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Genetic parameters for cow-specific digestibility predicted by near infrared reflectance spectroscopy

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ABSTRACT

Digestibility traits included in this study were dry matter digestibility (DMD, g/kg), which was calculated based on the indigestible neutral detergent fibre (iNDF, g/kg of dry matter) content in faeces ($iNDF_f$) and in diet ($iNDF_d$), and $iNDF_f$ predicted directly from faecal samples by near infrared reflectance spectroscopy (NIRS). The data set was collected at three research herds in Finland and one in Norway including in total 931 records from 328 lactating Nordic Red Cattle and Holstein cows. Observations were associated with different accuracy, due to the differences in sampling protocols used for collecting faecal samples. Heritability estimates varied between different sampling protocols and ranged from 0.14 ± 0.06 to 0.51 ± 0.24 for DMD and from 0.13 ± 0.05 to 0.48 ± 0.18 for $iNDF_f$. Estimated genetic standard deviations were 10.5 g/kg and 6.2 g/kg dry matter for DMD and $iNDF_f$, respectively. Results of our study indicated that recording only the iNDF content in the faeces is sufficient to determine genetic variation in cows' ability to digest feed. The coefficient of genetic variation for DMD was rather small (1.7%), but could be utilized if it is supported by a positive analysis of benefits over costs.

1. Introduction

Improving feed efficiency of dairy cows through genetic selection would be beneficial for farmers and for the environment (Connor, 2015). Diet digestibility is one important factor affecting feed utilization efficiency in dairy cows. This is because a cow with a higher ability to digest feed will make more metabolizable energy available for production and body functions. Nevertheless between-cow variation in digestibility has been reported to be small (Cabezas-Garcia et al., 2017; Huhtanen et al., 2016; Mehtiö et al., 2016), and the contribution of dry matter digestibility to feed efficiency variability among dairy cows has been estimated to be between 0 and 31% (Fischer et al., 2018; Potts et al., 2017a). Fischer et al. (2018) found apparent confounding with other biological traits like behaviour, activity, rumen temperature, and suggested that these other traits may either contribute to or be the consequence of digestibility, and thus conclusions on biological traits explaining feed efficiency differences among cows were not possible to make. Potts et al. (2017a) reported that the relationship between feed efficiency and digestibility is dependent on the diet and that digestibility contributed more on feed efficiency when cows were fed low starch diets than when fed high starch diets. In addition to diet composition, it is well established that the rate of digesta passage through the digestive tract has an effect on digestive efficiency, and increasing feed intake reduces diet digestibility (Tyrell and Moe, 1975). Therefore, it may be expected that increase in milk production, and related increase in dry matter intake, may reduce diet digestibility, and thus improving dairy cows' ability to digest feed is desirable. Genetic evaluations for cow-specific digestibility could be one means to select among cows that are high producing and also have higher ability to digest feed.

Cow-specific diet digestibility can be determined by total faecal collection, but this method is expensive and time-consuming, especially when a large number of animals are involved for breeding purposes. An alternative is to determine diet digestibility using different feed marker methods. Although these methods have been used in earlier studies for the estimation of genetic parameters for diet digestibility, the

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applicability for animal breeding purposes has been hampered by the cost and high logistical demand of the measuring techniques. Lee et al. (2002) used the paired alkane technique and reported that genetic variation in diet digestibility exists in sheep. They reported heritability estimates of 0.17 ± 0.06 and 0.13 ± 0.08 for diet digestibility in young and adult sheep, respectively. In dairy cattle, such reports are scarce in the literature, and to our knowledge only Berry et al. (2007) attempted to estimate genetic parameters for diet digestibility. They used the ratio of feed and faecal contents of the natural odd carbon-chain *n*-alkane pentatriacontane from 238 grazing Irish dairy cows, and reported a moderate heritability ranging from 0.08 at 50 days in milk (DIM) to 0.45 at 350 DIM based on random regression model analyses (Berry et al., 2007).

Near infrared reflectance spectroscopy (NIRS) is a relatively cheap and quick tool for predicting marker contents in faeces or even directly cow-specific digestibility (Brogna et al., 2018; Decruyenaere et al., 2009; Nyholm et al., 2009). Mehtiö et al. (2016) evaluated the ability of NIRS to predict three diet digestibility traits: directly organic matter digestibility (OMD) from faecal samples, indigestible neutral detergent fibre (iNDF) content in faeces ($iNDF_f$), and dry matter digestibility (DMD) using iNDF content in diet and faecal samples in dairy cows. The coefficient of determination (R^2) for OMD prediction was 0.69, and low repeatability and small cow-wise variability indicated that direct OMD predictions by NIRS may be inaccurate to quantify the small differences in OMD between cows. In contrast to OMD, the prediction of $iNDF_f$ was more accurate (R^2 = 0.85) and also repeatability estimates (DMD 0.32; $iNDF_f$ 0.46) were reasonable (Mehtiö et al., 2016), indicating that it should be possible to develop NIRS predictions for diet digestibility. Based on these findings, increasing the reference data for NIRS predictions was initiated, and more faecal spot samples were collected in Finland and Norway to generate a useful data set for the estimation of genetic parameters for diet digestibility in dairy cows. Thus, the main aim of this study was to estimate genetic parameters for DMD and $iNDF_f$ when both are predicted by NIRS.

2. Materials and methods

2.1. Traits

The digestibility traits considered in this study were based on iNDF content in diet and faeces, and were: dry matter digestibility (DMD, g/kg) and indigestible neutral detergent fibre content in the faeces ($iNDF_f$, g/kg dry matter). Thus iNDF was used as an internal marker for calculating DMD using the formula:

$$DMD = (1 - \frac{iNDF_d}{iNDF_f}) \times 1000. \quad (1)$$

The iNDF in the diet ($iNDF_d$) was determined by assessing the iNDF contents of silages and concentrates. The iNDF content of the silage was obtained by applying the NIRS prediction equations from the routine silage analyses. The iNDF content of the concentrates were determined based on a 12 d *in situ* incubation in the rumen of dairy cows as described in Ahvenjärvi et al. (2006), or calculated based on an earlier determined average iNDF content of the concentrate ingredients. When silages and concentrates were fed separately, the $iNDF_d$ content was calculated based on cow's DM intake of silage and concentrate as an average over two previous days of each faecal sampling day. Near infrared spectroscopy scans of faecal samples were used to get direct predictions for $iNDF_f$.

The trait $iNDF_f$ is simpler to record and should be equally as good to describe DMD as the actual DMD trait. Approximating formula [1] by a first-order Taylor expansion and evaluating it at the mean will yield:

$$DMD_{ik} \cong \left[1 - \frac{\mu_d}{\mu_f} - \frac{1}{\mu_f}(iNDF_{dk} - \mu_d) + \frac{\mu_d}{{\mu_f}^2}(iNDF_{fi} - \mu_f)\right] \times 1000, \quad (2)$$

where DMD_{ik} is the approximated DMD observation for cow i of the contemporary group (CG) k, μ_d is the mean iNDF content (g/kg) in diets, μ_f is the mean iNDF content (g/kg) in faeces, $iNDF_{dk}$ is the iNDF content (g/kg) in the diet of CG k, and $iNDF_{fi}$ is the iNDF content (g/kg) in the faeces of cow i. Considering Eq. [2] it can be shown that the phenotypic variance of DMD depends on $iNDF_{fi}$ only, if cows of the same CG are fed the same diet and a fixed CG effect is included into the analysis. Therefore, it can be shown that the genetic variance for DMD (σ^2_{aDMD}) is approximately $\hat{\sigma}^2_{aDMD} \cong (\frac{1000\,\mu_d}{{\mu_f}^2})^2 \hat{\sigma}^2_{aiNDF_f}$, [3]where $\hat{\sigma}^2_{aiNDF_f}$ is the estimated genetic variance of $iNDF_f$.

2.2. NIRS predictions

All feed and faecal samples were prepared for scanning as described by Mehtiö et al. (2016). Samples were scanned using FOSS NIRSystems 6500 spectrometer (Foss Electric A/S, Hillerød, Denmark) at Valio Ltd. Laboratory in Helsinki, Finland. The NIRS prediction equations applied on $iNDF_f$ were updated in 2016 with an increased reference data that included 476 samples collected from earlier trials. For the new NIRS calibration model, the standard error of cross-validation (SECV), the ratio of performance to deviation of cross validation (RPD_{cv}), the coefficient of determination for calibration (R^2) and R^2 for cross validation (R^2_{cv}) were 16.6 g/kg, 2.4, 0.86 and 0.83, respectively. This indicated a slight improvement compared to the estimates (SECV = 16.8 g/kg, RPDcv = 2.3, R2 = 0.85, R2cv = 0.82) from a previous model that was based on a 236 sample reference data. During data edition, observations for DMD < 500 g/kg and $iNDF_f$ > 300 g/kg of DM were treated as outliers and were removed from the data set. The NIRS prediction equation applied on $iNDF_d$ is based on a silage calibration consisting of grass, legume and whole-crop silages, and hay and haylage samples giving a total of 448 observations for iNDF (SECV = 14.9 g/kg, RPD_{cv} = 2.6, R^2 = 0.87, R^2_{cv} = 0.85).

2.3. Research herds

The data for this study were collected from 328 dairy cows belonging to three research herds located in Finland and from one research herd in Norway. From Finland, in the data there were 153 Nordic Red Dairy Cattle (RDC) cows, 49 RDC and 45 Holstein (HOL) cows, and 34 RDC cows, respectively from Luke Jokioinen research farm, Luke Maaninka research farm and from University of Helsinki research farm in Viikki. From Norway there were 47 RDC cows from Norwegian University of Life Sciences research farm in Ås.

In general, cows in all the research herds were fed on grass silage prepared mostly from mixed timothy (*Phleum pratense)* and meadow fescue (*Festuca pratensis*) sward and a home blend concentrate mix including mostly barley, oat, wheat, rapeseed meal, sugar beet pulp and a mineral and vitamin mix. The proportion of concentrates in the diet depended on the stage of lactation and digestibility of the grass silage. At the Luke Jokioinen research herd the proportion of concentrate in the diet of the cows was on average 48% on dry matter (DM) basis.

At the Luke Maaninka research herd, during the collection of the first data set in 2012–13, cows were fed two different diets; with concentration proportions of either 22% or 49%. The diets were fed as total mixed ration. In the following data collection period at Maaninka research herd, all cows were fed on a partial mixed ration, and also commercial concentrate from concentrate feeders. The average proportion of concentrate, in the diet on DM was 44%. In addition, during 2013–14, 10 cows at the Maaninka research herd were fed silage and home blend concentrate separately. For these cows, the average proportion of concentrate constituted about 35% of the DM of the diet.

Cows maintained at the University of Helsinki Viikki research herd were fed a partial mixed ration. In addition, the cows were given access to commercial concentrate and protein supplement during milking. The average proportion of concentrate was about 47% of the DM of the diet.

Feeding of cows at the Norwegian University of Life Sciences research herd was based on grass/clover silages which were considered to be either low in crude protein (LCP) or optimal (OCP). The cows in each group had *ad libitum* access to their feed. In addition, cows were given a concentrate feed in amounts estimated to meet the requirements for the expected milk yield based on 305 days lactation curve, and nutrient balance according to the Nordic Feed Evaluation System feeding standards (NorFor, 2011). Detailed description of the diets and feeding can be found in Kidane et al. (2018). The proportion of concentrate in the diet was 33% and 35% in the LCP and OCP groups, respectively.

In all the research herds, feed intake of the cows was recorded during the collection week. Feed samples for analyses were then collected one day before the faecal sampling and feed samples from each collection week were combined into one composite sample.

2.4. Sampling protocols for faecal samples

The data used in this study comprised of different trials with the aim to serve for two different purposes. The first was to develop a protocol for the collection of faecal spot samples to assess individual iNDF content in the faeces of cows, whilst the second was to utilize the obtained iNDF information for the estimation of genetic variance in diet digestibility of dairy cows. Developing a sampling protocol has been addressed by Mehtiö et al. (2016) and the second purpose is addressed in this study ensuring that all available data is effectively utilized. In general, because sampling protocols were varying, it can be expected that observations from the different trials and herds have different measurement errors, and this has been taken into account during the data analysis. The description of the data including different sampling protocols is presented in Table 1.

In the first trial, during 2012–13, cow-specific faecal samples were collected at specific stages of lactation. All cows in the trial were located at Maaninka research farm, and faecal samples were collected for five consecutive days every morning and every evening when the cows were at lactation stages around 50, 150 and 250 DIM. Ten individual samples from each lactation stage were then combined into one composite sample (protocol **C10**) and used for predicting iNDF content in faeces.

In the second trial, during April 2013 and December 2014, the first prototype of the sampling protocol (which was based on preliminary results from the first trial), was used on all Finnish research farms. The protocol involved the collection of faecal samples for three consecutive days every morning, and at the same stages of lactation as in the first trial (around DIM 50, 150 and 250). The collected three samples were then combined into one composite sample (protocol **C3**).

The third trial was carried out during January 2015 and April 2016 at the Finnish research farms for which the final protocol was used. Here samples were collected bi-monthly for three consecutive days every morning from all cows lactating between 29 and 294 DIM. This was done to form larger contemporary groups of cows which have been fed on the same diet (protocol **B3**). In Norway, composite samples from three consecutive days, following protocol B3, were collected from all cows in milk during February and March 2015.

The data for this study consists of two parts, the FULL and BI-MONTHLY data sets. The FULL data set comprised of all composite faecal samples collected from the four different farms between 2012 and 2016, including 931 records from 328 cows. The BI-MONTHLY data set is a subset of the FULL data set which specifically consisted of 441 records from 144 cows that were collected according to the bi-monthly protocol used in Jokioinen, Viikki and Maaninka research farms during 2015-16 (protocol **B3**). In addition, for the BI-MONTHLY data set, there were additional individual observations retained, which were based on one spot sample from day one and the composite of the spot samples from day one and two. Thus, the data set **B1** consisted of day one faecal and feed samples, the data set **B2** consisted of composite samples from day one and two and the data set B3 consisted of composite samples from day one, two and three as explained above.

2.5. Pedigree

The pedigree used for the genetic analyses for the FULL data set was traced back 6 generations from the animals with observations and included 4034 informative animals. The 328 cows with digestibility records descended from 170 different sires, and 13 of those sires had daughters in different herds. A second pedigree was prepared for the genetic analyses of the BI-MONTHLY data set. Also here the pedigree was traced back for 6 generations and it included 2389 animals.

2.6. Modelling diet digestibility

A univariate repeatability animal model was fitted to the FULL data set. The model for the FULL data set was:

$$y_{ijklmno} = B_i + P_j + LS_k + FL_l + HYM_m + b\times iNDF_{d_n} + a_o + pe_o + e_{ijklmno}, \quad (3)$$

where $y_{ijklmno}$ = DMD or $iNDF_f$ record of cow o, B_i = fixed effect of breed i (RDC or HOL), P_j = fixed effect of parity j (primiparous or multiparous), LS_k = fixed effect of lactation stage k (<100 DIM, 100–199 DIM and >199 DIM), FL_l = fixed effect of feeding level l (three levels; the basic and the two divergent levels), HYM_m = fixed effect of herd-year-month m (54 classes), b is a regression coefficient, $iNDF_{d_n}$ is the diet-specific iNDF content of diet n, a_o is the random additive genetic effect for animal o [$a \sim N(0, \mathbf{A}\sigma_g^2)$, where **A** is the additive genetic relationship matrix among animals and σ_a^2 is the additive genetic variance], pe_o is the random permanent environmental effect for animal o [$pe \sim N(0, \mathbf{I}\sigma_{pe}^2)$, where **I** is an identity matrix and σ_{pe}^2 is the permanent environmental variance], and $e_{ijklmno}$ is the random error term.

The fixed effect of feeding level was included in the model to comprise the difference between two concentrate levels in the Maaninka research herd data C10 (diet with on average 22% concentrate proportion was treated as a divergent and diet with on average 49% concentrate proportion was treated as a basic feeding level) and two silage crude protein levels in Norway data (LCP was treated as a divergent and OCP was treated as a basic feeding level). The HYM

Table 1
Description of the data by different protocols, including years of collection, number of research herds, the number of individual faecal spot samples combined to a composite sample (N samples), collection period (samples collected in three lactation stages ~50, 150 and 250 days in milk, monthly or bi-monthly), number of observations (N obs) and number of Nordic Red Dairy Cattle cows (N RDC cows) and number of Holstein cows (N HOL cows).

Protocol	Years of collection	Research herds	N samples	Collection period	N obs	N RDC cows	N HOL cows
C_{10}	2012–2013	1	10	3 stages	99	12	31
C_3	2013–2014	3	3	3 stages	300	133	0
NOR	2015	1	3	Monthly	91	47	0
B3	2015–2016	3	3	Bi-monthly	441	130	14
B2	2015–2016	3	2	Bi-monthly	441	130	14
B1	2015–2016	3	1	Bi-monthly	441	130	14

interaction consisted of four research herds, five years (2012–16), and months that were clustered to classes including samples from two consecutive months. In the data from University of Helsinki Viikki and Luke Maaninka research herds more than two consecutive month classes had to be clustered to achieve sizable contemporary groups. Thus, the HYM-variable was designed to describe the CGs of animals that were fed on same diet. Almost half (47%) of the data were collected using the B3 protocol, *i.e.*, all cows were sampled bi-monthly at the same time resulting in larger CGs with same diet. However, there was some variation between iNDF content in diet within the same HYM-class of observations collected under the C10 and C3 protocols where cows were sampled based on stage of lactation. To account for this variation in the diet, $iNDF_d$ was included in the model as a covariate. In the model a heterogeneous residual variance was fitted because different sampling protocols (C10, C3 and B3) were used for the collection of the data. Furthermore, the data collection in Norway deviated from the other protocols, and thus four different residual variance classes were considered.

For the BI-MONTHLY data sets (B3, B2 and B1), the model used was otherwise the same as in [3] but the fixed effect of feeding level and different residual variances were omitted. In addition to the univariate models, we fitted a bivariate model for DMD and $iNDF_f$ on the B3 data set to estimate the genetic correlation between the traits. Variance components were estimated by REML applying expectation maximization (EM-REML) method as implemented in MiX99 software (Vuori et al., 2006). Standard errors for heritability and repeatability estimates were approximated using Taylor series expansions.

3. Results

Means of DMD, $iNDF_f$ and $iNDF_d$ observations differed between herds and protocols reflecting the differences in the composition of the diets fed across herds and time, whereas differences in standard deviations of the observations reflected the applied sampling protocol (Table 2). Standard deviations were smaller when sampling was based on the BI-MONTHLY protocol, because under this protocol all cows from the same comparison group were fed the same diet.

From the genetic analysis of FULL data set, the estimates of genetic variances for DMD and $iNDF_f$ were 110.67 ± 58.97 and 38.90 ± 16.89, respectively (Table 3). Estimated genetic variance for $iNDF_f$ was consistent with the estimate of genetic variance for DMD as was expected from Eq. [3]: $\hat{\sigma}^2_{a_{DMD}} \cong (\frac{1000\,\mu_d}{\mu_f{}^2})^2 \hat{\sigma}^2_{a_{iNDF_f}} = 2.9*38.9 = 112.8$. The permanent environmental variance explained only a small fraction of the phenotypic variance for both digestibility traits. Residual variance estimates varied between different protocols, resulting in varying heritability estimates. Heritability estimates were lower for data collected according to the sampling protocol C3 compared to protocol B3. This was because under the B3 protocol the residual variance was clearly smaller. Under the C3 protocol, cows of the same CG were sampled over a longer time window and day-to-day variation in the diet most likely results in high residual variance. Similarly in the data from Norway, the $iNDF_d$ within the same CG varied markedly, which resulted in high residual variance and lower heritability estimates. The highest heritability estimates were obtained for data set C10, which was comprised of more accurate observations, resulting in relatively smaller estimates of residual variances. The heritability estimates for $iNDF_f$ and DMD were on a same level. For the B3 data higher heritability estimates were found for $iNDF_f$. The FULL data set available for genetic analyses was somewhat small and this is reflected by high standard errors associated especially with the permanent environmental effect. However, the standard errors of the heritability estimates were low indicating that the estimates are reasonable and are statistically significant.

Repeatability and heritability estimates based on the BI-MONTHLY data sets are presented in Table 4. The repeatability estimates were lowest for B1 and highest for B3 sampling protocol in both DMD (0.17 to 0.36) and $iNDF_f$ (0.19–0.40). This is because the estimated measurement error variance reduced for the composite samples based on two or three spot samples. On the contrary, the estimated genetic variance increased for the composite samples. Consequently, heritability estimates were smallest in B1 (0.03 for both DMD and $iNDF_f$) and largest in B3 data (0.25 ± 0.22 for DMD and 0.31 ± 0.23 for $iNDF_f$). Due to the small data set with 144 cows with observations, standard errors were large for the estimated genetic variances and heritabilities and estimates have to be interpreted with caution. Nevertheless, the heritability estimates and genetic standard deviations of B3 data set were in line with the estimates from the FULL data set.

Analyses from BI-MONTHLY data set resulted in higher repeatability and heritability estimates for $iNDF_f$ than for DMD. When a bivariate model for the B3 data set was fitted, higher heritability estimates were obtained. These estimates were closer to those ones estimated from the FULL data set, especially for DMD. The estimated genetic correlation between both traits was very high 0.998 ± 0.01, confirming that genetic variation in DMD is determined by the genetic variation in $iNDF_f$. In the BI-MONTHLY data set the heritability estimates were slightly lower for both traits compared to those estimated from the FULL data set for the same sampling protocol (B3) (Table 3).

Table 2
Statistics of the FULL data set (including C10, C3, B3 protocols and Norway data) and the BI-MONTHLY data set (B1 one day sample, B2 two day and B3 three day composite samples) including number of observations in herds with different protocols, means and standard deviations (SD) for iNDF content in faeces ($iNDF_f$, g/kg DM), dry matter digestibility (DMD, g/kg) and iNDF content in diet ($iNDF_d$, g/kg).

Herd	Breed†	Protocol	N obs	DMD		$iNDF_f$		$iNDF_d$	
				mean	SD	mean	SD	mean	SD
Jokioinen	RDC	C3	211	616.8	39.5	221.7	29.1	84.9	13.2
		B3	269	593.8	33.1	204.1	24.8	82.4	8.5
		B2	270	594.8	33.6	204.6	24.6	82.4	8.5
		B1	264	594.7	35.6	204.9	26.1	82.4	8.5
Viikki	RDC	C3	51	630.0	32.8	209.5	24.9	77.3	9.8
		B3	26	712.5	27.7	209.1	11.6	59.9	4.1
		B2	26	710.9	28.4	208.1	11.3	59.9	4.1
		B1	26	710.5	30.6	207.8	13.6	59.9	4.1
NMBU	RDC	C3	91	629.6	33.0	240.7	27.6	88.3	4.2
Maaninka	RDC	C10	30	680.4	53.1	211.6	13.3	67.8	13.0
		C3	38	669.5	38.8	213.4	27.4	70.0	8.5
		B3	103	660.9	33.0	216.8	16.0	73.2	6.1
		B2	107	659.4	31.2	215.3	14.9	73.2	6.1
		B1	108	654.7	35.1	213.3	17.5	73.2	6.1
Maaninka	HOL	C10	69	694.4	60.0	205.5	12.3	62.7	12.3
		B3	43	646.1	33.0	208.4	19.6	73.7	9.1
		B2	43	646.3	36.6	208.6	18.3	73.7	9.1
		B1	43	644.7	37.3	207.5	18.6	73.7	9.1

† RDC = Nordic Red Dairy Cattle; HOL = Holstein.

4. Discussion

According to the literature, between-cow phenotypic variation in digestibility is small (Cabezas-Garcia et al., 2017; Huhtanen et al., 2016; Mehtiö et al., 2016), but there are genetic differences between cows (Berry et al., 2007) and between breeds (Beecher et al., 2014). In this study, we found small genetic variation in diet digestibility of dairy cows, which is in agreement with that reported by Berry et al. (2007). Scientific literature on the genetic background of diet digestibility is scarce, and to our knowledge only a few studies can be found (Lee et al., 2002; Berry et al., 2007). Collecting faecal samples is expensive and laborious, and therefore in most of the limited studies so far relatively small data sets were used for genetic analyses. In our study, a heterogeneous data set was compiled to generate a reasonable data size for genetic analyses that necessitated the fitting of heterogeneous residual variances. Furthermore, to increase the size of CG's and thereby the statistical power, data was collected from all contemporaries of in a

Table 3
Estimates of genetic parameters[†] with standard errors, when fitting heterogeneous residual variances for different protocols (C3, B3, NOR = Norway, C10) as analysing dry matter digestibility (DMD) and iNDF content in faeces ($iNDF_f$) using the FULL data set (328 cows with 931 observations).

	σ^2_{pe} ± se	σ^2_a ± se	σ^2_e ± se	h^2 ± se
DMD	3.15 ± 50.76	110.67 ± 58.97		
C3			687.05 ± 73.36	0.14 ± 0.06*
B3			281.44 ± 22.36	0.28 ± 0.13*
NOR			609.24 ± 102.05	0.15 ± 0.07*
C10			102.55 ± 22.98	0.51 ± 0.24*
$iNDF_f$	1.11 ± 14.20	38.90 ± 16.89		
C3			242.16 ± 24.64	0.14 ± 0.05**
B3			75.05 ± 5.32	0.34 ± 0.12**
NOR			253.66 ± 45.61	0.13 ± 0.05**
C10			40.35 ± 7.32	0.48 ± 0.18**

[†] σ^2_{pe} = permanent environmental variance, σ^2_a = additive genetic variance, σ^2_e = residual variance, h^2 = heritability estimate.
* $p < 0.05$.
** $p < 0.01$.

herd. Consequently, observations came from two breeds (RDC and HOL cows), which was accounted for by including the fixed effect of breed into the analytical model. Thus, a possible difference in the genetic levels of the breeds does not bias variance component estimates. The heritability estimates found in our study are slightly higher than the estimates reported for sheep (Lee et al., 2002), but they are in line with Berry et al. (2007) who found estimates ranging from 0.08 to 0.45 in diet digestibility fitting a random regression model for a data collected from 238 HOL dairy cows.

Earlier studies have shown that NIRS can be used to predict iNDF content in faeces (Brogna et al., 2018; Mehtiö et al., 2016; Nyholm et al., 2009). In this study, we have demonstrated that genetic variance in cows' ability to digest feed can be predicted based on NIRS scans of faeces. This is beneficial, because it will not require predictions of iNDF in diets, which may be associated with prediction errors. Results from our analysis showed that recording iNDF in faeces is sufficient to determine the genetic variation in diet digestibility and therefore there will be no need for analyzing feed samples as long as cows of the same CG consume the same diet. In fact, the repeatability and heritability estimates were even higher using $iNDF_f$, which indicates that $iNDF_f$ could be more accurate than DMD.

The varying residual variances between different sampling protocols, and thus varying heritability estimates, found in this study clearly showed how important it is to design sampling protocols with sizable contemporary groups of cows consuming the same diet and measured at the same time. This should also be considered when collecting data for other feed efficiency traits in dairy cattle. The heritability estimates were in general higher when the B3 protocol, where all cows in the herd were sampled simultaneously every second month, was used rather than recording only during specific lactation windows. Moreover, the higher repeatability estimates showed, that the prediction of digestibility was much more accurate when using three faecal samples combined into one composite sample, compared to a composite of two samples or using just one individual sample. These results confirmed the protocol which has been proposed in Mehtiö et al. (2016).

Potts et al. (2017b) found that dry matter digestibility in dairy cows has declined by two percent from 1970 to 2014. However, they also suggested that when differences in the diet composition and dry matter intake of the cows are taken into account, no significant differences should exist in the ability to digest feed between the cows born in the 70's and cows of today. In addition, Fischer et al. (2018) found a relatively weak phenotypic correlation (−0.26; $P = 0.05$) between dry matter digestibility and residual energy intake, indicating that the higher the digestibility, the higher is the feed utilization efficiency of cows. These findings indicate that the potential of improving digestibility by selection has not been utilized and cow-specific digestibility has not improved indirectly via improvement in production and feed efficiency. The coefficients of genetic variation found in this study were 1.7% and 2.9% for DMD and $iNDF_f$, respectively. These are lower than coefficients for production traits (6%, Berry et al., 2003), but shows that selection for digestibility could be beneficial. In addition, because every unit improvement in diet digestibility corresponds to same amount of savings in feed requirement, it may become of significant interest in the future. Nevertheless, although predicting iNDF content in faeces by NIRS is possible, the sampling and processing pipeline would need to be optimized and advanced to provide iNDF records at acceptable costs for establishing a suitable genomic prediction cow reference population.

Table 4
Variance components[†] with standard errors, heritability (h^2) and repeatability (r) estimates using univariate and bivariate ($B3_{bivariate}$) animal models for dry matter digestibility (DMD) and iNDF content in faeces ($iNDF_f$) in B1, B2 and B3 data sets (441 observations from 144 cows).

	σ^2_{pe} ± se	σ^2_a ± se	σ^2_e ± se	r ± se	h^2 ± se
DMD					
B1	91.9 ± 79.4	18.6 ± 81.6	534.2 ± 41.1	0.17 ± 0.05***	0.03 ± 0.13^{NS}
B2	86.9 ± 68.6	20.2 ± 55.1	335.6 ± 29.0	0.24 ± 0.06***	0.05 ± 0.12^{NS}
B3	69.0 ± 83.1	76.9 ± 93.3	267.7 ± 23.6	0.35 ± 0.06***	0.19 ± 0.22^{NS}
$B3_{bivariate}$	44.3 ± 77.8	104.2 ± 93.9	269.1 ± 25.3	0.36 ± 0.07***	0.25 ± 0.22^{NS}
$iNDF_f$					
B1	27.4 ± 29.2	5.8 ± 26.8	145.4 ± 14.4	0.19 ± 0.06**	0.03 ± 0.15^{NS}
B2	35.4 ± 24.5	5.9 ± 24.5	128.5 ± 9.7	0.24 ± 0.04***	0.03 ± 0.14^{NS}
B3	13.9 ± 39.9	34.3 ± 42.5	71.8 ± 5.7	0.40 ± 0.06***	0.29 ± 0.35^{NS}
$B3_{bivariate}$	11.5 ± 23.7	36.9 ± 28.6	72.4 ± 6.9	0.40 ± 0.06***	0.31 ± 0.23^{NS}

[†] σ^2_{pe} = permanent environmental variance, σ^2_a = additive genetic variance, σ^2_e = residual variance, NS = non-significant.
*** $p < 0.001$.
** $p < 0.01$.

5. Conclusion

In this study cow-specific diet digestibility predictions from NIRS were used for genetic analyses of digestibility traits. The estimated genetic standard deviations were 10.5 g/kg and 6.2 g/kg for DMD and for $iNDF_f$, respectively. The heritability estimates for diet digestibility ranged from 0.13 to 0.51 depending on the trait and sampling protocol. Our results confirm that sizable contemporary groups of cows recorded at the same time and consuming the same diet are needed for genetic analyses to get reliable estimates. Results of our study also indicated that recording only the iNDF content in the faeces is sufficient to determine the genetic variation in cows' ability to digest feed. The coefficient of genetic variation for DMD was rather small (1.7%), but could be utilized if it is supported by a positive analysis of benefits over costs.

Declaration of Competing Interest

The authors declare no conflict of interest.

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