effects.

The ME requirement for maintenance (**ME<sub>m</sub>**, MJ/kg of  $\text{BW}^{0.75}$ ) of individual cows was estimated from net energy requirement for maintenance (**NE<sub>m</sub>**) divided by the efficiency of utilization of ME for maintenance ( $k_m$ ). The **NE<sub>m</sub>** was calculated from the current data using the intercept (0.50 MJ/kg of  $\text{BW}^{0.75}$ ) from Figure 1, and  $k_m$  was calculated using the equation of AFRC (1993):

$$\begin{aligned} \text{ME}_m = & \text{NE}_m / k_m = \\ & 0.50 / (0.35 \times \text{ME/GE} + 0.503). \end{aligned} \quad [8]$$

The efficiency of ME use for lactation ( $k_l$ ) for individual cows used in the present study was calculated using the equation of AFRC (1993):



**Figure 1.** Linear regression of milk energy output adjusted to zero energy balance [ $E_{l(0)}$ ] against ME intake for lactating dairy cows, consisting of 809 cow/period observations from 31 chamber studies:  $E_{l(0)} = 0.68 (\pm 0.007) \times \text{ME intake} - 0.50 (\pm 0.013; \text{SE of the coefficients})$ .

$$k_l = E_{l(0)} / (\text{ME intake} - \text{ME}_m), \quad [9]$$

where  $E_{l(0)}$  is milk energy output ( $E_l$ ) adjusted to zero energy balance (MJ/d), calculated from Equations [10] and [11]:

$$\text{if } EB > 0, E_{l(0)} = E_l + (1/0.95) \times EB; \quad [10]$$

$$\text{if } EB < 0, E_{l(0)} = E_l + 0.84 \times EB. \quad [11]$$

Energy efficiency measures were defined and estimated as follows: residual feed intake (**RFI**) was calculated by regressing DMI (kg/d) on major energy sinks metabolic BW ( $\text{kg}^{0.75}$ , related to maintenance), energy-corrected milk (ECM, kg/d), and body energy change (i.e., EB, MJ/d). The regression was adjusted for random experiment, period within experiment, and diet within experiment, to account for potential differences in accuracy of intake records across experiments and for differences in growth and lactation for different experimental periods and diets. The prediction equation residual was defined as RFI. Residual energy-corrected milk (**RECM**) was also estimated from the current data with multiple linear regression including

GE intake (MJ/d), metabolic BW ( $\text{kg}^{0.75}$ ; related to maintenance), and EB (MJ/d), to model ECM (kg/d). The estimated partial regression coefficients of the models are reported and discussed in our companion paper (Guinguina et al., 2020).

### Statistical Analysis

The relationships between energy metabolism variables (DE/GE,  $\text{CH}_4\text{E}/\text{GE}$ , and UE/GE) and animal variables were determined using multiple linear regression equations by running iterations in the MIXED model procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC), using the following model:

$$Y_{ij} = B_0 + B_1X_{1ij} + b_0 + b_iX_{1ij} + B_2X_{2ij} + \dots + B_nX_{nij} + e_{ij},$$

where  $Y_{ij}$  = the expected value for the dependent variable  $Y$  observed at level of  $j$  of the independent variable  $X$  in study  $i$ ;  $B_0$  = the overall intercept (fixed effect);  $b_0$  = the random effect of study  $i$  on the intercept ( $i = 1, \dots, 31$ );  $B_1, B_2, \dots$ , and  $B_n$  are the regression coefficients of  $Y$  on  $X_1, X_2, \dots$ , and  $X_n$  across all

studies (fixed effects),  $X_{1ij}$ ,  $X_{2ij}$ , . . . , and  $X_{nij}$  = value  $j$  of the continuous variables  $X_1$ ,  $X_2$ , . . . , and  $X_n$  in study  $i$ ;  $b_i$  = is the random effect of study  $i$  on the regression coefficient of  $Y$  on  $X_1$  in study  $i$  ( $i = 1, \dots, 31$ ); and  $e_{ij}$  = the residual error. The models included 2 random statements: a random intercept and slope of  $X_1$  with SUBJECT = Diet(Exp) and a random intercept with SUBJECT = Period(Exp), using the TYPE = VC (variance components) covariance structure for all random statements. The method = ML (maximum likelihood) statement was used in the PROC MIXED model syntax. Only 1 random independent variable was used, to avoid over-parameterized models and to improve convergence (St-Pierre, 2001).

Variance components of energy intake (GE, MJ/d) and output ( $CH_4E$ , UE, HP, and  $E_l$ , expressed in kJ/MJ of GE), as well as energy utilization efficiencies (DE and ME, expressed as kJ/MJ of GE, and  $k_i$ ) and FE measures (RECM and RFI), were estimated using the PROC MIXED procedure of SAS. Experiment (Exp), diet within experiment [Diet(Exp)], period within experiment [Period(Exp)], and cow within experiment [Cow(Exp)] were specified as random factors, and grams of DMI per kilogram of BW (**DMIBW**) was added as a covariate to take into account the dilution of maintenance effect of feeding level. Covariance structure was specified using the TYPE = VC option in the RANDOM statement. From these estimates, repeatability values (Rep) for all variables were calculated as

$$\text{Rep} = \frac{\sigma_{\text{Cow}}^2}{\sigma_{\text{Cow}}^2 + \sigma_{\text{Residual}}^2}, \text{ where } \sigma_{\text{Cow}}^2 \text{ and } \sigma_{\text{Residual}}^2 \text{ are}$$

Cow(Exp) and residual variances, respectively. Repeatability values estimated the correlation between values from consecutive samples on the same cow, on the same diet, and within the same period of the same experiment. The standard deviation (SD) and coefficient of variation (CV) for each factor were calculated as the square root of the variance estimate, and SD divided by the corresponding mean value of each factor, respectively. Only data from changeover studies ( $n = 641$ ) were used for the variance components analysis because of multiple measurements on the same individual.

The regression technique was also used to determine  $k_i$ . The relationship between  $E_{l(0)}$  (MJ/kg of  $BW^{0.75}$ ) and ME intake (MJ/kg of  $BW^{0.75}$ ) was fitted within the MIXED linear regression model procedure of SAS (Littell et al., 2006) using the following model:

$$Y_{ij} = B_0 + B_1X_{1ij} + b_0 + b_iX_{1ij} + e_{ij},$$

where  $Y_{ij}$  = the expected value for the dependent variable  $Y$  observed at level of  $j$  of the independent variable

$X$  in the study  $i$ ;  $B_0$  = the overall intercept (fixed effect);  $b_0$  = the random effect of study  $i$  on the intercept ( $i = 1, \dots, 31$ );  $b_i$  = the random effect of study  $i$  on the regression coefficient of  $Y$  on  $X_1$  in study  $i$  ( $i = 1, \dots, 31$ );  $B_1$  is regression coefficient of  $Y$  on  $X_1$  across all studies (fixed effects);  $X_{1ij}$  = value  $j$  of the continuous variable  $X_1$  in study  $i$ ; and  $e_{ij}$  = the residual error. The prediction models included 1 independent variable ( $X_1$ ) and 1 random statement: a random intercept and slope of  $X_1$  with SUBJECT = Exp using the TYPE = UN (unstructured covariance). Outlier observations for dependent variables were investigated for leverage and influence by the diagnostics DFFITS and DFBETAS (Belsley et al., 1980). Cutoff values suggesting that an observation was an outlier were set at  $|DFFITS_i| > 2\sqrt{(p/n)}$  and  $|DFBETAS_{ij}| > 2\sqrt{n}$ , where  $p$  = number of variables estimated in the model and  $n$  = total number of observations in the model.

Partial correlation coefficients among energy metabolism variables were determined using MANOVA in PROC GLM of SAS, controlling for DMIBW, Exp, [Diet(Exp)], and [Period(Exp)].

## RESULTS

### Data Description

The animal, diet, and energy metabolism data used in the present study are presented in Table 1. The data set had a wide range in BW (379 to 847 kg) and DMI (7.5 to 30.9 kg/d). The average ECM of the cows was 25.6 kg/d, varying from 6.2 to 52.0 kg/d. The cows were offered either forage-only diets or TMR representing various CP concentrations (113 to 250 g/kg of DM) and fiber (NDF) contents (224 to 604 g/kg of DM). The data represented a wide range of GE intakes and correspondingly large differences in energy outputs from urine,  $CH_4$ , and HP. Metabolizable energy intake ranged from 84 to 379 MJ/d and milk energy output from 19.0 to 163 MJ/d. The range in EB was relatively high (−49 to 50 MJ/d) as the data included studies with different feeding levels. Sixty-three percent of the 841 estimates of EB were zero and positive (range = 0.0 to 50.0 MJ/d). Cows produced on average 21.6 MJ of  $CH_4$  per day.

Summary statistics for data on energy partitioning, energy utilization efficiency, and FE used in the present study are presented in Table 2. Gross energy digestibility (DE/GE) and metabolizability (ME/GE) exhibited low variation (CV = 0.053 and 0.060, respectively) considering they also included between-diet and between-period variation. Methane energy as a proportion of GE intake was 65.9 kJ/MJ on average, with minimum and

**Table 1.** Summary statistics for feed intake, diet composition, milk yield, and energy metabolism used in the present study

Item	n	Mean	SD	Minimum	Maximum
BW, kg	841	570	84.9	379	847
ECM, kg/d	841	25.6	8.4	6.2	52.0
Diet composition, g/kg of DM					
OM	705	922	13.0	854	949
CP	796	175	23.6	113	250
NDF	671	381	63.5	224	604
Intake, kg/d					
Forage DM	841	9.8	2.95	2.9	20.8
Concentrate DM	841	8.1	3.69	0.0	17.2
Total DM	841	18.0	4.00	7.5	30.9
OM	841	16.8	3.73	7.5	28.6
Forage proportion, kg/kg	841	0.56	0.175	0.25	1.00
DMIBW, <sup>1</sup> g/kg	841	31.7	5.34	15.8	54.6
Diet digestibility, g/kg					
DM	841	738	38.6	621	871
OM	841	752	37.2	640	883
Energy intake and output, MJ/d					
Gross energy	841	335	79.0	137	582
Digestible energy	841	247	54.4	104	427
Urinary energy	841	11.9	4.54	2.0	28.0
Methane energy	841	21.6	4.35	11.0	35.0
ME	841	214	48.6	84.0	379
Heat production	841	128	21.2	75.0	185
Milk energy	841	80.4	26.4	19.0	163
Energy balance	841	5.1	20.2	-49.0	50.0

<sup>1</sup>Dry matter intake per kg of BW.

maximum values of 36 and 108 kJ/MJ, respectively. Milk energy output as a proportion of GE intake averaged 237, varying from 99 to 401 kJ/MJ. The average  $ME_m$  was 0.68 MJ/kg  $BW^{0.75}$ . The mean  $k_l$  value was 0.65, and the CV was high (0.129). The determination of  $ME_m$  and  $k_l$  by regression is shown in Figure 1 as the relationship between milk energy adjusted to zero EB and ME intake. The  $ME_m$  from this figure was 0.73 MJ/kg  $BW^{0.75}$ , and the slope representing  $k_l$  was 0.68.

### Regression of Methane Yield, Digestibility, and Urine Energy on Animal Variables

The relationship between DE/GE,  $CH_4E/GE$ , UE/GE, and animal variables is shown in Table 3. Gross energy digestibility was not related to DMI but was positively related to BW ( $P = 0.04$ ). Both DE/GE ( $P < 0.01$ ) and BW ( $P < 0.01$ ) were positively related to  $CH_4E/GE$ , whereas increases in total DMI were lin-

**Table 2.** Summary statistics for data on energy partitioning, energy utilization efficiency, and feed efficiency used in the present study

Item <sup>1</sup>	n	Mean	SD	Minimum	Maximum
Energy partitioning, kJ/MJ					
DE/GE	841	740	38.9	620	877
UE/GE	841	35.7	10.6	5.1	79.3
$CH_4E/GE$	841	65.9	10.9	36	108
ME/GE	841	639	38.1	487	741
HP/GE	841	390	48.9	261	578
$E_l/GE$	841	237	41.3	99	401
EB/GE	841	11.7	60.6	-238	165
Energy utilization					
$ME_m$ , MJ/kg of $BW^{0.75}$	841	0.68	0.013	0.65	0.74
$k_l$	841	0.65	0.087	0.28	0.95
Feed efficiency measures					
RFI, kg/d	841	0.29	1.39	-4.50	4.72
RECM, kg/d	841	0.09	3.31	-9.02	11.0

<sup>1</sup>GE = gross energy; DE = digestible energy; UE = urinary energy output;  $CH_4E$  = methane energy output; HP = heat production;  $E_l$  = milk energy output; EB = energy balance;  $ME_m$  = ME requirement for maintenance;  $k_l$  = efficiency of ME use for lactation, calculated from Equation [9]; RFI = residual feed intake; RECM = residual energy-corrected milk.

**Table 3.** Influence of animal variables on digestible, methane, and urine energy as proportions of gross energy (GE) intake (kJ/MJ), estimated by multiple mixed model regression derived from 31 chamber studies in lactating dairy cows ( $n = 841$ )<sup>1</sup>

Variable	CH <sub>4</sub> E/GE			DE/GE			UE/GE		
	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value
Intercept	44.2	7.64	<0.01	687	12.7	<0.01	36.9	7.54	<0.01
DMI, kg/d	-1.38	0.113	<0.01	0.17	0.489	0.73	-0.70	0.136	<0.01
DE/GE, kJ/MJ	0.041	0.010	<0.01	—	—	—	0.017	0.010	0.08
CH <sub>4</sub> E/GE, kJ/MJ	—	—	—	—	—	—	-0.0021	0.0322	0.95
BW, kg	0.028	0.004	<0.01	0.031	0.0148	0.04	-0.0015	0.0042	0.72
AIC <sup>2</sup>	5,678			7,729			5,584		
Residual variance	36.7			371			31.3		

<sup>1</sup>CH<sub>4</sub>E = methane energy output; DE = digestible energy; UE = urinary energy output.

<sup>2</sup>AIC = Akaike's information criterion.

early associated ( $P < 0.01$ ) with decreases in CH<sub>4</sub>E/GE. Urine energy as a proportion of GE intake was related to neither BW, DE/GE, nor CH<sub>4</sub>/GE, but was strongly and negatively correlated with DMI.

### Variance Component

Feeding level has often influenced measures of digestion and metabolism. Therefore, the feeding level parameter (DMIBW) was added to the variance component analysis as a covariate in the present study. In general, the effect of experiment (Exp) was the largest source of variation observed in the data set. The variance components of GE intake and energy output traits are shown in Table 4. Gross energy intake had the highest repeatability, as the between-cow CV (0.10) in this trait was 1.4 times the CV due to diet. For UE/GE, which was the least repeatable (0.10), Diet(Exp) variance was more than double the between-cow variance. For CH<sub>4</sub>E/GE, HP/GE, and E<sub>l</sub>/GE, the between-cow CV was higher than the CV due to diet. Among all energy output measures, the highest between-cow CV (0.084) and repeatability estimate (0.50) was observed in E<sub>l</sub>/GE.

The variance components for energy use and efficiency measures are presented in Table 5. For DE/GE and ME/GE, the CV associated with diet was greater than the between-cow CV, with moderate repeatability estimates. For  $k_l$ , the between-cow CV (0.038) was greater than the CV associated with diet (0.019), with a low repeatability estimate (0.15). For RECM, the CV due to diet was about half the between-cow CV, whereas they were similar for RFI.

### Partial Correlations Among Components of Feed Efficiency

Table 6 shows the partial correlation coefficients among FE components and measures of FE. Increased

GE intake was associated with increased EB/GE ( $r = 0.12$ ) but decreased UE/GE ( $r = -0.17$ ). An increase in DE/GE was associated with increased CH<sub>4</sub>E/GE ( $r = 0.24$ ), HP/GE ( $r = 0.12$ ), EB/GE ( $r = 0.35$ ), and  $k_l$  ( $r = 0.10$ ). A strong positive correlation between DE/GE and ME/GE ( $r = 0.91$ ) was found. Higher ME/GE was associated with increased E<sub>l(0)</sub>/GE ( $r = 0.68$ ), EB/GE ( $r = 0.50$ ), and  $k_l$  ( $r = 0.27$ ) but decreased UE/GE ( $r = -0.29$ ). Milk energy output adjusted to zero energy balance as a proportion of GE intake was positively correlated with DE/GE (0.51), EB/GE ( $r = 0.74$ ), and  $k_l$  ( $r = 0.87$ ) but negatively associated with UE/GE ( $r = -0.21$ ), CH<sub>4</sub>E/GE ( $r = -0.37$ ), and HP/GE ( $r = -0.74$ ).

## DISCUSSION

Variations in energy losses and utilization are believed to contribute to the between-cow variation in FE (VandeHaar et al., 2016). Our ability to quantify both the variability among cows in each component and any potential trade-offs is critical if we are to improve FE in the future. However, little information is available on between-cow variations in the components underpinning FE and any potential trade-offs. Therefore, the aim of the present study was to take the research further to quantify the between-cow variation at each step of energy conversion and to evaluate the trade-offs among these components in lactating dairy cows, using energy metabolism data measured in calorimeter chambers. The data set represented a very wide variation in milk production and, in particular, included some very high milk yields from cows of high genetic merit. It covered the expected ranges in dietary chemical composition and feed intake of dairy cows in the Northern European countries. It should be noted that these results were derived from indoor-feeding cows offered diets based on grass silage, corn silage, and fresh grass.



### Between-Cow Variation and Repeatability

The repeatability and between-cow CV estimated by variance components were used to identify the mechanisms related to between-cow differences in FE. The effects of experiment, diet, and period within experiment were statistically removed from the data set so that the differences in the processes contributing to variation in FE of individual cows could be detected. It is well known that feeding level influences digesta passage rate, which has consequences on energy partitioning variables such as digestibility and CH<sub>4</sub>E output (Yan et al., 2010; Ramin and Huhtanen, 2013). Therefore, in the determination of between-cow CV in the components of FE, feeding level (DMIBW) was used as a covariate, and the components were expressed in kilojoules per megajoule of GE intake to standardize intake.

Feed intake, defined as DM or GE intake is an important component of all available FE traits in dairy cattle. In the present study, we adopted the energy unit for feed intake. The between-cow CV in GE intake was 0.10. We estimated a similar between-cow CV (0.094) in DMI from the data set of Huhtanen et al. (2015). Our results showed that the between-cow CV was 1.4-fold the CV due to diet, indicating that genetics has a greater consequence on feed intake than diet does. The repeatability for GE intake (0.68) was the highest among all component traits evaluated. The estimated value in the present study is consistent with the across-lactation repeatability estimate of 0.66 documented in 5,162 lactating dairy cows (Berry et al., 2014). In a recent study, Guinguina et al. (2019) also reported a repeatability estimate of 0.65 for DMI in lactating dairy cows in digestion studies. We estimated a repeatability

**Table 4.** Variance component estimates for gross energy intake and energy output variables, using DMIBW<sup>1</sup> as a covariate with data set derived from 22 changeover studies in dairy cows (n = 641)

Item <sup>2</sup>	Estimate	SE	P > Z <sup>3</sup>	SD <sup>4</sup>	CV <sup>5</sup>	REP <sup>6</sup>
GE, MJ/d						0.68
Exp	2,505	858	<0.01	50.0	0.155	
Diet(Exp)	518	122.0	<0.01	22.76	0.071	
Period(Exp)	308	81.6	<0.01	17.6	0.054	
Cow(Exp)	1,039	135	<0.01	32.2	0.100	
Residual	499	39.9	<0.01	22.3	0.069	
UE/GE, kJ/MJ						0.10
Exp	61.4	20.5	<0.01	7.84	0.234	
Diet(Exp)	11.9	3.81	<0.01	3.45	0.103	
Period(Exp)	5.50	1.97	<0.01	2.34	0.070	
Cow(Exp)	2.71	1.29	0.02	1.65	0.049	
Residual	25.2	1.95	<0.01	5.02	0.150	
CH <sub>4</sub> E/GE, kJ/MJ						0.46
Exp	37.8	14.8	<0.01	6.15	0.093	
Diet(Exp)	17.6	3.81	<0.01	4.20	0.063	
Period(Exp)	4.0	1.47	<0.01	1.99	0.030	
Cow(Exp)	19.2	3.01	<0.01	4.38	0.066	
Residual	22.9	1.80	<0.01	4.79	0.072	
HP/GE, kJ/MJ						0.20
Exp	893	294	<0.01	29.9	0.076	
Diet(Exp)	61	35.0	0.04	7.80	0.020	
Period(Exp)	70	25.7	<0.01	8.34	0.021	
Cow(Exp)	113	30.4	<0.01	10.7	0.027	
Residual	443	35.8	<0.01	21.1	0.053	
E <sub>1</sub> /GE, kJ/MJ						0.50
Exp	493	208	<0.01	22.2	0.096	
Diet(Exp)	31	23.7	0.10	5.5	0.024	
Period(Exp)	452	89.2	<0.01	21.3	0.092	
Cow(Exp)	376	62.2	<0.01	19.4	0.084	
Residual	383	31.9	<0.01	19.6	0.085	

<sup>1</sup>DMI per kg of BW.

<sup>2</sup>Exp = experiment; Diet(Exp) = diet within experiment; Period(Exp) = period within experiment; Cow(Exp) = cow within experiment; GE = gross energy intake; UE = urinary energy output; CH<sub>4</sub>E = methane energy output; HP = heat production; E<sub>1</sub> = milk energy output.

<sup>3</sup>Probability of Z-value.

<sup>4</sup>Calculated as square root of variance component estimate.

<sup>5</sup>Calculated as SD divided by the respective mean value of the variable.

<sup>6</sup>Repeatability =  $\sigma_{\text{Cow}}^2 / (\sigma_{\text{Cow}}^2 + \sigma_{\text{Residual}}^2)$ , where  $\sigma_{\text{Cow}}^2$  and  $\sigma_{\text{Residual}}^2$  are Cow(Exp) and residual variances, respectively.

**Table 5.** Variance component estimates for energy utilization variables and feed efficiency measurements, using DMIBW<sup>1</sup> as a covariate with data set derived from 22 changeover studies in dairy cows (n = 641)

Item <sup>2</sup>	Estimate	SE	P > Z <sup>3</sup>	SD <sup>4</sup>	CV <sup>5</sup>	REP <sup>6</sup>
DE/GE, kJ/MJ						0.28
Exp	434	164	<0.01	20.8	0.028	
Diet(Exp)	235	52.5	<0.01	15.3	0.021	
Period(Exp)	58	20.4	0.002	7.61	0.010	
Cow(Exp)	110	23.9	<0.01	10.5	0.014	
Residual	281	22.1	<0.01	16.8	0.023	
ME/GE, kJ/MJ						0.23
Exp	162	85.8	0.03	12.7	0.020	
Diet(Exp)	247	55.3	<0.01	15.7	0.024	
Period(Exp)	59	21.0	<0.01	7.71	0.012	
Cow(Exp)	92	23.4	<0.01	9.59	0.015	
Residual	315	24.7	<0.01	17.7	0.028	
k <sub>l</sub>						0.15
Exp	43.9	14.6	<0.01	6.62	0.103	
Diet(Exp)	1.5	1.94	0.22	1.21	0.019	
Period(Exp)	3.9	1.74	0.01	1.98	0.031	
Cow(Exp)	5.9	1.90	<0.01	2.43	0.038	
Residual	32.2	2.57	<0.01	5.68	0.088	
RECM, kg/d						0.25
Exp	3.34	1.33	0.01	1.83	0.076	
Diet(Exp)	0.41	0.224	0.04	0.64	0.026	
Period(Exp)	1.43	0.368	<0.01	1.20	0.050	
Cow(Exp)	0.98	0.233	<0.01	0.99	0.041	
Residual	2.92	0.238	<0.01	1.71	0.071	
RFI, kg/d						0.22
Exp	0.40	0.167	<0.01	0.632	0.036	
Diet(Exp)	0.17	0.049	<0.01	0.408	0.023	
Period(Exp)	0.11	0.040	<0.01	0.325	0.019	
Cow(Exp)	0.12	0.034	<0.01	0.352	0.020	
Residual	0.45	0.036	<0.01	0.669	0.038	

<sup>1</sup>DMI per kg of BW.<sup>2</sup>GE = gross energy intake; DE = digestible energy; k<sub>l</sub> = efficiency of ME use for lactation, calculated from Equation [9] and expressed as a percentage; RECM = residual energy-corrected milk; RFI = residual feed intake; Exp = experiment; Diet(Exp) = diet within experiment; Period(Exp) = period within experiment; Cow(Exp) = cow within experiment.<sup>3</sup>Probability of Z-value.<sup>4</sup>Calculated as square root of variance component estimate.<sup>5</sup>Calculated as SD divided by the respective mean value of the variable.<sup>6</sup>Repeatability =  $\sigma_{\text{Cow}}^2 / (\sigma_{\text{Cow}}^2 + \sigma_{\text{Residual}}^2)$ , where  $\sigma_{\text{Cow}}^2$  and  $\sigma_{\text{Residual}}^2$  are Cow(Exp) and residual variances, respectively.**Table 6.** Partial correlation coefficients<sup>1</sup> of the associations among energy metabolism variables (n = 641)

Item <sup>2</sup>	DE/GE	UE/GE	CH <sub>4</sub> E/GE	ME/GE	HP/GE	E <sub>l(0)</sub> /GE	EB/GE	k <sub>l</sub>
GE	-0.016	-0.17**	-0.076	0.045	-0.033	0.051	0.12**	0.010
DE/GE		-0.029	0.24**	0.91**	0.12*	0.51**	0.35**	0.10*
UE/GE			0.036	-0.29**	0.025	-0.21**	-0.16**	-0.10*
CH <sub>4</sub> E/GE				-0.091†	0.44**	-0.37**	-0.37**	-0.44**
ME/GE					-0.032	0.68**	0.50**	0.27**
HP/GE						-0.74**	-0.60**	-0.91**
E <sub>l(0)</sub> /GE							0.74**	0.85**
EB/GE								0.64**
k <sub>l</sub>								

<sup>1</sup>Correlations were controlled for feeding level, experiment, diet within experiment, and period within experiment effects.<sup>2</sup>GE = gross energy; DE = digestible energy; UE = urinary energy output; CH<sub>4</sub>E = methane energy output; HP = heat production; E<sub>l(0)</sub> = milk energy output adjusted to zero energy balance; EB = energy balance; k<sub>l</sub> = efficiency of ME use for lactation, calculated from Equation [9].

†P &lt; 0.10; \*P &lt; 0.05; \*\*P &lt; 0.01.

of 0.81 for DMI from the data set of Huhtanen et al. (2015). The high repeatability suggests that feed intake is mostly influenced by additive genetic and permanent environmental effects rather than management practices. However, because the genetic correlation between feed intake and ECM or BW is positive (Spurlock et al., 2012), caution must be exercised when evaluating FE using only feed intake, as we risk selecting for cows that become too thin or have low milk production.

The between-cow CV in DE/GE and ME/GE were 0.014 and 0.015, respectively. In a recent meta-analysis by Cabezas-Garcia et al. (2017), a value of 0.013 for between-cow CV in OMD was reported. In the experiment reported by Flatt et al. (1969), slightly higher estimates of between 0.019 and 0.025 in the ratio of DE or that of ME to GE were obtained. These results demonstrate that little variability exists among cows in their ability to digest and metabolize a given diet, especially when intakes are standardized. The increased degree of homogeneity of cows in their ability to digest and absorb nutrient observed in our study compared with the study of Flatt et al. (1969) could be attributed to improvements in feeding and management of cows as well as methods of measuring digestibility that are more consistent than they were 50 years ago. In our study, the between-cow CV for energy digestibility and metabolizability was smaller than the CV due to diet. Many years of considerable research have shown that digestibility and metabolizability can be greatly influenced by dietary factors (Mertens, 1993; Huhtanen et al., 2006; Nousiainen et al., 2009). In the data used for the current meta-analysis, these dietary factors varied greatly across studies; hence, a greater effect of diet on digestibility and metabolizability was expected. Overall, these results suggest that considerable improvement in digestibility and metabolizability could be achieved through dietary manipulation with less improvement via selection.

In recent years, interest has been increasing in selecting animals that emit less CH<sub>4</sub>. Genetic progress through selection requires that the between-animal CV is large enough to make improvement and that the trait is heritable and can be reliably measured. Earlier studies have shown that methane emission is a heritable trait, with heritability estimates ranging from 0.12 to 0.44 depending on the method of measurement (de Haas et al., 2011; van Engelen et al., 2015; Lassen and Løvendahl, 2016). Garnsworthy et al. (2012a) reported approximately 19% between-cow CV in CH<sub>4</sub> emission rate (g/min) using the sniffer method. In the studies of Bell et al. (2014) and van Engelen et al. (2018), even greater between-cow variabilities in CH<sub>4</sub> emission (g/d) were reported using the same methods. In contrast, the present results derived from respiration chamber data

indicate much smaller (CV = 10.0%; results not shown) variability in CH<sub>4</sub> emission (MJ/d). When expressed as a proportion of GE intake, the between-cow variation in CH<sub>4</sub> yield (kJ/MJ of GE) was 6.6%. Blaxter and Clapperton (1965) reported slightly greater variability (from 7.2 to 8.1%) in CH<sub>4</sub> yield (g/kg of DMI) for sheep in closed-circuit respiration chambers. In 10 studies using the GreenFeed system (C-Lock Inc., Rapid City, SD), the average between-cow CV in CH<sub>4</sub> yield (g/kg of DMI) was 10.7% (Cabezas-Garcia, 2017). It appears that the large between-animal CV with associated large random errors in the data are mainly observed when measurements of CH<sub>4</sub> are based on the sniffer method. Small between-cow variability in CH<sub>4</sub> yield in the present study is consistent with the small between-cow variability (6.7%) in CH<sub>4</sub> yield (g/kg of DMI) estimated from rumen fermentation pattern using stoichiometric principles (Cabezas-Garcia et al., 2017). On an energy basis, the effect of between-cow variability in CH<sub>4</sub> yield is small. Assuming a DMI of 20 kg/d (GE concentration of 18.5 MJ/kg of DM),  $\pm 1$  SD variation in CH<sub>4</sub> yield corresponds to  $\pm 1.6$  MJ of energy—that is, the requirement of approximately  $\pm 0.3$  kg of ECM. The true effect is likely to be even smaller because of the positive relationship between digestibility and CH<sub>4</sub> production. This is discussed further in our companion paper (Guinguina et al., 2020). The CH<sub>4</sub> yield in the present study was moderately repeatable (0.46). Using the GreenFeed system in 28 lactating dairy cows, Huhtanen et al. (2013) reported a higher repeatability value (0.78) for CH<sub>4</sub> yield (g/kg of DMI). The lower repeatability of CH<sub>4</sub> yield in the present study could be related to the shorter measurement periods (3 to 5 d) in respiration chambers, which will reduce variation between cows (Garnsworthy et al., 2012b) and subsequently repeatability.

The between-cow CV of the ratio of E<sub>1</sub> to GE intake was 0.084. From the experiment reported by Arndt et al. (2015), we estimated that between-cow CV in the ratio of E<sub>1</sub> to DMI was 0.119. A similar value of 0.113 was estimated for ECM/DMI from data reported in the meta-analysis by Huhtanen et al. (2015). The moderate to high repeatability estimates observed in the current study for E<sub>1</sub>/GE (0.50) and for ECM/DMI (0.85) in the data reported in the study by Huhtanen et al. (2015) suggest that variation among cows in proportional milk energy output potentially has a high heritability. Indeed, previous studies have reported significant levels of heritability (0.14–0.37) for the ratio of ECM to DMI (Van Arendonk et al., 1991; Vallimont et al., 2011).

A relatively limited number of studies have attempted to evaluate the between-cow CV in ME<sub>m</sub> in producing animals. Graham (1982) discussed how the response in ME<sub>m</sub> to a change in feed intake is rather

slow in lactating cows. This makes it difficult to evaluate the between-individual CV in  $ME_m$ , especially in changeover studies, where cows are placed on different diets after every 21 to 28 d. Moreover, the simultaneous measurements of  $ME_m$  and  $k_l$  in lactating cows are not practically feasible, because  $ME_m$  requires that animals are fed only to meet their basic metabolic functions plus some activity, without any gain or loss in body tissue. Therefore, in the present study, a fixed  $NE_m$  was assumed for all cows in estimating  $ME_m$ , leading to an infinitesimal CV (0.5%,  $P < 0.01$ ; results not shown) in  $ME_m$  between cows. This variation was due to differences in  $q$ -value ( $ME/GE$ ). van Es (1961) estimated values of between 0.04 and 0.08 in dry dairy cows and between 0.05 and 0.10 in a review of an additional 237 energy balance studies in dairy cows and steers. Yan et al. (1997) reported  $ME_m$  of between 0.61 and 0.75 MJ/kg of  $BW^{0.75}$ , indicating a large range of variation. However, consensus is lacking on whether genetic variation among dairy cows exists in their requirements for maintenance. Neither Ferris et al. (1999) nor Dong et al. (2015a) identified significant differences in  $ME_m$  between breeds and between cows of different genetic merit for milk production. In direct contrast, Moraes et al. (2015), using calorimetric data from 284 Holstein cows, reported an increase in  $ME_m$  over the years, which may be correlated with higher genetic merit of cattle for milk production. In the present study, the between-diet CV (0.8%) in  $ME_m$ , although small, was significant ( $P < 0.01$ ; results not shown). This is in agreement with earlier studies (Yan et al., 1997, Dong et al., 2015b), which reported significant diet effects on  $ME_m$ . The results from Dong et al. (2015b) demonstrated that cows offered forage-only diets or TMR with forage proportion above 60% required approximately 11% more energy for maintenance than did those offered mixed diets with forage proportion  $< 30\%$ . The increased  $ME_m$  reported for cows offered high-forage diets has been attributed to increased energy expenditure associated with the digestive tract and other internal organs (Steen et al., 1998).

Between-cow CV in the efficiency of ME utilization for lactation ( $k_l$ ) is more difficult to evaluate, as only a few experiments have addressed this in essence. In our meta-analysis, the estimated between-cow CV in  $k_l$  was 0.038. However, the residual CV was substantially high, leading to a low repeatability estimate for  $k_l$ . The large residual CV is an accumulation of errors associated with measuring multiple variables needed in the calculation of  $k_l$ . Although the repeatability estimate was low, the between-cow CV was significant, indicating genetic influence and scope to increase  $k_l$  via selection. The CV due to diet in  $k_l$  was considerably low and not significant ( $P = 0.22$ ). Yan et al. (1997) combined

data from 221 lactating dairy cows across experiments and reported that the proportion of grass silage in the diet did not significantly influence  $k_l$  values. Because dietary manipulation can influence  $ME_m$  of cows, as discussed previously, Agnew and Yan (2000) concluded that the lower performance of dairy cows offered high-forage diets is due to higher  $ME_m$ , which leaves less energy for production, instead of the high-forage diet resulting in lower  $k_l$ . The results from the present study support this hypothesis that variation due to diet was significant for  $ME_m$  but not for  $k_l$ .

If FE is to be included as an economically important trait worthy of consideration in selection strategies, an animal's rank for the trait must be repeatable across periods and a range of diets commonly used on dairy farms, and ideally also across production systems in general (feeding regimen, type of housing, milking system, etc). The repeatability of RFI across diets and periods in this study was lower than that shown in Holstein dairy cows in mid-lactation. Potts et al. (2015) studied the repeatability of RFI in lactating Holstein dairy cows in mid-lactation ( $n = 109$ ) fed low- and high-starch diets. They found that RFI was highly repeatable (0.73) across diet and that 44% ( $n = 48$ ) of the cows changed their FE ranking from low RFI to medium or high RFI and vice versa when diets were switched. In the same study, the average repeatability of RFI within diet across experimental week was 0.65, whereas that across-diet and experimental week repeatability was 0.56. Studies in growing beef cattle given the same diet across 2 separated periods (Kelly et al., 2010) and 2 consecutive periods (Durunna et al., 2012) have found repeatability estimates of 0.62 and 0.33, respectively, for RFI. In a nutshell, the results of these studies indicate that RFI is moderately repeatable across diets and periods in both beef and dairy cattle. However, the occurrence of some animal re-ranking suggests the existence of a genotype  $\times$  environment interaction for the trait (Kenny et al., 2018). A possible explanation for the lower repeatability of RFI in our study could be that the diets differed greatly in forage proportion (CV = 35%), whereas the diets in the previous studies had similar forage proportions. Short measurement periods in respiration chamber studies can also increase random errors, as all errors are accumulated in the EB term. Moreover, the cows in our study were at different stages of lactation, as some were in negative and some in positive EB. Repeatability of RFI could be improved if measurements are taken from periods when cows are in similar lactation stages and over longer periods of time. Using rank correlations, Prendiville et al. (2011) compared RFI of individual stages of lactation with average RFI over a full lactation and concluded that RFI cannot be successfully determined over a short period.

Genetic gain is a function of variation between individuals; all conditions remaining the same, the greater the between-cow variation, the greater the potential genetic gain. The between-cow CV in RECM was 2-fold that of RFI, suggesting greater scope for genetic gain in RECM as a measure of FE compared with RFI. The repeatability of RECM was 12% greater than the repeatability of RFI. Repeatability for both definitions of FE, combined with the existence of significant between-cow CV, suggests that both traits may be heritable, with maximum repeatability (broad-sense heritability) of approximately 0.25 in this study.

### Correlation Among Components of Feed Efficiency

The variation between cows in DE/GE was positively associated with the differences between cows in CH<sub>4</sub>E/GE. Increased CH<sub>4</sub> yield (g/kg of DMI) with incremental digestibility is expected because more substrate is fermented in the rumen (Cabezas-Garcia et al., 2017). In a respiration chamber study involving 8 cows fed at either maintenance or production level (Schiemann et al., 1971; cited by Løvendahl et al., 2018), a strong positive relationship between digestibility and CH<sub>4</sub> yield (g/kg of DMI) was found in both cases. Løvendahl et al. (2018) reported a positive relationship between CH<sub>4</sub> yield (g/kg of DMI) and digestibility in lactating dairy cows and indicated that some 25 to 30% of incremental DE can be lost as CH<sub>4</sub> in response to a slower passage rate and improved digestibility. Also, in sheep studies, positive correlations (0.66 and 0.74) have been reported between CH<sub>4</sub> yield (g/kg of DMI) and cellulose digestibility (Pinares-Patiño et al., 2003) and between CH<sub>4</sub> yield and NDF digestibility (Pinares-Patiño and Clark, 2010). Pinares-Patiño et al. (2003) further showed that CH<sub>4</sub> yield was positively associated ( $r = 0.84$ ) with rumen digesta pool size (i.e., high mean retention time). Using model simulations, Huhtanen et al. (2016) demonstrated that digesta passage rate was inversely proportional to CH<sub>4</sub> yield (g/kg of DMI) and digestibility, with CH<sub>4</sub> yield and digestibility changing concomitantly. In the present study, on average, a decrease of 10 kJ/MJ of GE in diet digestibility was associated with a 0.41 kJ/MJ reduction in CH<sub>4</sub> yield. The positive relationship between CH<sub>4</sub> yield and digestibility is a drawback, as it limits the potential for improving FE by selecting cows for low CH<sub>4</sub> emission and high digestibility at the same time. Therefore, caution must be exercised in selecting for low-emitting animals, as we risk selecting for animals with reduced NDF digestibility, thereby compromising an important characteristic of ruminant nutrition (Løvendahl et al., 2018).

The partial regression coefficient of CH<sub>4</sub> yield on BW was positive and significantly different from zero, indicating that CH<sub>4</sub> yield decreases when body weight is decreased. The magnitude of the CH<sub>4</sub> yield response to BW in our study was 0.041 (CH<sub>4</sub> kJ/MJ of GE per kg of BW), suggesting an average increase of 0.041 kJ/MJ in CH<sub>4</sub> yield for every kilogram increase in BW at standardized feeding level. The significance of BW in explaining CH<sub>4</sub> yield from enteric fermentation can be ascribed to the relationship between BW and gut capacity because gut volume is positively related to BW (Demment and Van Soest, 1985). Low CH<sub>4</sub> yield (g/kg of DMI) has been reported in sheep and cows with smaller rumen volume and short mean retention time (Goopy et al., 2014; Huhtanen et al., 2016). This suggests that larger animals will exhibit slower ruminal digesta passage kinetics and greater amounts of fermented feed than smaller cows when consuming similar amounts of a common diet. Therefore, the negative relationship between CH<sub>4</sub> yield (kJ/MJ of GE) and DMI in the present study was expected, as low DMI favors longer retention time, which increases digestibility and then increases CH<sub>4</sub> production per unit of intake.

Methane production represents an energetic loss for the ruminant. Thus, reducing it could result in the repartition of more energy toward production (Judy et al., 2019). Bell et al. (2010) observed a 12% difference in CH<sub>4</sub> intensity (g of CH<sub>4</sub>/kg of milk) between control and selected (for kg of milk fat and protein production) genetic lines, whereby genetically selected cows partitioned more of their nutrient intake toward milk production and less to CH<sub>4</sub>. They concluded that an effective way to reduce enteric CH<sub>4</sub> emissions per kilogram of milk in dairy cows is breeding for increased ECM. In the present study, CH<sub>4</sub>E, expressed as a ratio of GE intake, negatively correlated with E<sub>1(0)</sub>/GE. The negative relationship between CH<sub>4</sub> intensity and ECM (Bell et al., 2010) and between CH<sub>4</sub> yield and E<sub>1(0)</sub>/GE (present study) are likely because total CH<sub>4</sub> production is positively related to both DMI and ECM. This indicates that high milk-producing cows produce less CH<sub>4</sub> per unit of feed, which has desirable effects for genetic selection. Also, increasing ME intake has been shown to increase the proportion of energy directed to milk production and body tissue retention or low HP/ME, which consequently increases the possibility of low proportional CH<sub>4</sub>E output for high-yielding cows (Yan et al., 2010). Accordingly, we observed that CH<sub>4</sub>E/GE was negatively associated with E<sub>1(0)</sub>/GE and positively correlated with HP/GE.

Bauman et al. (1985) concluded that increased milk yield is not accompanied by large changes in nutrient digestibility. This is because differences in milk yield

among cows on the same diet are not associated with differences in digestibility among cows (Bauman et al., 1985). Similarly in our study, no correlation was detected between DE/GE and  $E_1/GE$  ( $r = 0.039$ ,  $P = 0.40$ ; results not shown), which indicates no direct effect of digestibility on milk energy output. In production studies, however, a 1 percentage unit increase in digestibility was associated with 0.25 kg/d greater ECM yield (Løvendahl et al., 2018). When milk energy output was adjusted to zero EB ( $E_{1(0)}/GE$ ), a moderate positive correlation ( $r = 0.51$ ) was observed with DE/GE. That  $E_{1(0)}/GE$ , but not  $E_1/GE$ , correlates with DE/GE suggests that cows more efficiently digesting diets partitioned a greater proportion of the incremental energy to body tissues instead of milk production. This is supported by a moderate positive correlation between EB and digestibility in the current study.

The correlation between  $E_1/GE$  and EB/GE was strongly negative ( $r = -0.69$ ,  $P < 0.001$ ; results not shown). This suggests that selecting for high genetic merit for milk production will likely result in cows with severe negative EB, especially in early lactation. However, the correlation between  $E_{1(0)}/GE$  and EB/GE was strongly positive ( $r = 0.74$ ). In a study involving 35 Israeli Holstein cows, Asher et al. (2014) replaced  $E_1$  with recovered energy ( $E_1 + EB$ ) and found a positive correlation ( $r = 0.38$ ) between recovered energy and EB. The positive effect of EB/GE on  $E_{1(0)}/GE$  could be related to the way  $E_{1(0)}$  is calculated, from energy retained in milk and body tissue. It suggests that the values of  $E_{1(0)}$  are largely dependent on the range in EB estimates. When the efficiency of ME use for body tissue gain is underestimated, as seen in this study (Guinguina et al., 2020), the effect of EB on  $E_{1(0)}$  is large.

No correlation was detected between  $E_1/GE$  and  $k_l$ , indicating that production level is not related to the efficiency of ME utilization above maintenance. Earlier works also reported that  $k_l$  was independent of the level of animal production (Agnew and Yan, 2000; Yan et al., 2006). A moderate negative correlation was observed between  $k_l$  and  $CH_4E/GE$ . Similarly, Yan et al. (2010) reported a negative relationship between  $k_l$  and  $CH_4E$  as a proportion of GE intake. This clearly suggests that putting selection pressure on high energy efficiency is an effective way of reducing  $CH_4$  emissions in dairy cows. However, the assessment of energy efficiency demands the use of energy metabolism data, which may not always be available.

## CONCLUSIONS

The present analysis showed that the between-cow variation and repeatability estimates for GE intake and milk energy as a proportion of GE intake were the

greatest among all traits evaluated. The between-cow variation in RECM as an estimate of FE was larger than for RFI, which suggests greater scope for genetic gain in RECM than RFI, assuming they have similar heritability estimates. Milk energy output corrected for zero EB per unit of GE intake was positively related to digestibility and metabolizability of the diet and negatively to  $CH_4$  energy as a proportion of GE intake at the same DMI/BW. If between-cow variation in  $CH_4$  yield is related to differences among cows in their ability to digest a given diet, caution should be exercised when selecting against  $CH_4$  emission in breeding programs, as we risk selecting for reduced digestibility, which is an essential factor of ruminant nutrition. On the other hand, breeding for cows with high efficiency of ME utilization for lactation is an effective approach to reduce  $CH_4$  emission.

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## REFERENCES

- Agnew, R., and T. Yan. 2000. Impact of recent research on energy feeding systems for dairy cattle. *Livest. Prod. Sci.* 66:197–215. [https://doi.org/10.1016/S0301-6226\(00\)00161-5](https://doi.org/10.1016/S0301-6226(00)00161-5).
- Agricultural and Food Research Council (AFRC). 1993. Energy and Protein Requirements of Ruminants. CAB International, Wallingford, UK.
- Arndt, C., J. Powell, M. Aguerre, P. Crump, and M. Wattiaux. 2015. Feed conversion efficiency in dairy cows: Repeatability, variation in digestion and metabolism of energy and nitrogen, and ruminal methanogens. *J. Dairy Sci.* 98:3938–3950. <https://doi.org/10.3168/jds.2014-8449>.
- Asher, A., A. Shabtay, A. Haim, Y. Aharoni, J. Miron, G. Adin, A. Tamir, A. Arieli, I. Halachmi, U. Moallem, A. Orlov, and A. Brosh. 2014. Time required to determine performance variables and production efficiency of lactating dairy cows. *J. Dairy Sci.* 97:4340–4353. <https://doi.org/10.3168/jds.2013-7265>.
- Bauman, D. E., S. N. McCutcheon, W. D. Steinhour, P. J. Eppard, and S. J. Sechen. 1985. Sources of variation and prospects for improvement of productive efficiency in the dairy cow: A review. *J. Anim. Sci.* 60:583–592. <https://doi.org/10.2527/jas1985.602583x>.

- Bell, M., E. Wall, G. Russell, C. Morgan, and G. Simm. 2010. Effect of breeding for milk yield, diet and management on enteric methane emissions from dairy cows. *Anim. Prod. Sci.* 50:817–826. <https://doi.org/10.1071/AN10038>.
- Bell, M. J., S. Potterton, J. Craigon, N. Saunders, R. Wilcox, M. Hunter, J. Goodman, and P. Garnsworthy. 2014. Variation in enteric methane emissions among cows on commercial dairy farms. *Animal* 8:1540–1546. <https://doi.org/10.1017/S1751731114001530>.
- Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. *Regression Diagnostics: Identifying Influential Data and Sources of Collinearity*. John Wiley and Sons Inc., New York, NY.
- Berry, D. P., M. P. Coffey, J. Pryce, Y. De Haas, P. Løvendahl, N. Krattenmacher, J. Crowley, Z. Wang, D. Spurlock, K. Weigel, K. Macdonald, and R. F. Veerkamp. 2014. International genetic evaluations for feed intake in dairy cattle through the collation of data from multiple sources. *J. Dairy Sci.* 97:3894–3905. <https://doi.org/10.3168/jds.2013-7548>.
- Blaxter, K. L., and J. L. Clapperton. 1965. Prediction of the amount of methane produced by ruminants. *Br. J. Nutr.* 19:511–522. <https://doi.org/10.1079/BJN19650046>.
- Brouwer, E. 1965. Report of sub-committee on constants and factors. Pages 441–443 in *Energy Metabolism of Farm Animals*. EAAP Publ. No. 11. Academic Press, London, UK.
- Cabezas-Garcia, E. H., S. J. Krizsan, K. J. Shingfield, and P. Huhtanen. 2017. Between-cow variation in digestion and rumen fermentation variables associated with methane production. *J. Dairy Sci.* 100:4409–4424. <https://doi.org/10.3168/jds.2016-12206>.
- Cabezas-Garcia, E. H. 2017. *Methane Production in Dairy Cows*. PhD Thesis, Department of Agricultural Research for Northern Sweden, Swedish Univ. of Agricultural Sciences, Umeå, Sweden.
- Coleman, J., D. Berry, K. Pierce, A. Brennan, and B. Horan. 2010. Dry matter intake and feed efficiency profiles of 3 genotypes of Holstein-Friesian within pasture-based systems of milk production. *J. Dairy Sci.* 93:4318–4331. <https://doi.org/10.3168/jds.2009-2686>.
- Collard, B. L., P. J. Boettcher, J. C. Dekkers, D. Petitclerc, and L. R. Schaeffer. 2000. Relationships between energy balance and health traits of dairy cattle in early lactation. *J. Dairy Sci.* 83:2683–2690. [https://doi.org/10.3168/jds.S0022-0302\(00\)75162-9](https://doi.org/10.3168/jds.S0022-0302(00)75162-9).
- de Haas, Y., J. J. Windig, M. P. L. Calus, J. Dijkstra, M. de Haan, A. Bannink, and R. F. Veerkamp. 2011. Genetic parameters for predicted methane production and potential for reducing enteric emissions through genomic selection. *J. Dairy Sci.* 94:6122–6134. <https://doi.org/10.3168/jds.2011-4439>.
- De Vries, M. J., S. van der Beek, L. M. Kaal-Lansbergen, W. Ouweltjes, and J. B. Wilmink. 1999. Modeling of energy balance in early lactation and the effect of energy deficits in early lactation on first detected estrus postpartum in dairy cows. *J. Dairy Sci.* 82:1927–1934. [https://doi.org/10.3168/jds.S0022-0302\(99\)75428-7](https://doi.org/10.3168/jds.S0022-0302(99)75428-7).
- Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641–672. <https://doi.org/10.1086/284369>.
- Dong, L. F., C. P. Ferris, D. A. McDowell, and T. Yan. 2015b. Effects of diet forage proportion on maintenance energy requirement and the efficiency of metabolizable energy use for lactation by lactating dairy cows. *J. Dairy Sci.* 98:8846–8855. <https://doi.org/10.3168/jds.2015-9465>.
- Dong, L. F., T. Yan, C. P. Ferris, and D. A. McDowell. 2015a. Comparison of maintenance energy requirement and energetic efficiency between lactating Holstein-Friesian and other groups of dairy cows. *J. Dairy Sci.* 98:1136–1144. <https://doi.org/10.3168/jds.2014-8629>.
- Durumna, O. N., M. G. Colazo, D. J. Ambrose, D. McCartney, V. S. Baron, and J. A. Basarab. 2012. Evidence of residual feed intake reranking in crossbred replacement heifers. *J. Anim. Sci.* 90:734–741. <https://doi.org/10.2527/jas.2011-4264>.
- Ferris, C., F. Gordon, D. Patterson, M. Porter, and T. Yan. 1999. The effect of genetic merit and concentrate proportion in the diet on nutrient utilization by lactating dairy cows. *J. Agric. Sci.* 132:483–490. <https://doi.org/10.1017/S0021859699006553>.
- Flatt, W. P., P. W. Moe, A. W. Munson, and T. Cooper. 1969. Energy utilization by high producing dairy cows: II. Summary of energy balance experiments with lactating Holstein cows. In *Energy Metabolism of Farm Animals*. K. L. Blaxter, J. Kielanowski, and G. Thorbeck, ed. Oriel Press, Newcastle-Upon-Tyne, UK.
- Garnsworthy, P. C., J. Craigon, J. H. Hernandez-Medrano, and N. Saunders. 2012a. Variation among individual dairy cows in methane measurements made on farm during milking. *J. Dairy Sci.* 95:3181–3189. <https://doi.org/10.3168/jds.2011-4606>.
- Garnsworthy, P. C., J. Craigon, J. H. Hernandez-Medrano, and N. Saunders. 2012b. On-farm methane measurements during milking correlate with total methane production by individual dairy cows. *J. Dairy Sci.* 95:3166–3180. <https://doi.org/10.3168/jds.2011-4605>.
- Goopy, J. P., A. Donaldson, R. Hegarty, P. E. Vercoe, F. Haynes, M. Barnett, and V. H. Oddy. 2014. Low-methane yield sheep have smaller rumens and shorter rumen retention time. *Br. J. Nutr.* 111:578–585. <https://doi.org/10.1017/S0007114513002936>.
- Graham, J. F. 1982. The effect of body condition of beef cows at calving and post-calving nutrition on calf growth rate and cow fertility. *Proc. Aus. Soc. Anim. Prod.* 14:309–312.
- Guinguina, A., S. Ahvenjärvi, E. Prestløkken, P. Lund, and P. Huhtanen. 2019. Predicting feed intake and feed efficiency in lactating dairy cows using digesta marker techniques. *Animal* 13:2277–2288. <https://doi.org/10.1017/S1751731119000247>.
- Guinguina, A., T. Yan, A. R. Bayat, P. Lund, and P. Huhtanen. 2020. The effects of energy metabolism variables on feed efficiency in respiration chamber studies with lactating dairy cows. *J. Dairy Sci.* <https://doi.org/10.3168/jds.2020-18259>. In press.
- Hansen, L. B. 2000. Consequences of selection for milk yield from a geneticist's viewpoint. *J. Dairy Sci.* 83:1145–1150. [https://doi.org/10.3168/jds.S0022-0302\(00\)74980-0](https://doi.org/10.3168/jds.S0022-0302(00)74980-0).
- Huhtanen, P., E. Cabezas-Garcia, S. Krizsan, and K. Shingfield. 2015. Evaluation of between-cow variation in milk urea and rumen ammonia nitrogen concentrations and the association with nitrogen utilization and diet digestibility in lactating cows. *J. Dairy Sci.* 98:3182–3196. <https://doi.org/10.3168/jds.2014-8215>.
- Huhtanen, P., S. Krizsan, M. Hetta, H. Gidlund, and E. C. Garcia. 2013. Repeatability and between cow variability of enteric CH<sub>4</sub> and total CO<sub>2</sub> emissions. *Adv. Anim. Biosci.* 4:588.
- Huhtanen, P., E. Nousiainen, and M. Rinne. 2006. Recent developments in forage evaluation with special reference to practical applications. *J. Agric. Food Sci.* 15:293–323. <https://doi.org/10.2137/145960606779216317>.
- Huhtanen, P., M. Ramin, and E. Cabezas-Garcia. 2016. Effects of ruminal digesta retention time on methane emissions: A modelling approach. *Anim. Prod. Sci.* 56:501–506. <https://doi.org/10.1071/AN15507>.
- Huhtanen, P., M. Rinne, and J. Nousiainen. 2009. A meta-analysis of feed digestion in dairy cows. 2. The effects of feeding level and diet composition on digestibility. *J. Dairy Sci.* 92:5031–5042. <https://doi.org/10.3168/jds.2008-1834>.
- Judy, J. V., G. C. Bachman, T. M. Brown-Brandl, S. C. Fernando, K. E. Hales, P. S. Miller, R. R. Stowell, and P. J. Kononoff. 2019. Reducing methane production with corn oil and calcium sulfate: Responses on whole-animal energy and nitrogen balance in dairy cattle. *J. Dairy Sci.* 102:2054–2067. <https://doi.org/10.3168/jds.2018-14567>.
- Kelly, A. K., M. McGee, D. H. Crews Jr., T. Sweeney, T. M. Boland, and D. A. Kenny. 2010. Repeatability of feed efficiency, carcass ultrasound, feeding behavior, and blood metabolic variables in finishing heifers divergently selected for residual feed intake. *J. Anim. Sci.* 88:3214–3225. <https://doi.org/10.2527/jas.2009-2700>.
- Kenny, D. A., C. Fitzsimons, S. M. Waters, and M. McGee. 2018. Invited review: Improving feed efficiency of beef cattle—the current state of the art and future challenges. *Animal* 12:1815–1826. <https://doi.org/10.1017/S1751731118000976>.
- Kriss, M. 1930. Quantitative relations of the dry matter of the food consumed, the heat production, the gaseous outgo, and the insensible loss in body weight of cattle. *J. Agric. Res.* 40:283–295.

- Lassen, J., and P. Løvendahl. 2016. Heritability estimates for enteric methane emissions from Holstein cattle measured using noninvasive methods. *J. Dairy Sci.* 99:1959–1967. <https://doi.org/10.3168/jds.2015-10012>.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for Mixed Models. 2nd ed. SAS Institute Inc., Cary, NC.
- Løvendahl, P., G. Difford, B. Li, M. Chagunda, P. Huhtanen, M. Lidauer, J. Lassen, and P. Lund. 2018. Selecting for improved feed efficiency and reduced methane emissions in dairy cattle. *Animal* 12(Suppl. 2):s336–s349. <https://doi.org/10.1017/S1751731118002276>.
- MAFF. 1975. Energy allowance and feeding systems for ruminants. *Tech. Bull.* 33, page 79, London, UK.
- Mertens, D. 1993. Kinetics of cell wall digestion and passage in ruminants. Forage cell wall structure and digestibility page 535–570. *Am. Soc. Agron.*, Madison, WI.
- Moraes, L. E., E. Kebreab, A. B. Strathe, J. Dijkstra, J. France, D. P. Casper, and J. G. Fadel. 2015. Multivariate and univariate analysis of energy balance data from lactating dairy cows. *J. Dairy Sci.* 98:4012–4029. <https://doi.org/10.3168/jds.2014-8995>.
- Nousiainen, J., M. Rinne, and P. Huhtanen. 2009. A meta-analysis of feed digestion in dairy cows. 1. The effects of forage and concentrate factors on total diet digestibility. *J. Dairy Sci.* 92:5019–5030. <https://doi.org/10.3168/jds.2008-1833>.
- NRC. 2001. Nutrient Requirements of Dairy Cattle. 7th rev. ed. National Academies Press, Washington, DC.
- Pinares-Patiño, C., M. Ulyatt, K. Lassey, T. Barry, and C. W. Holmes. 2003. Rumen function and digestion parameters associated with differences between sheep in methane emissions when fed chaffed lucerne hay. *J. Agric. Sci.* 140:205–214. <https://doi.org/10.1017/S0021859603003046>.
- Pinares-Patiño, C. S., and H. Clark. 2010. Rumen function and digestive parameters associated with methane emissions in dairy cows. Paper presented at the 4th Australasian Dairy Science Conference, Aug. 31–Sep. 2, 2010, Christchurch, New Zealand. Caxton Press, Christchurch, New Zealand.
- Potts, S. B., J. P. Boerman, A. L. Lock, M. S. Allen, and M. J. VandeHaar. 2015. Residual feed intake is repeatable for lactating Holstein dairy cows fed high and low starch diets. *J. Dairy Sci.* 98:4735–4747. <https://doi.org/10.3168/jds.2014-9019>.
- Prendiville, R., K. M. Pierce, L. Delaby, and F. Buckley. 2011. Animal performance and production efficiencies of Holstein-Friesian, Jersey and Jersey × Holstein-Friesian cows throughout lactation. *Livest. Sci.* 138:25–33. <https://doi.org/10.1016/j.livsci.2010.11.023>.
- Ramin, M., and P. Huhtanen. 2013. Development of equations for predicting methane emissions from ruminants. *J. Dairy Sci.* 96:2476–2493. <https://doi.org/10.3168/jds.2012-6095>.
- Rogers, W., and J. Cooper. 2011. Genetic differences in fertility among US dairy cattle breeds. *Progressive Dairyman* 26:112–117.
- Schiemann, R., W. Jentsch, and H. Wittenburg. 1971. Zur Abhängigkeit der Verdaulichkeit der Energie und der Nährstoffe von der Höhe der Futtermittelaufnahme und der Rationszusammensetzung bei Milchkühen [Dependence of energy and nutrient digestibility upon the level of food uptake and composition of diet of dairy cows]. *Arch. Anim. Nutr.* 21:223–240. <https://doi.org/10.1080/17450397109424178>.
- Spurlock, D. M., J. C. M. Dekkers, R. Fernando, D. A. Koltes, and A. Wolc. 2012. Genetic parameters for energy balance, feed efficiency, and related traits in Holstein cattle. *J. Dairy Sci.* 95:5393–5402. <https://doi.org/10.3168/jds.2012-5407>.
- St-Pierre, N. R. 2001. Invited review: Integrating quantitative findings from multiple studies using mixed model methodology. *J. Dairy Sci.* 84:741–755. [https://doi.org/10.3168/jds.S0022-0302\(01\)74530-4](https://doi.org/10.3168/jds.S0022-0302(01)74530-4).
- Steen, R., S. Johnston, D. Kilpatrick, and D. Chestnutt. 1998. Responses in the growth of body components of finishing lambs to additional metabolizable energy supplied from either grass silage or concentrates. *J. Anim. Sci.* 67:503–512. <https://doi.org/10.1017/S1357729800032938>.
- Vallimont, J. E., C. D. Dechow, J. M. Daubert, M. W. Dekleva, J. W. Blum, C. M. Barlieb, W. Liu, G. A. Varga, A. J. Heinrichs, and C. R. Baumrucker. 2011. Short communication: Heritability of gross feed efficiency and associations with yield, intake, residual intake, body weight, and body condition score in 11 commercial Pennsylvania tie stalls. *J. Dairy Sci.* 94:2108–2113. <https://doi.org/10.3168/jds.2010-3888>.
- Van Arendonk, J., G. Nieuwhof, H. Vos, and S. Korver. 1991. Genetic aspects of feed intake and efficiency in lactating dairy heifers. *Livest. Prod. Sci.* 29:263–275. [https://doi.org/10.1016/0301-6226\(91\)90103-W](https://doi.org/10.1016/0301-6226(91)90103-W).
- van Engelen, S., H. Bovenhuis, J. Dijkstra, J. A. M. van Arendonk, and M. H. P. W. Visker. 2015. Short communication: Genetic study of methane production predicted from milk fat composition in dairy cows. *J. Dairy Sci.* 98:8223–8226. <https://doi.org/10.3168/jds.2014-8989>.
- van Engelen, S., H. Bovenhuis, P. van der Tol, and M. Visker. 2018. Genetic background of methane emission by Dutch Holstein Friesian cows measured with infrared sensors in automatic milking systems. *J. Dairy Sci.* 101:2226–2234. <https://doi.org/10.3168/jds.2017-13441>.
- van Es, A. J. H. 1961. Between-animal variation in the amount of energy required for the maintenance of cows. PhD thesis, Department of Animal Physiology, Wageningen University & Research, Wageningen, the Netherlands.
- VandeHaar, M. J., L. E. Armentano, K. Weigel, D. M. Spurlock, R. J. Tempelman, and R. Veerkamp. 2016. Harnessing the genetics of the modern dairy cow to continue improvements in feed efficiency 1. *J. Dairy Sci.* 99:4941–4954. <https://doi.org/10.3168/jds.2015-10352>.
- VandeHaar, M. J. 2016. Understanding the physiological aspects to improving feed efficiency in dairy cows. Pages 27–34 in *Proc. Tri-State Dairy Nutrition Conference*, Apr. 18–20, 2016, Fort Wayne, IN. 25th Anniversary. The Ohio State University, Columbus, OH.
- VandeHaar, M. J., and N. St-Pierre. 2006. Major advances in nutrition: Relevance to the sustainability of the dairy industry. *J. Dairy Sci.* 89:1280–1291. [https://doi.org/10.3168/jds.S0022-0302\(06\)72196-8](https://doi.org/10.3168/jds.S0022-0302(06)72196-8).
- Yan, T., F. Gordon, R. Agnew, M. Porter, and D. Patterson. 1997. The metabolizable energy requirement for maintenance and the efficiency of utilization of metabolizable energy for lactation by dairy cows offered grass silage-based diets. *Livest. Prod. Sci.* 51:141–150. [https://doi.org/10.1016/S0301-6226\(97\)00065-1](https://doi.org/10.1016/S0301-6226(97)00065-1).
- Yan, T., C. S. Mayne, F. G. Gordon, M. G. Porter, R. E. Agnew, D. C. Patterson, C. P. Ferris, and D. J. Kilpatrick. 2010. Mitigation of enteric methane emissions through improving efficiency of energy utilization and productivity in lactating dairy cows. *J. Dairy Sci.* 93:2630–2638. <https://doi.org/10.3168/jds.2009-2929>.
- Yan, T., C. S. Mayne, T. W. J. Keady, and R. E. Agnew. 2006. Effects of dairy cow genotype with two planes of nutrition on energy partitioning between milk and body tissue. *J. Dairy Sci.* 89:1031–1042. [https://doi.org/10.3168/jds.S0022-0302\(06\)72170-1](https://doi.org/10.3168/jds.S0022-0302(06)72170-1).

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