



Correlations of feed intake predicted with milk infrared spectra and breeding values in the Dutch Holstein population

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ABSTRACT

Feed is a major cost in dairy production, and substantial genetic variation in feed efficiency exists between cows. Therefore, breeders aim to improve feed efficiency of dairy cattle. However, phenotypic data on individual feed intake on commercial farms is scarce, and accurate measurements are very costly. Several studies have shown that information from Fourier-transformed infrared spectra of milk samples (milk infrared, milk IR) can be used to predict phenotypes such as energy balance and energy intake, but this is usually based on small data sets obtained under experimental circumstances. The added value of information from milk IR spectra for estimation of breeding values is unknown. The objectives of this study were (1) to develop prediction equations for dry matter intake (DMI) and residual DMI (rDMI) from milk IR spectra; (2) to apply these for a data set of milk IR spectra from commercial Dutch dairy farms; (3) to estimate genetic parameters for these traits; and (4) to estimate correlations between these predictions and other traits in the breeding goal. We used data from feeding trials where individual feed intake was recorded daily and for which milk IR spectra were determined weekly to develop prediction equations for DMI and rDMI with partial least squares regression. This data set contained over 7,600 weekly averaged DMI records linked with milk IR spectra from 271 cows. The equations were applied for a data set with test day information from 676 Dutch dairy herds with 621,567 records of 78,488 cows. Both milk IR-predicted DMI and rDMI were analyzed with an animal model to obtain genetic parameters and sire effect estimates that could be correlated with breeding

values. A partial least squares regression model with 10 components from the milk IR spectra explained around 25% of DMI variation and less than 10% of rDMI variation in the validation set. Nearly all variation in the milk IR spectra was captured by 7 components; additional components contributed marginally to the spectral variation but decreased prediction errors for both traits. Accuracies of predictions of DMI and rDMI from milk IR spectra for a large feeding experiment were 0.47 and 0.26 on average, respectively, with small differences between ration treatments (ranging from 0.43 to 0.55 and from 0.21 to 0.34, respectively) and among lactation stages (ranging from 0.24 to 0.59 and from 0.13 to 0.36, respectively), with the highest prediction accuracies in early lactation. The estimated heritabilities for predicted DMI and rDMI were 0.3 and 0.4, respectively, which suggests genetic potential for both predicted traits. The correlations of sire estimates for milk IR-predicted DMI with official Dutch breeding values were strongest with milk production (0.33), longevity (0.26), and fertility (−0.27), indicating that cows that eat more produce more, live longer, and have poorer fertility. The correlations of sire estimates for predicted DMI and rDMI with the official breeding values for DMI were low (0.14 and 0.03, respectively). This implies that the added value of including milk IR-predicted DMI information in the estimation procedure of breeding values for DMI would be considered insufficient for practical application.

Key words: feed intake, milk IR spectra, genetic parameters, dairy cattle

INTRODUCTION

Feed is the major variable cost in dairy production (Hemme et al., 2014). Several studies have shown that genetic variation for both feed intake and feed efficiency exist (Berry and Crowley, 2013; de Haas et al., 2015). In line with this, breeding goals of dairy cattle in many countries now also include a measure for feed intake

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or feed efficiency (Egger-Danner et al., 2015; Pryce et al., 2015; de Jong et al., 2016). An important bottleneck for genetic improvement of feed efficiency is that phenotypic data from commercial farms on feed intake of individual cows are scarce, because measurement of true feed intake is very costly and labor intensive. Moreover, validated, practically applicable, alternative ways to measure feed intake in dairy cows are currently lacking. Several authors (e.g., De Marchi et al., 2014, and McParland and Berry, 2016) have suggested that Fourier-transformed milk mid-infrared spectroscopy (milk infrared; **milk IR**) is a potentially rich source of information for prediction of animal phenotypes. Currently, milk IR spectra are used globally to determine fat, protein, and lactose content of milk samples (Soyeurt et al., 2011), and empirical evidence is available that energy balance and energy intake can be predicted from milk IR spectra as well (McParland et al., 2012). However, measurements of feed intake and efficiency used to develop prediction equations in practice are incomplete (i.e., feed intake is not recorded during the entire lifetime), which limits the possible accuracy of predictors.

Breeding values for feed intake that are currently published in the Netherlands rely mostly on genomic predictions of DMI from a relatively small population with individual recordings, and on additional information on milk production, milk composition, and body weight. The question that is not addressed yet is how much new information DMI predicted from milk IR spectra for a large (national) population adds to those information sources when estimating breeding values. Therefore, the objectives of this study were (1) to develop prediction equations for DMI and residual DMI (**rDMI**) from milk IR spectra using data from feeding experiments conducted on a Dutch research farm, (2) to apply these prediction equations for a data set of milk IR spectra from 676 commercial Dutch dairy farms, (3) to estimate genetic parameters for milk IR-predicted DMI and rDMI, and (4) to estimate correlations between these predictions and other traits in the breeding goal, to investigate the added value of (r) DMI predictions from milk IR spectral information for estimation of breeding values.

MATERIALS AND METHODS

Milk IR Spectra, Individual Feed Intake, and Farm Data

Individual feed intake data from feeding trials carried out at Dairy Campus research farm (Lelystad, the Netherlands), stored in a relational database together

with regular farm data, were used for this study. During all experiments the cows were kept in cubicle housing with concrete slatted floors and had access to RIC feeding troughs (Insentec) and concentrate feeders (Manus VC5, DeLaval), where their feed intake was recorded individually. The cows were milked twice daily in a conventional parlor where milk yields were recorded. They were weighed each time they entered the milking parlor. During all feeding experiments, milk was sampled according to 2 protocols in parallel: (1) regular 4-weekly DHI sampling with a combined sample from 1 evening and 1 morning milking (**EM** samples), and (2) weekly sampling on 2 consecutive days with combined samples from the 2 morning milkings (**MM** samples) and from the 2 evening milkings (**EE** samples), as described in van Hoeij et al. (2017a). Milk infrared spectral data with unique identification, such that they can be linked with other cow information, were available from February 1, 2013, onward.

Data Processing

Individual feed intake data from experiments carried out from February 1, 2013, until May 8, 2016, were selected from the database. Moreover, milk yields, body weights, calving dates, parity numbers, and codes for experiment and treatment within experiment were retrieved. Dry mater intake was calculated from the intakes recorded and the percentages of DM of the rations that were fed. After aggregating these DMI records to totals per cow per day, all records with calculated DMI <5 or >99 kg were discarded. Next, weekly averages of daily DMI were calculated when at least 3 daily DMI records were present in that week. These weekly averages were calculated separately for weeks with EM, MM, and EE samplings from 5 d before until 1 d after the milk sampling date. All daily intakes that were <50 or >150% of the week average were discarded. This procedure was applied iteratively until no more records were discarded. In total, 1% of the daily DMI records were discarded. Week averages for daily milk yield (**MY**) and BW were calculated without filtering of potential outliers. After these edits, 3,265, 12,129, and 12,130 weekly average DMI records of 552 Holstein cows could be linked with milk IR spectra of EM, MM, and EE milk samples, respectively.

Preprocessing Milk IR Spectra

The milk samples were analyzed in the laboratory of Qlip B.V. (Zutphen, the Netherlands) using MilkoScan FT 6000 spectrometers (Foss Analytical A/S) equipped with diamond cuvettes. The spectra consisted of 1,060

infrared frequencies (wavenumbers), representing infrared light absorption through the milk samples ranging from 925 to 5,008 cm^{-1} . From all available wavenumbers in the FTIR spectra, 323 wavenumbers were selected for further processing: 925 to 1,596, 1,692 to 1,896, and 2,702 to 3,061 cm^{-1} . As argued by Shetty et al. (2017), the remaining wavenumbers are not informative for DMI and have low heritabilities (Zaalberg et al., 2019). After selection, the data were smoothed with polynomial order 2 and a filter width of 7, similar to the procedures of Shetty et al. (2017).

Calculation of Residual DMI

A priori it is expected that a large part of the variation in DMI can be explained by differences in BW, MY, and feed characteristics (Zom et al., 2012). Residuals of the week averages of individual DMI were calculated with ASReml (Gilmour et al., 2015) with the following model:

$$DMI_{ijklmno} = \mu + Tr_i P_j M_k + pol(BW_{jlm}, 2) + pol(MY_{jlm}, 2) + Tr_i D_n + e_{ijklmno}, \quad [1]$$

where DMI = week average daily DMI (kg); μ = common mean; $Tr_i P_j M_k$ = combined effect of experimental treatment within experiment i , parity j ($j = 1, 2$, or >2), and 4-weekly period in milk of cow k ($k = 1-11$); $pol(BW_{jlm}, 2)$ = polynomial effect of week average BW of animal l in parity j and m weeks in milk, of order 0–2; $pol(MY_{jlm}, 2)$ = polynomial effect of week average MY of animal l in parity j and m ($m = 1-44$) weeks in lactation, of order 0–2; $Tr_i D_n$ = random effect of combination of treatment i and day n of sampling; and $e_{ijklmno}$ = random error.

One experiment contributed substantially more than all other experiments in the overall data set of week average DMI. Therefore, 2 subsets of the data set were analyzed with model [1]:

- Subset A—Records from all experiments with, in addition to a weekly DMI average, also a weekly average for MY and BW in wk 1–44 in lactation, from cows with at least 10 week averages per lactation and treatment within experiment.
- Subset B—A selection of subset A with only records from the largest experiment. Details of this experiment are described in van Hoeij et al. (2017a,b).

After evaluation of the results of a preliminary analysis, additional calculations were carried out for subset B, where “4-weekly period in milk” in model [1] was re-

placed by “weeks in milk.” Numbers of classes of model terms, animals, and records of the 2 subsets are shown in Table 1.

Partial Least Squares Regression of Milk IR Spectra on DMI and rDMI

Partial least squares regression (PLS) was used to model DMI and rDMI with milk IR spectral information (Wallén et al., 2018). All DMI and rDMI records of subsets A and B were linked with milk IR spectra, and because in general both an EE and MM sample were available during each week, this resulted in data sets with 15,885 (subset A) and 11,329 (subset B) records. Both DMI and rDMI were analyzed, and prediction equations were developed for both traits from the same selection of wavenumbers. In the PLS analyses, up to 20 components were fitted with the PLS package in R (version 4.0.2; R Foundation for Statistical Computing). The data were split into a training and a validation set by assigning cows randomly to one of the subsets. Leave-one-out cross validation was applied for internal validation, and predictor variables were standardized by dividing them by their standard deviations. Subset A was analyzed per experiment as a next step to investigate whether the results of predictions could be generalized across experiments and to determine the number of components to be used in the remainder of the study. Hereafter, subset B was analyzed in more detail to derive the prediction equations for DMI and rDMI to be applied in the next step of the study:

- Per stage of lactation (1–100 DIM, 101–200 DIM, and >200 DIM);
- Per treatment, with treatment factors length of dry period (0 or 30 d) and concentrate level (low or standard); see van Hoeij et al. [2017b; the fact that the energy source was either glucogenic or

Table 1. Number of classes of model terms, animals and records in subsets used for calculation of residual DMI

Term	Subset	
	A (all experiments)	B (largest experiment)
Treatment within experiment (Tr)	13	3
Tr \times parity ¹ \times 4 wk in milk	202	66
Tr \times parity ¹ \times week in milk		527
Date	151	117
Tr \times date	465	345
Animal \times parity	317	126
Animal	271	120
No. records	7,619	5,374

¹Parity: 1, 2, or >2 .

lipogenic from wk 8 postpartum onward (van Hoesj et al., 2017a) was ignored for this analysis, because this affected neither EB nor lactation curve characteristics];

- Per type of sample (EM, MM, EE, all, or MM + EE).

Genetic Analysis of Milk IR-Predicted DMI and rDMI

The data set to perform genetic analyses contained all herd test day information from year 2016 of 676 Dutch dairy herds that are contracted to provide additional information for the breeding program of CRV (Arnhem, the Netherlands). The milk IR spectra of the test day samples were used to predict DMI and rDMI with the prediction equations developed with PLS. Moreover, additional phenotypic data of the cows in the data set (MY, conformation scores), pedigree information, and breeding values of sires with offspring in the data set were selected from the CRV database. The following requirements for inclusion were applied on the merged data: (1) The cow was herd book registered; (2) predicted DMI and rDMI were ≥ 12.4 and ≤ 30.4 kg and ≥ -3.89 and ≤ 3.01 kg, respectively; (3) age at calving was ≥ 630 d; (4) the cow was between 2 and 60 wk in lactation at the herd test day; (5) MY was between 5 and 70 kg; (6) the cow breed was at least 75% Holstein-Friesian (**HF**); (7) at least 5 daughters per sire were present in the data set; and (8) there were at least 10 records per herd test day and at least 4 test days per herd in 2016.

After these edits, a data set with 621,567 records representing 78,488 cows (112,653 lactations) with 1,585 sires and 6,637 herd test days remained (77.3% of the initial records, 72.7% of the cows). The pedigree of the data set contained 308,152 animal identification numbers. The data set was analyzed with ASReml (Gilmour et al., 2015) using the following univariate animal model with the same fixed effects as for the national breeding value estimation for DMI:

$$Y_{ijklmnop} = \mu + Hm_i + B_j + M_k + \text{leg}(W_l, 5) + A_m + Pe_n + Anim_o + e_{ijklmnop}, \quad [2]$$

where Y = DMI or rDMI (values predicted from milk IR spectra); μ = common mean; Hm_i = effect of herd-month i ($i = 1-6,637$); B_j = effect of breed j of cow ($j = 1-3$, where 1 = 75% HF, 2 = 87.5% HF, and 3 = 100% HF); M_k = effect of month k of calving ($k = 1-12$); $\text{leg}(W_l, 5)$ = Legendre polynomials describing effect of weeks in milk l , of order 0-5 ($l = 2-60$); A_m = effect of age at calving class m ($m = 1-123$); Pe_n = permanent

environmental effect of repeated records on the same animal n ($n = 1-78,488$); $Anim_o$ = genetic effect of animal o ($o = 1-308,152$); and $e_{ijklmnop}$ is the error term. Pe , $Anim$, and e were random effects; the other model terms were fixed effects. For both DMI and rDMI, heritability and genetic variation were estimated, as well as reliabilities of the $Anim$ estimates. Correlations of sire estimates from the analysis and official breeding values for DMI and a selection of other traits were calculated according to the Calo method (Calo et al., 1973), which considers the reliabilities of breeding values and sire estimates. Only breeding values and sire estimates with a reliability of at least 50% were included in the calculations. To further investigate the genetic associations, correlations between the sire estimates and official Dutch breeding values for DMI were calculated with REML, using sire breeding values and taking into account their reliabilities and the genetic relationships among bulls (Schaeffer, 1994; Larroque and Ducrocq, 1999; Sullivan and Wilton, 2001).

RESULTS

General

Variations and ranges for DMI, MY, BW, parity, and DIM in subsets A and B (which is a subset of A) were similar (Table 2). When adjusting DMI with model [1] to obtain rDMI, the standard deviation (SD) was substantially reduced (to 1.76 and 1.81 kg/d for subsets A and B, respectively). Standard deviations of the residuals after correction of DMI for the model term only (in), and after correction for model [1] while omitting the model term (out), indicate the relevance of each individual term. The most important terms from model [1] were $Tr_i P_j M_k$ and $pol(MY_{jlm}, 2)$, because these terms resulted in the largest reduction of the SD of the residuals for both subsets (Table 3). Removing terms from the full model resulted in a smaller increase of the SD than the variation explained when solely including them, probably because of interrelationships between model terms. The contribution of the other terms in model [1] was small but significant. More refined correction for treatment and stage of lactation effects (with a term for each week in milk instead of each 4 wk) for subset B resulted in an SD of the residuals of 1.74 instead of 1.81 kg/d of DM.

Partial Least Squares Regressions

Prediction errors of the PLS model to estimate DMI or rDMI using milk IR spectra decreased when the number of components in the model was increased

Table 2. Characteristics of the data sets used to calculate residual (r)DMI

Item	Subset A (all experiments)				Subset B (largest experiment)			
	Mean	Minimum	Maximum	SD	Mean	Minimum	Maximum	SD
DMI (kg)	21.2	6.8	36.2	3.1	21.1	6.8	29.7	3.0
Milk yield (kg)	28.7	1.7	56.4	9.3	27.2	1.7	54.0	9.0
BW (kg)	683	412	966	78	687	425	966	79
Parity (no.)	2.9	1	5		2.9	2	5	
DIM (d)	151	1	308	83	150	1	308	87
rDMI (kg)	0.0	-10.8	13.1	1.8	0.0	-10.9	8.5	1.8

to 10 (Figure 1), but hardly changed with addition of more components. Prediction errors for DMI were larger than those for rDMI. Prediction errors for both DMI and rDMI were larger for the validation set than for the training set. Similarly, more variation could be explained for the training set than for the validation set, particularly when adding more than 10 components to the prediction models. A model with 10 components could explain around 25% of DMI variation and less than 10% of rDMI variation in the validation set. Nearly all variation in the milk IR spectra could be explained by 7 components; the additional components contributed only marginally.

As a next step, subset A was analyzed per feeding experiment. This analysis (results not shown) showed large consistency across the results: for all experiments nearly all variation in the milk IR spectra could be explained by between 5 and 10 components; root mean squared errors of prediction were greater and R^2 lower in the validation sets than in the training sets; and R^2 values were consistently higher for DMI than for rDMI. Only for the largest experiment could a small portion of the rDMI variance be explained. Based on these results, it was decided to include 6 components in the models to calculate the weights for the wavenumber

values in the remainder of the study. More detailed analysis of the results of that experiment (subset B), with separate predictions per treatment, showed that prediction equations had similar R^2 when predicting DMI or rDMI among treatments (Table 4). Use of the results from different milk sampling recording schemes did not affect the prediction accuracy. Spectra from MM and EE samples gave very similar prediction accuracy compared with spectra from EM samples (Table 5).

Predictions from all samples based on spectra for 1 to 100 DIM, 101 to 200 DIM, and 201 to 308 DIM were compared with predictions based on samples from entire lactations (Table 6) to investigate the influence of stage of lactation on the correlation between calculated and predicted DMI and rDMI. The results show that samples from 1 to 100 DIM can be used to predict DMI and rDMI throughout the lactation, with accuracies similar to samples from 101 to 200 or 201 to 308 DIM. Based on these results, the final prediction equations to be applied for the data set with test day information were derived from the data from the largest experiment in d 1 to 100 in lactation.

Genetic Parameters and Correlations with Breeding Values

Weights of the standardized wavenumber values in the prediction equations of DMI and rDMI applied for a national data set of milk IR spectra from regular herd tests are shown in Figure 2; the model intercepts (12.93 and -5.10, respectively) are not shown. Both DMI and rDMI were predicted for individual cows for each test day. Averages and SD for DMI and rDMI were 21.55 ± 1.47 and -0.42 ± 0.67 kg/cow per day, respectively. Variance components and heritabilities were calculated with an animal model (see Table 7). Correlations between the sire estimates for DMI and rDMI and official Dutch breeding values, as published August 2017, calculated according to the Calo method with a threshold of 50% for reliability, are shown in Table 8. Correlations were also calculated with a threshold of 60% reliability,

Table 3. Standard deviation (kg/d) of the residuals of DMI after solely including each term (in) and when omitting the term (out) from the full model [1] to calculate residual DMI

Model term ¹	Subset A (all experiments)		Subset B (largest experiment)	
	In	Out	In	Out
$Tr_i P_j M_k$	2.29	2.05	2.36	2.11
$pol(BW_{jlm}, 2)$	2.99	1.86	3.00	1.92
$pol(MY_{jlm}, 2)$	2.50	2.10	2.40	2.18
$Tr_i D_n$	2.83	1.91	2.89	1.94

¹ $Tr_i P_j M_k$ = combined effect of experimental treatment within experiment i , parity j ($j = 1, 2$, or >2), and 4-weekly period in milk of cow k ($k = 1-11$); $pol(BW_{jlm}, 2)$ = polynomial effect of week average BW of animal l in parity j and m weeks in milk, of order 0-2; $pol(MY_{jlm}, 2)$ = polynomial effect of week average milk yield of animal l in parity j and m ($m = 1-44$) weeks in lactation, of order 0-2; $Tr_i D_n$ = random effect of combination of treatment i and day n of sampling.

Table 4. Performance of partial least squares regression models using milk infrared spectra to predict DMI and residual (r)DMI per treatment for subset B (largest experiment)

Trait	Treatment ¹	No. of tests ²	Validation set			Rest of data set		
			No. of rec ³	Corr ⁴	Dif ⁵	No. of rec ⁶	Corr	Dif
DMI	0-d DP (LOW)	1,790	1,897	0.45	2.1	7,642	0.48	2.1
	0-d DP (STD)	1,979	1,580	0.55	2.2	7,770	0.45	2.2
	30-d DP (STD)	1,954	2,129	0.43	2.2	7,246	0.56	2.1
	All	5,723	5,606	0.47	2.2			
rDMI	0-d DP (LOW)	1,790	1,897	0.32	1.1	7,642	0.26	1.3
	0-d DP (STD)	1,979	1,580	0.34	1.2	7,770	0.29	1.3
	30-d DP (STD)	1,954	2,129	0.21	1.4	7,246	0.24	1.2
	All	5,723	5,606	0.26	1.3			

¹DP = dry period; LOW = low level of concentrate (up to 6.7 kg/d); STD = standard level of concentrate (up to 8.5 kg/d).

²Number of records in test set.

³Number of records in validation set.

⁴Correlation between calculated and predicted values.

⁵Average absolute difference between calculated and predicted values (in kg).

⁶Number of records in remainder of the data set [e.g., representing treatments 0-d DP (STD) and 30-d DP (STD) when prediction is based on treatment 0-d DP (LOW)].

but the results were very similar and are therefore not presented. The REML calculations with deregressed values as records also resulted in low estimated correlation (0.11) between DMI sire estimates and official Dutch breeding values for DMI using predictors.

DISCUSSION

Large-scale phenotypic data of individual cow feed intake on commercial dairy farms are scarce but could be very useful for genetic improvement. Therefore, in this study, we investigated whether nationally and routinely available milk IR data could be used to predict DMI and rDMI of individual dairy cows and estimate genetic parameters from these predictions.

The first objective of this study was to develop prediction equations for DMI and rDMI from milk IR spectra using data from feeding experiments. When calculating rDMI, we corrected for factors that affect DMI, and our results show that average absolute differences between predicted and calculated values for rDMI are smaller than those for DMI. We probably could have improved the prediction of DMI by including, for instance, DIM and MY in the prediction models with milk IR spectra, but it can be doubted whether this would have affected the results of the genetic analysis, since these components of the predictions would be removed by the factors in model [2]. According to cross validation (half of the cows were randomly assigned to the training set and the other half to a validation set), we achieved

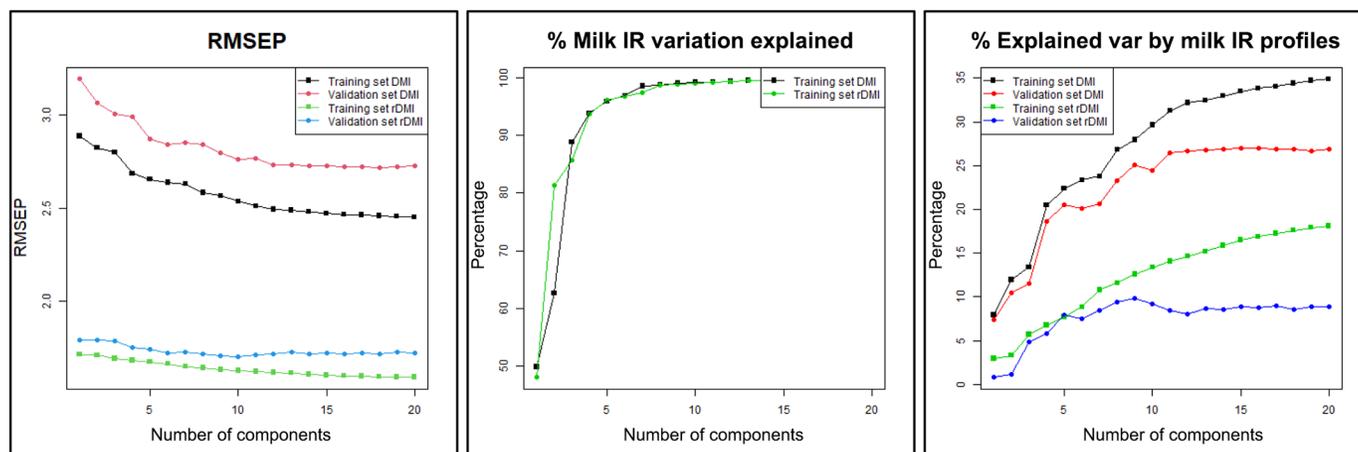


Figure 1. Root mean squared error of prediction (RMSEP), percentage of milk infrared (milk IR) spectra variation (var) explained by components, and percentage of DMI and residual (r)DMI variation explained by milk IR spectra with partial least squares regression analysis of DMI and rDMI for subset A with 1–20 components.

Table 5. Performance of partial least squares regression models using milk infrared spectra from different types of milk samples to predict DMI and residual (r)DMI for subset B

Trait	Sample ¹	No. of tests ²	Validation set			Rest of data set		
			No. of rec ³	Corr ⁴	Dif ⁵	No. of rec ⁶	Corr	Dif
DMI	EM	575	560	0.49	2.2	10,194	0.53	2.0
	MM	2,574	2,523	0.48	2.2	6,232	0.53	2.0
	EE	2,574	2,523	0.47	2.2	6,232	0.52	2.0
	All	5,723	5,606	0.47	2.2			
	MM+EE	5,148	5,046	0.47	2.2	1,135	0.53	2.0
rDMI	EM	575	560	0.24	1.3	10,194	0.33	1.2
	MM	2,574	2,523	0.25	1.3	6,232	0.32	1.2
	EE	2,574	2,523	0.26	1.3	6,232	0.32	1.2
	All	5,723	5,606	0.26	1.3			0.0
	MM+EE	5,148	5,046	0.26	1.3	1,135	0.29	1.2

¹EM = milk sample from evening and morning milkings; MM = milk sample from 2 consecutive morning milkings; EE = milk sample from 2 consecutive evening milkings.

²Number of records in test set.

³Number of records in validation set.

⁴Correlation between calculated and predicted values.

⁵Average absolute difference between calculated and predicted values (in kg).

⁶Number of records in remainder of the data set (e.g., representing MM and EE samples when prediction is based on EM samples).

accuracies of predictions of DMI and rDMI of 0.47 and 0.26 on average, respectively, using PLS regression. This shows that indeed these predictions are possible to some extent, but also that ignoring systematic effects of, for example, MY and BW did not reduce the accuracy of the predictions of DMI. Brand et al. (2021) achieved better predictions of pregnancy status from milk IR spectra with a machine learning approach than with PLS, but Tedde et al. (2021) found very similar DMI prediction accuracies using either PLS regression or machine learning. This suggests that improvement of predictions using milk IR spectra using machine learning compared with PLS regression is trait dependent.

The experiments were performed under specific circumstances and with experimental rations. If prediction equations for DMI or rDMI were to differ substantially between experiments or between treatments within experiments, this would limit the applicability of prediction equations. Our results, however, show that prediction equations can be applied across treatments, even though the rations fed were substantially distinct (van Hoeij et al., 2017b). Several authors have concluded that prediction equations were not adequate when variability in the validation set was not represented in the calibration set (McParland and Berry, 2016; Grelet et al., 2020), and this is often used as an

Table 6. Performance of partial least squares regression models using milk infrared spectra from different stages of lactation to predict DMI and residual (r)DMI for subset B

Trait	DIM	No. of tests ¹	Validation set			Rest of data set		
			No. of rec ²	Corr ³	Dif ⁴	No. of rec ⁵	Corr	Dif
DMI	1–100	1,987	1,878	0.59	2.0	7,464	0.35	2.4
	101–200	1,885	1,869	0.34	2.1	7,575	0.50	2.2
	201–308	1,851	1,859	0.24	2.1	7,619	0.42	2.7
	1–308	5,723	5,606	0.47	2.2			
rDMI	1–100	1,987	1,878	0.36	1.3	7,464	0.30	1.2
	101–200	1,885	1,869	0.27	1.2	7,575	0.29	1.3
	201–308	1,851	1,859	0.13	1.4	7,619	0.32	1.2
	1–308	5,723	5,606	0.26	1.3			

¹Number of records in test set.

²Number of records in validation set.

³Correlation between calculated and predicted values.

⁴Average absolute difference between calculated and predicted values (in kg).

⁵Number of records in remainder of the data set (e.g., samples representing 101–308 DIM when prediction is based on samples representing 1–100 DIM).

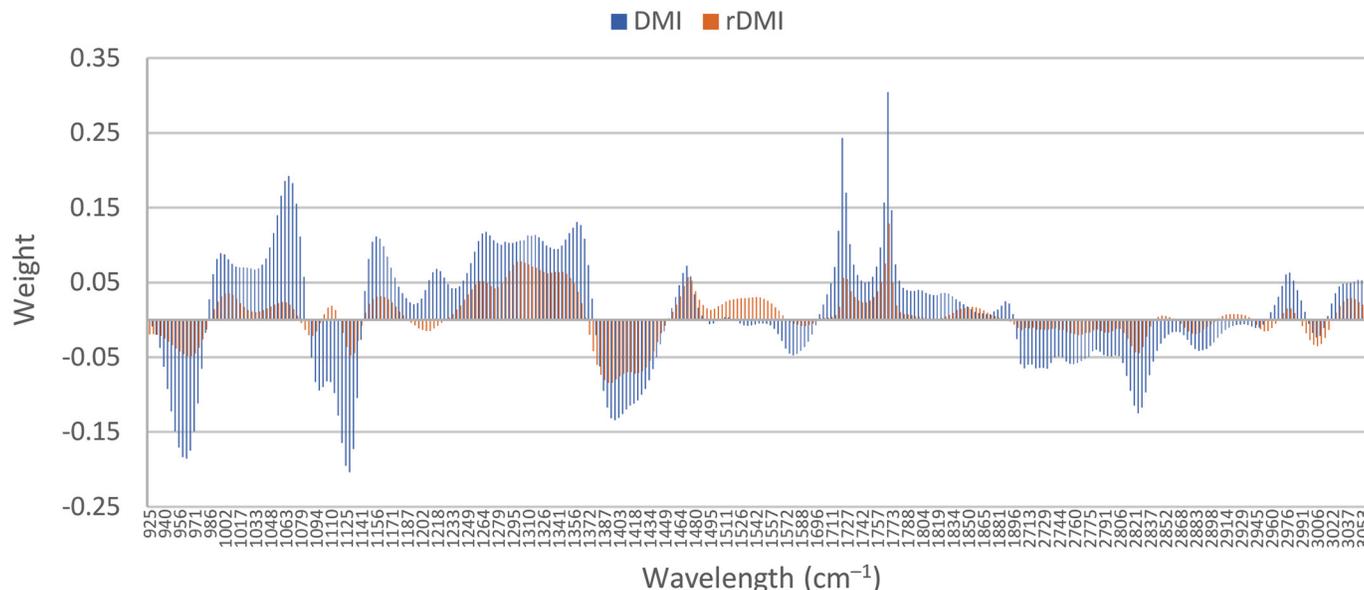


Figure 2. Weights of standardized wavenumber values of milk mid-infrared spectra used in the prediction equations for DMI and residual (r)DMI.

argument for random cross validation, as applied in this study. However, as argued by Wang and Bovenhuis (2019), such validation can also lead to overfitting and over-optimism regarding the accuracy of prediction models. It is likely that not all variability in the DHI data set from the commercial farms was represented in calibration set, and thus that the predictive ability for this data set is lower than for the validation set. However, real external validation with data from farms, cows, and test dates other than those represented in the training set is not possible because we have no DMI information from commercial farms.

For commercial Dutch herds, the milk IR spectra for individual cows usually are obtained from EM samples,

whereas the majority of milk IR spectra that could be linked to DMI in our data set were from EE and MM samples. On average, EE, MM, and EM samples have a different milk composition and thus different spectra, and it can be questioned whether prediction equations for DMI should take into account the type of sample. McParland et al. (2014) consistently found better predictions of energy intake and efficiency from p.m. than from a.m. milk samples. Our results show that, despite the differences in milk composition, prediction equations for DMI and rDMI derived from EE and MM samples performed very similarly to prediction

Table 7. Estimates of heritability (h^2), additive genetic variance (σ_a^2), permanent environmental variance (σ_{pe}^2), and residual variance (σ_e^2) for DMI and residual (r)DMI predicted from milk infrared spectra

Trait	Parameter	Estimate (\pm SE)
DMI	h^2	0.34 \pm 0.01
	σ_a^2	0.44 \pm 0.01
	σ_{pe}^2	0.12 \pm 0.01
	σ_e^2	0.73 \pm 0.00
rDMI	h^2	0.43 \pm 0.01
	σ_a^2	0.12 \pm 0.00
	σ_{pe}^2	0.02 \pm 0.00
	σ_e^2	0.13 \pm 0.00

Table 8. Correlations (corr) between sire estimates for DMI and residual (r)DMI based on milk infrared (milk IR) spectra and official Dutch breeding values for a selection of traits

Trait	Sire estimates based on milk IR spectra ¹			
	DMI		rDMI	
	Corr	No. of sires	Corr	No. of sires
Milk yield (kg)	0.33	2,019	-0.06	2,139
BW	0.08	1,997	-0.08	2,115
BCS	-0.11	1,996	-0.05	2,114
Longevity	0.26	1,920	0.06	2,038
SCC	0.07	2,019	-0.08	2,139
Udder health	-0.03	2,016	-0.10	2,136
Claw health	0.03	1,904	0.12	2,010
Fertility	-0.27	2,009	-0.07	2,129
DMI	0.14	100	0.03	102

¹Correlation of milk IR-predicted sire estimates for DMI and rDMI was 0.57, based on 2,073 sires.

equations derived from EM samples. Both differences in predicted variables and differences in experimental conditions (grazing vs. indoor feeding of conserved feeds) may have influenced these contradictory results.

Phenotypic means and variations of DMI in our data set were in line with the findings of Manzanilla Pech et al. (2014; 19.2 ± 3.3 kg/cow per day), Shetty et al. (2017; 22.2 ± 3.4 kg/cow per day), and Wallén et al. (2018; 19.8 ± 3.5 kg/cow per day). Although prediction of DMI from milk IR is more straightforward than prediction of rDMI, the latter is presumably more directly linked to efficiency (McParland et al., 2014; Shetty et al., 2017). Moreover, VandeHaar et al. (2016) reported that rDMI is more independent from other breeding goal traits, such as production (which is in line with our results) and live weight (which does not agree with our results). In our study, around two-thirds of the variation in DMI could be explained by systemic factors (parity, stage of lactation, MY and BW, treatment) when calculating rDMI. Inclusion of an animal term in model [1] reduced the SD of rDMI down from 1.76 to 1.35 and from 1.81 to 1.40 kg of DM for subsets A and B respectively. This indicates substantial individual differences in DMI per kilogram of milk, as well as considerable within-cow variation. However, information regarding individual variation is not available unless feed intake is actually measured, and therefore is not suited for DMI prediction models using routinely available data. Potentially, variation represented in milk IR spectra may be physiologically linked with differences in efficiency of converting feedstuffs, but this can be related both to within- and between-animal variations in DMI and rDMI.

Genetic Parameters of Milk IR-Predicted DMI

Our second set of objectives was to apply the prediction equations for rDMI and DMI for a data set of milk IR spectra from regular herd tests of commercial Dutch dairy farms, estimate genetic parameters for milk IR-predicted DMI and rDMI, and estimate correlations between these predictions and other traits in the breeding goal. To our knowledge, this study is the first where a large data set with milk IR-predicted DMI and rDMI was analyzed and where genetic correlations with currently available breeding values were calculated. Heritabilities reported in literature ranged from 0.2 to 0.63 for DMI (Spurlock et al., 2012; Berry et al., 2014; de Haas et al., 2015; de Jong et al., 2016; Hardie et al., 2017) and from 0.1 to 0.35 for rDMI (Pryce et al., 2015; Tempelman et al., 2015; Hardie et al., 2017; Li et al., 2017). Thus, our heritability estimate for DMI was in line with values reported in literature, but our esti-

mate for rDMI was relatively high. This could be due to the fact that we predicted rDMI solely from milk IR spectral data that is partly heritable. For both traits, estimated additive genetic variation was low compared with values reported from other studies (Pryce et al., 2015; de Jong et al., 2016; Hardie et al., 2017). This is in line with the low accuracies of the predictions of DMI and rDMI. Correlations of sire estimates for milk IR-predicted DMI and rDMI and official breeding values for DMI were low, despite accounting for the reliabilities of these values. The correlations of sire estimates for milk IR-predicted DMI with official Dutch breeding values were strongest with milk production (0.33), longevity (0.26), and fertility (-0.27), indicating that cows that eat more produce more, live longer, and have poorer fertility. It could be argued that the positive correlation between DMI and longevity results from improved energy balance, but this is not in line with the small but negative correlation with BCS and ignores the fact that milk IR-predicted DMI was also positively correlated with MY. Current Dutch breeding values for DMI also take into account milk, fat, and protein yields and BW, in addition to recorded values of feed intake (de Jong et al., 2016). Information on DMI is rather limited in practice, and milk IR-predicted DMI can be calculated for each test day record. However, due to both low additive genetic variation and low genetic correlation with DMI, the reliability of breeding values for DMI would increase only 1% when including milk IR-predicted DMI or rDMI. This was considered to be insufficient for practical application.

The amount of nutrients becoming available for the animal with each kilogram of DM is determined by the ration composition and its digestibility, and this is ignored in our study. Differences between rations can be corrected for by the treatment effect when composition of feed within treatments is fixed, but, in practice, ignoring ration composition will have increased residual variation. Apart from feed ingested, body reserves are a potential source of or sink for, for instance, energy. Regarding milk production and maintenance, the calculation of rDMI figures could theoretically be refined by taking the milk composition into account (e.g., fat- and protein-corrected milk yield instead of MY, and metabolic BW or BCS instead of BW and changes in BW; VandeHaar et al., 2016; Hurley et al., 2018). Preliminary investigations with fat- and protein-corrected milk yield and metabolic BW replacing MY and BW in model [1], however, revealed that predictions of rDMI did not improve. An explanation for the lack of improvement from using metabolic BW instead of BW is that composition of the body—and, thus, the amount of energy reserves—is ignored. Using BCS could be

an alternative, but presumably this trait is not sufficiently precise to model body energy reserves. We did not include pregnancy status when calculating rDMI, although gestation might have a significant effect on energy requirements. However, averages of rDMI per week until the next calving did not show a trend deviating from zero. Therefore, we assume that pregnancy status can be ignored when calculating rDMI and that this does not affect the predictions of rDMI from milk IR spectra. Wallén et al. (2018) found that predictions of DMI were less accurate [R (accuracy of prediction) ~ 0.54] than predictions of net energy intake (R ~ 0.65) when using milk IR spectra for prediction models. For both, MY and BW were included in the best-performing prediction models. Similar results were obtained by Shetty et al. (2017) for residual feed intake and DMI. It can be argued that adding information from milk IR spectra to models also containing MY and BW resulted in marginal improvement of predictions of DMI, particularly if milk composition routinely calculated from milk IR spectra is considered.

In line with Wallén et al. (2018), preliminary calculations revealed that smoothing of milk IR spectra had no effect on results. However, McParland and Berry (2016) suggested that pre-processing of spectral data is particularly useful when more than one spectrometer is used. Our data were obtained from multiple spectrometers but all from the same laboratory. Preliminary analysis clearly showed that variation in milk IR spectra could largely be explained by between 5 and 10 components of the spectra. Similar numbers of components from milk IR spectra contributing to prediction models for DMI, net energy intake, and residual feed intake were reported by Shetty et al. (2017) and Wallén et al. (2018), whereas McParland et al. (2014) used on average 14 explanatory factors for explanation of energy intake and efficiency traits. Allowing more than 10 components in PLS prediction models for DMI and rDMI in our study resulted in higher percentages of explained variation in the training sets but also resulted in increasing differences compared with the validation sets. We assume this is due to overfitting. The percentage of DMI variation that could be explained by milk IR spectra in this study was in line with the results of Wallén et al. (2018). Higher prediction accuracies for training sets in comparison with validation sets agreed with findings of McParland et al. (2014).

Applications for DMI Predicted from Milk IR Spectra

One reason that DMI can, to some extent, be predicted from milk IR spectra is that milk composition is known to vary throughout lactation, and is determined

from the spectra, and DMI also changes during lactation (Wallén et al., 2018). In line with some other recent studies (Shetty et al., 2017; Wallén et al., 2018), however, our study shows that rDMI is less predictable from milk IR spectra, which indicates that animals that differ in feed conversion efficiency do not have clear differences in milk constituents. The phenotypes discussed by De Marchi et al. (2014), for which better predictability from milk IR is expected, are all more directly linked to milk composition.

McParland et al. (2014) and Shetty et al. (2017) reported that prediction of residual feed intake from milk IR in early lactation was more accurate than in late lactation, but Shetty et al. (2017) also mentioned the opposite for prediction of DMI. Our results showed that cross validation of prediction equations for early lactation both for DMI and rDMI had somewhat higher accuracy than those for mid- and late lactation. Accuracy of predictions for the remainder of the data, however, were not clearly better for early-lactation data, but despite that we have used the data from 1 to 100 DIM to estimate the prediction equations. We assume that the final prediction equations developed for DMI and rDMI are valid for all Dutch dairy herds, and that prediction accuracy is not reduced due to our estimation procedure.

CONCLUSIONS

We developed prediction equations for DMI and rDMI from milk IR spectra, applied these equations for a large data set of commercial Dutch dairy farms, and estimated genetic parameters. We achieved accuracies of predictions of DMI and rDMI of 0.47 and 0.26, on average, using PLS regression for our data set, with cows randomly assigned to either the training or the validation set for cross validation. The estimated heritabilities for predicted DMI and rDMI were 0.3 and 0.4, respectively, and the estimated additive genetic variances were 0.4 and 0.1, respectively. The correlations of sire estimates for predicted DMI and rDMI with the official breeding values for DMI were low (0.14 and 0.03, respectively). The reliability of breeding values for DMI would increase only by 1% when including milk IR-predicted DMI or rDMI. Although such predictions can be obtained at low cost, the added value of including milk IR-predicted DMI information when estimating breeding values for DMI was considered insufficient for practical application.

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