Identification of biological traits associated with differences in residual energy intake among lactating Holstein cows

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ABSTRACT

Residual feed intake, which is usually used to estimate individual variation of feed efficiency, requires frequent and accurate measurements of individual feed intake to be carried out. Developing a breeding scheme based on residual feed intake in dairy cows is therefore complicated, especially because feed intake is not measurable for a large population. Another solution could be to focus on biological determinants of feed efficiency, which could potentially be directly and broadband measurable on farm. Several phenotypes have been identified in literature as being associated with differences in feed efficiency. The present study therefore aims to identify which biological mechanisms are associated with residual energy intake (REI) differences among dairy cows. Several candidate phenotypes were recorded frequently and simultaneously throughout the first 238 d in milk for 60 Holstein cows fed on a constant diet based on maize silage. A multiple linear regression of the 238 d in milk average of net energy intake was fitted on the 238 d in milk averages for milk energy output, metabolic body weight, the sum over the 238 d in milk of both, body condition score loss and gain, and the residuals were defined as REI. A partial least square regression was fitted over all biological traits to explain REI variability. Linear multiple regression explained 93.6% of net energy intake phenotypic variation, with 65.5% associated with lactation requirement, 23.2% with maintenance, and 4.9% with body reserves change; the 6.4% residuals represented REI. Overall, measured biological traits contributed to 58.9% of REI phenotypic variability, which were mainly explained by activity (26.5%) and feeding behavior (21.3%). However, apparent confounding was observed between behavior, activity, digestibility, and rumen-temperature variables. Drawing a conclusion on biological traits that explain feed efficiency differences among dairy

cows was not possible due to this apparent confounding between the measured variables. Further investigation is needed to validate these results and to characterize the causal relationship of feed efficiency with feeding behavior, digestibility, body reserves change, activity, and rumen temperature.

Key words: feed efficiency, dairy cow, phenotype

INTRODUCTION

The world population is expected to increase by 32% by 2050 compared with 2015 (United Nations Department of Economic and Social Affairs Population Division, 2015). Demand for animal products is therefore expected to increase (IAASTD, 2009). To increase animal production, one possibility is to improve feed efficiency by selection, which means increased animal production or decreased use of resources. Selection for feed efficiency is complicated because individual variability of feed efficiency is not easily measurable on a large population. The classic indicator of individual variability in feed efficiency is residual feed or energy intake (**RFI** or **REI**; Dekkers and Gilbert, 2010; Aggrey and Rekaya, 2013; Berry and Crowley, 2013). By definition, RFI is the residual of a linear regression of feed intake fitted over a population, on the biological traits associated with the main energy expenditures.

Direct selection on RFI is often mentioned to improve feed efficiency (Pryce et al., 2015). Its heritability was moderate and variable in literature (Berry and Crowley, 2013; Yao et al., 2017); even when estimated over a large population (Tempelman et al., 2015), heritability was only 0.18. Given this moderate heritability, a large reference population is needed to develop a reliable EBV for RFI; at least 30,000 or 100,000 cows would be needed, respectively, with a heritability of 0.3 or 0.05 (Gonzalez-Recio et al., 2014). Because DM intake is difficult and expensive to measure on farm, especially in cattle, building a large reference population would therefore be difficult, and thus, developing EBV for RFI seems limited. To avoid measuring RFI in lactating cows, a possibility could be to measure it as grow-

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ing heifers if RFI is repeatable throughout age. When cows were identified as efficient or inefficient as calves, Macdonald et al. (2014) found that differences in DMI differed significantly but slightly between the most and the least efficient cows.

The major problem with RFI is that by definition of model residuals, RFI does not only reflect feed efficiency variability but also model fitting and measurement errors (Robinson, 2005). This sensitivity to model errors may contribute to the difficulty of building a reliable EBV of RFI. To have a better indication of feed efficiency variability, the possibilities are either to isolate RFI variability that is specific to animals and not to errors or to sum up feed efficiency in its main biological determinants. Literature poorly documents methods to identify animal-specific variability of RFI. Using frequent and accurate measurements of DMI and energy expenditure traits should reduce part of RFI associated with measurement errors (Robinson, 2005) and render RFI more representative of feed efficiency variability. Characterizing feed efficiency with its main biological determinants is an alternative to DMI modeling that could help to identify more heritable traits. Identification of feed efficiency biological determinants is largely documented in literature. Only Richardson and Herd (2004) have simultaneously analyzed the main biological traits expected to be involved in feed efficiency variability in beef cattle. In dairy cows, most studies have focused only on a group of these traits at the same time (Table 1). A more complete study with simultaneous measures of the identified biological traits is required to reach a conclusion on the biological determinants of RFI variability in dairy cows.

The present study is a preliminary analysis aiming at identifying potential determinants of long-term feed efficiency, estimated over the first 238 DIM, in dairy cow. Most potential determinants of feed efficiency cited in literature were therefore recorded for all cows to estimate the contribution of each determinant to residual energy intake phenotypic variability (Table 1). To reduce the part of REI variability that can be associated with measurement errors, REI was estimated with accurate and frequent measurements.

MATERIALS AND METHODS

An experiment on lactating dairy cows was established to frequently record as many phenotypes as possible among those that are potentially determinants of feed efficiency. Experimentation was carried out indoors to minimize the effect of changes in environmental conditions. This experiment was carried out from August 2014 to June 2015 in the INRA UMR PEGASE Méjusseume (Le Rheu, France) experimental farm in

western France. The data set consisted of 60 Holstein cows with 50% primiparous among them that were housed in a freestall barn. Data were available from calving to 238 DIM, which was the minimum number of DIM reached by all cows and will be referred to as the whole experimental period in the rest of the paper. Calving was seasonal, with a calving-season length of 56 d between August 27 and October 22, 2014.

A same TMR was fed from calving to the end of the experiment. The diet was offered ad libitum with a daily target level of 10% refusals per cow. Diet energy and protein densities were assessed according to the French system [INRA, 2010: UFL (unité fourragère lait) are amounts of NE_L , with 1 UFL equating to 7.1 MJ of NE_L , and PDIE (protein digested in the small intestine supplied by rumen-undegraded dietary protein and by microbial protein from rumen-fermented OM) are amounts of MP]. The TMR was based on maize silage, energy concentrate, soybean cake, dehydrated alfalfa, and minerals (Table 2). This diet had a net energy density of 0.936 UFL/kg of DM (6.65 MJ of NE_L /kg of DM) and a MP concentration of 94.3 g of PDIE/kg of DM. All cows were also fed the same diet at least 3 wk before calving. This precalving diet was based on a DM basis on corn silage (84.5%), soybean meal (9%), energy concentrate (4%), and straw (2.5%).

Feed Efficiency

Measurements to Calculate Feed Efficiency.

Each cow had its own individual feed trough and was fed ad libitum. To enable feed distribution, access to the feed trough was closed from 0730 to 0900 h and from 1400 to 1600 h. Conversely, all cows were locked at the feed fence from 0900 to 1000 h and in the afternoon after milking, starting at 1530 until 1800 h; the rest of the day (17 h) they had free access to their feed trough, with a maximum of 10% refusals daily. Feed intake was measured daily for each cow as the difference between distributed and next morning refusals weight. A bulk sample of each ingredient was analyzed for composition. Analyses for DM were based on samples taken 5 times weekly for wet forages and once weekly for concentrates. Cows were gathered for milking around 0630 and 1530 h and were waiting in a standing position for milking. Milk yield was recorded at each milking. Twice a week, 2 consecutive milkings were analyzed for milk protein and fat concentrations. Milk net energy (MNE) was estimated according to the French standard energy requirement equation (INRA, 2010):

$$MNE = 7.12 \times \{MY \times [0.44 + 0.0055 \times (MFC - 40) + 0.0033 \times (MPC - 31)]\}, \quad [1]$$

Table 1. Review of biological traits recorded to explain residual feed intake variability

Reference	Milk ¹	Body comp. and reserves change ²	Digestion ³	Thermo-regulation	Morphology	Behavior	Activity	Genes CNV study ⁴
Coleman et al., 2010	MY, MSOL	BCS			BW			
Hou et al., 2012								x
Mantysaari et al., 2012	ECMY, MSOL	BCS, BCS change, NEFA			BW			
Connor et al., 2013	ECMY				BW	Eating	Pedometer	
DiGiacomo et al., 2014				Rectal and skin temperature				
Thornhill et al., 2014	MY, MSOL, lactose		DMd, rumen metabolite					
Manafiazar et al., 2016	ECMY	BCS			BW, conformation traits			
Xi et al., 2015								x
Manzanilla-Pech et al., 2016	MilkE, MY	BCS			BW, conformation traits			
Xi et al., 2016	MY, FCM, MSOL, lactose, urea				BW, chest girth	Eating		
Present study	MY, MSOL, lactose	BCS, BCS change, NEFA, glucose	DMd	Rumen temperature	BW	Eating, ruminating	Overactivity, standing	

¹MY = milk yield; MSOL = milk solids; ECMY = ECM yield; MilkE = milk energy output.²Body comp. = body composition traits; NEFA = nonesterified fatty acid.³DMd = DM digestibility.⁴CNV = copy number variation.

Table 2. Diet composition and feed analysis

Item	Corn silage				Dehydrated alfalfa	Soybean meal	Concentrate ¹	Mineral–vitamin supplement ²	Diet
	1	2	3	4					
Composition ³ (%)	3.8	17.0	27.2	15.8	10.0	10.7	14.0	1.5	100
DM (%)	33.6	32.1	32.7	35.8	87	87	87	100	53
OM (g/kg of DM)	966	962	963	965	886	926	953	0	936
CP (g/kg of DM)	66	61	74	67	170	502	113	0	130
NDF (g/kg of DM)	385	462	375	388	449	111	229	0	345
ADF (g/kg of DM)	207	250	214	215	334	63	94	0	196
ADL (g/kg of DM)	18	17	23	22	84	4	14	0	24
Starch (g/kg of DM)	307	257	315	349	35	54	466	0	271
P (g/kg of DM)	1.6	1.6	1.9	1.8	2.7	6.7	3.4	60.0	3.5
Ca (g/kg of DM)	1.8	2.4	2.2	1.7	17.7	3.6	3.1	240.0	7.5
Mg (g/kg of DM)	1.2	1.2	1.2	1.2	1.5	3.3	1.5	40.0	2.1
Net energy (UFL/kg of DM) ⁴	0.93	0.88	0.95	0.97	0.60	1.17	1.11	0.00	0.94
Net energy (MJ/kg of DM)	6.61	6.25	6.77	6.86	4.21	8.32	7.90	0.00	6.65
PDIN ⁵ (g/kg of DM)	40.6	37.5	45.5	41.2	114.7	365.2	74.4	0.0	88.2
PDIE ⁶ (g/kg of DM)	65.2	64.6	70.5	71.0	92.7	250.3	95.5	0.0	94.3

¹The energy concentrate was composed of 20% corn, 20% wheat, 20% barley, 20% dehydrated beet pulp, 15% wheat bran, 3% molasses, 1% rapeseed oil, and 1% NaCl (expressed as a percentage of as-fed matter).

²Mineral composition: 5.5% phosphorus, 27% calcium, 4% magnesium, 0.1% sodium, 0.4% zinc, 0.4% manganese, 0.1% copper, 0.008% iodine, 0.002% cobalt, 0.002% selenium, 0.15% vitamin E, 600,000 IU of vitamin A, and 80,000 IU vitamin D₃.

³The composition is calculated on proportion of each ingredient during the whole experiment. The proportion of each ingredient was constant during the experiment. For corn silage, the 4 different silos had to be used sequentially to feed all cows during the whole experimentation.

⁴UFL = French forage units for NE_L (unité fourragère lait), 1 UFL = 7.1 MJ (INRA, 2010).

⁵PDIN = protein digested in the small intestine supplied by rumen-undegraded dietary protein and by microbial protein from rumen-degraded dietary nitrogen (INRA, 2010).

⁶PDIE = protein digested in the small intestine supplied by rumen-undegraded dietary protein and by microbial protein from rumen-fermented OM (INRA, 2010).

where MNE represented net energy in milk in megajoules of NE per day, MY is the milk yield in kilograms per day, MFC is the milk fat concentration in grams per kilogram, and MPC is the milk protein concentration in grams per kilogram.

Body weight was measured after each morning milking using an automatic electronic scale. Body condition was scored on a scale from 0 for an emaciated cow to 5 for a fat cow, with 0.25-unit increments (Bazin, 1984). At Méjusse farm, body condition score is routinely assessed monthly, including the dry period, by the same 3 trained and experienced scorers who regularly do a recalibration training. Average BCS of the 3 scorers was used. These values were then smoothed using a cubic spline using measuring days as the knots to interpolate daily BCS. The last BCS done during the dry period and the BCS done after experiment end were added to the data to improve the smoothing quality at lactation start and after the 238 DIM. The difference between BCS of 2 consecutive days was defined as daily BCS loss when the difference was negative and daily BCS gain when the difference was positive.

Calculation of Repeatable Feed Efficiency.

Building heritable RFI requires at least a repeatable RFI to identify cows repeatedly more efficient throughout time. Indeed cows repeatedly more efficient throughout time are also cows more efficient on average over a long period. Feed efficiency was therefore estimated over whole experimental period using averaged data. Feed efficiency variability was therefore calculated using REI over almost the whole lactation period (i.e., first 238 DIM) using variables either averaged or summed over this period. Given the 2-mo offset of calving date and the 4 silo changes for maize silage during experimentation, diet quality changed throughout lactation. Intake was therefore expressed in net energy and not in DM to avoid biasing intake estimation due to a variable diet quality throughout lactation. A linear multiple regression regressed the whole experimental period average of net energy intake (NEI) on the main energy expenditure traits calculated over the whole experimental period as follows: MNE average, metabolic BW average, body reserves loss and gain. Body reserves loss was estimated with the sum of daily BCS loss multiplied by the BW average, and conversely, body reserves gain was defined as the sum of daily BCS gain multiplied by BW average. This multiplication by BW was to correct BCS change for body size differences between cows that may exist for a given BCS change. Body reserves change was split in loss and gain because gaining body reserves expends more than the energy supply associated with the corresponding loss of body reserves (Chilliard et al., 1987). The cost for body reserves gain and released energy for body reserves loss are higher for adipose

tissue than for protein. Because primiparous-cow feed efficiency appears associated with growth requirements (Hardie et al., 2017), a parity effect was added to the model as an interaction with body reserves gain and loss to distinguish a slope for primiparous and multiparous cows. However, the slopes were not significantly different between primiparous and multiparous cows ($P = 0.61$ for body reserves loss slope and $P = 0.25$ for body reserves gain slope) and were therefore not kept in the model. Residual energy intake was expressed in the French energy system (INRA, 2010), UFL, and converted into the megajoules unit of net energy and calculated as residuals of the following model using the lm function in R (R Core Team, 2013):

$$\text{NEI} = \mu + a \times \text{MNE} + b \times (\text{BW}^{0.75}) + c \times (\text{BW} \times \Delta\text{BCS}^+) + d \times (\text{BW} \times \Delta\text{BCS}^-) + \text{REI}, [2]$$

where NEI represented net energy intake in megajoules of NE per day; μ is the intercept; MNE is the milk net energy in megajoules of NE per day; ΔBCS^+ is the gain of body condition score over the whole experimental period; ΔBCS^- is the loss of body condition score over the whole experimental period; REI is the residuals; and a , b , c , and d are the regression coefficients.

A final objective was to create efficiency groups of cows to compare them for the recorded biological traits. The most and the least efficient cows were identified using the 20% extreme (± 1.5 SD from mean REI of zero): the 10% most efficient were the 6 cows that had the lowest REI and the 10% least efficient were the 6 cows that had the highest REI. The remaining 80% were considered as the medium group. These 3 groups were compared for all measured phenotypes using an ANOVA performed with the Anova function of package car in R (R Core Team, 2013).

Biological Traits Measured as Potential Determinants of REI

The objective was to identify potential biological traits associated with REI estimated over almost the whole lactation (238 DIM) and that could then be potential indirect indicators of feed efficiency to include in the EBV index. These biological traits were described using variables calculated over the long-term period, 238 DIM, and not over shorter periods of lactation with repeated estimations. As for REI, this long-term period was required to identify repeatable characteristics of the cows and not characteristics having only effects on short-term feed efficiency. The recorded characters were divided into 8 biological traits: milk yield expenditure, maintenance, digestibility, body reserves change, rumen

temperature, feeding behavior, unidentified behavior, and physical activity. Phenotypes measured and calculated variables within each of these 8 biological traits are described below.

Milk Yield Expenditure. Lactation expenditure was described by 2 variables: lactation energy outputs, defined as MNE (model 1 above), and milk lactose concentration. Lactose was measured for one milking each week and was averaged per cow over the whole experimental period.

Maintenance. Maintenance expenditure was approached using 2 variables referring to body size and body composition to assess possible differences in maintenance cost of lean and fat mass: average metabolic BW and average BCS, both calculated over whole experimental period.

Digestibility. Digestibility was measured for 2 consecutive 14-d periods during the second half of lactation with a minimum of 150 DIM, and at the same calendar date for all cows to compare digestibility of cows fed with a diet having exactly the same ingredients and thus the same composition and digestibility. Average digestibility calculated across both periods was used as proxy of apparent DM digestibility. To measure DM digestibility, the reference method needs the measurement of DM excreted in feces, which requires total and individual feces collection over several days. Using total feces collection was therefore not adapted for a large population. An indirect method, described by Delagarde et al. (2010), usually used to estimate DM intake for grazing cows, was thus used to estimate DM fecal output. An indigestible marker, ytterbium (YbCl_3), was dosed to each cow twice a day in cellulosic stoppers: one in the morning and one in the afternoon over 14 consecutive days. Feces were collected by rectal sampling from each cow before meals, one in the morning and one in the afternoon during the 5 last days of the 14-d drugging period. A representative sample of the 10 fecal samples was taken for each cow. Ytterbium concentration was measured for each representative sample. Excreted DM in feces for each cow was calculated as follows:

$$\text{DMfeces}_i = \text{Yb}_i \times [\text{Yb}]_i,$$

where DMfeces_i represents excreted amount of daily DM for cow i ($i = 1-60$ cows), $[\text{Yb}]_i$ is ytterbium concentration in the representative sample of feces for cow i in milligrams per gram, and Yb_i is daily amount of dosed ytterbium for cow i in milligrams per day.

Body Reserves Change. Body reserves change was described with the variables included in the initial model used to estimate REI, BCS loss, and BCS

Figure 1. Curves of BCS for 2 cows throughout the lactation with one cow having 1 inflexion point (—) and one cow having 7 inflexion points (—). Each inflexion point is represented with an arrow.

gain multiplied by average BW and was also described by glucose and nonesterified fatty acid concentration in blood. From calving until the end of the experiment, caudal blood samples were collected 2 wk after calving and then every 4 wk to measure glucose and nonesterified fatty acid concentrations. Glucose and nonesterified fatty acid concentrations were averaged for each cow over the whole experimental period. Assuming that the way a cow mobilizes or accretes body reserves throughout lactation could affect NEI use, the number of inflexion points in BCS kinetic throughout the whole experimental period was calculated. To better understand how the number of inflexion points was estimated, 2 examples are given in Figure 1. In the end, body reserves change included 5 variables.

Rumen Temperature. Each cow had a SanPhone, which is a reticulorumen thermobolus (Medria, Châteaubourg, France, Timsit et al., 2011), during the entire experimental period. This thermobolus recorded rumen temperature every 5 min. Data outputs included 2 distinct temperatures: raw temperature and a drink-corrected temperature (Figure 2). Raw temperature decreases each time the cow drinks water. Drink-corrected temperature was the raw temperature corrected for these drinking effects, such that corrected temperature reflected body core temperature. For both temperatures, the whole experimental period average was calculated for each cow, resulting in 2 variables: one for the corrected temperature and one for the raw temperature. In the same way, the standard deviation of the daily rumen temperature was calculated for both

Figure 2. Daily kinetics of a given lactating dairy cow for a given day of raw rumen temperature (—) and of drinking-corrected rumen temperature (---). Each drinking begins at a decrease in raw rumen temperature (arrows).

temperatures to reflect the daily variation of the rumen temperature. In the end, rumen temperature trait included 4 variables.

Activity, Feeding Behavior, and Unidentified Activity. Each cow was equipped with the Medria Axel logger (Medria), which is an activity logger, placed on the neck. This logger was validated for eating and ruminating behavior on a collective feed trough using a diet similar to the one used in the present study (Delagarde and Lemonnier, 2015). This logger records standing or lying activity and 5 different behaviors: eating, ruminating, resting, overactivity, and unidentified activity. Unidentified activity refers to all activities that are not eating, ruminating, resting, or overactivity. Every 5 min the logger attributed these 5 min to the most dominant behavior out of the 5 recorded and also attributed these 5 min to the dominant position between standing and lying. For each behavior and for standing, the time spent daily was summed per day per cow and then averaged per cow over the whole experimental period. Additionally, to detect possible pattern differences for a given behavior between efficiency groups, for each of the daily 24 h, the hourly time spent on each behavior and on standing was calculated and averaged per cow over the whole experimental period. Additional information collected by the logger was the average intensity of unidentified activity and of overactivity every 5 min. This intensity was scored between 0 for a null activity and 10 for a high activity, with 1-unit increments. Both of these intensity variables were also averaged per cow over the whole experimental period.

Considering eating, ruminating, standing, and resting, each behavior was described by the 24 variables describing the 24 h of a day and by the daily total duration, which results in 25 variables per behavior.

Considering overactivity and unidentified activity, they both have one more variable that is the average score of activity, which results in 26 variables per behavior. In the end, the feeding behavior trait included 50 variables (25 for eating + 25 for ruminating), the activity trait included 76 variables (25 for standing + 25 for resting + 26 for overactivity), and the unidentified activity trait included 26 variables.

Calculating Determinants Contribution to REI and to NEI

To identify the most relevant variables to explain REI, a linear regression of REI was fitted on the previously described variables. A partial least squares regression (PLSr) was preferred in this case as opposed to a classic linear regression because PLSr is more effective and particularly relevant to fit linear regression for numerous and potentially correlated independent variables (Wold et al., 1984; Höskuldsson, 1988), such as in the present study. Indeed PLSr builds new orthogonal variables, called latent variables, from the original variables. This way PLSr reduces the number of independent variables. Then an ordinary linear least squares regression is fitted on these latent variables. The PLSr was fitted using the function `plsrf` of package `pls` in R (R Core Team, 2013). All potential variables, including the 4 used in model 2 to estimate REI, resulting in a total of 167 variables, were included in PLSr. To identify the biological traits that were the most relevant to explain REI variability, the variable selection procedure proposed by Lê Cao et al. (2011) for PLSr was used to select the most stable variables. This methodology is developed in 3 steps: first, by selecting the number of latent variables, then by estimating the

stability of the original variables, and finally by selecting which of these original variables are to be kept in PLSr. The number of latent variables is defined as the number of latent variables minimizing the root mean squared error of prediction (**RMSEP**). This error of prediction was defined as the average RMSEP from 30 cross-validations; each calibration was carried out on 50 different cows and validated on the 10 remaining cows (these 10 cows are different at each cross-validation). In the present study, RMSEP was minimal with 4 latent variables (Figure 3A). The stability of the original 167 variables used to explain REI variability was estimated using 2,500 PLSr, with each fitted on a permutation of REI values. The original variables were then added to PLSr, one at a time, according to their stability order. In the end we kept 27 original variables because this number minimized the cross-validation RMSEP (Figure 3B).

The estimation of the contribution of each of the 8 biological traits to NEI variability was made in 2 steps: one to estimate the contribution to NEI variability of the 4 variables included in model 2 and one to estimate the contribution to REI variability of each of the 8 biological traits (milk yield expenditure, maintenance, digestibility, body reserves change, rumen temperature, activity, feeding behavior, and unidentified activity) defined in the previous section. The contribution of a given trait to NEI or REI variability was calculated as the part of NEI or REI variability that was explained by the variability of this given trait in the model. By definition, the contribution of a given trait to NEI or REI variability was calculated as the sum of the variance of this trait and of each of the covariance of this

trait with the 7 other biological traits. For example contribution of maintenance trait to REI variability was calculated as follows and expressed as a percentage:

$$\text{contrib}_{\text{Maint}} = \text{contrib}\left(a \times \text{BW}^{0.75} + b \times \text{BCS}\right) = \left[\frac{\text{var}\left(a \times \text{BW}^{0.75} + b \times \text{BCS}\right)}{\text{var}(\text{REI})} + \frac{\sum_{i=1}^7 \text{cov}\left(a \times \text{BW}^{0.75} + b \times \text{BCS}, \text{Trait}_i\right)}{\text{var}(\text{REI})} \right] \times 100,$$

where $\text{contrib}_{\text{Maint}}$ represents maintenance contribution to REI variability, a and b are the slopes for the variables $\text{BW}^{0.75}$ and BCS in the PLSr, var is the variance, cov is the covariance, and Trait_i is trait i ($i = 1-7$ other biological traits in the model).

A final step was to check whether the estimated contributions to NEI variability of the 4 traits included in model 2 are relevant. The contributions of MNE, metabolic BW, and body reserves change to NEI variability estimated with model 2 coefficients were compared with the contributions calculated using the reference coefficients for MNE, metabolic BW, and body reserves change published by INRA (2010). The standard coefficients published by INRA (2010) are 1 for MNE and 0.045 for metabolic BW. These reference coefficients were used to estimate net energy required in the current population for milk production and metabolic BW. INRA (2010) does not provide reference coefficients for body reserves gain and loss. The reference coefficients for body reserves gain and loss were therefore

Figure 3. Evolution of the root mean squared error of prediction (RMSEP) (A) according to the number of latent variables kept in the partial least squares regression (PLSr) and (B) after selecting the right number of latent variables, according to the number of input variables kept in the PLSr to build the latent variables. The black diamond is the minimum RMSEP on both graphs, for a population including 60 lactating dairy cows. NE = net energy. Error bars represent SD of the RMSEP across 2,500 PLSr, with each PLSr run on a different permutation of the variable to explain.

Figure 4. Contribution of each biological trait averaged over the 238-DIM period and measured on 60 lactating dairy cows to net energy intake (NEI) averaged over the 238-DIM period and feed efficiency measured with residual energy intake (REI) averaged over the 238-DIM period.

the coefficients estimated in the linear model explaining the difference between NEI and the NE for both milk production and metabolic BW according to both $\Delta\text{BCS}^+ \times \text{BW}$ and $\Delta\text{BCS}^- \times \text{BW}$. The contributions of MNE, metabolic BW, and body reserves change were estimated as explained above using the aforementioned INRA (2010) reference coefficients. The contributions estimated with the INRA (2010) reference coefficients were compared with the contributions estimated with the coefficients obtained in the current study in model 2.

RESULTS AND DISCUSSION

Multitraits Contribution to REI Variability

The model used to estimate REI explained NEI variability with a coefficient of determination of 93.6% and a residual standard error of 4.6 MJ of NE/d (Figure 4). The PLSr model used to explain the 6.4% residual variance of NEI (i.e., REI) explained 58.9% of the observed variation of REI with a RMSEP of 3.6 MJ of NE/d (Figure 5). In a similar approach in beef steers, Richardson and Herd (2004) achieved to explain 52% of RFI variability when using a multitraits model. Moreover, they estimated that the biological traits that they could not include in the model such as activity, feeding patterns, and heat increment of fermentation accounted for additional 21% RFI variability. Because species are different in both studies, the results are not comparable.

Figure 5. Relationship between observed residual energy intake (REI) and REI predicted (predicted REI) from a partial least squares regression fitted over rumen temperature, digestibility, feeding behavior, activity, and body reserves change traits. The data set included 60 lactating dairy cows. The first bisector is shown with a dotted line, and the least squares regression line is shown with a solid line. NE = net energy.

The 58.9% of REI variability were explained by the 27 variables selected by the procedure (Table 3 and Figure 6), which included 6 biological traits: activity accounted for 26.5%; feeding behavior for 21.3%; other behavior for 10.6%; and overall body reserves change, rumen temperature, and digestibility for 0.5% of REI variability (Figure 4). In beef steers, Richardson and Herd (2004) also found that activity, feeding behavior, and digestibility explained part of RFI variability: 10% for activity, 10% for digestibility, and 2% for feeding patterns. The remaining explained part in their study

was explained by protein turnover and metabolism for 37.7%, heat fermentation for 9%, and body composition for 5%. However, as suggested by Richardson and Herd (2004) regarding their results, which is also valid for the present study, a major limit of the estimated contribution is the use of indirect and sometimes not accurate enough methods to estimate the variability of each determinant.

The contribution of each measured trait will be discussed in the following sections, as well as their interaction with other measured traits.

Table 3. Comparison of efficient (L-REI, 6 cows), medium (48 cows), and inefficient (H-REI, 6 cows) groups of cows based on net energy intake (NEI), residual energy intake (REI), and the potential determinants of feed efficiency¹

Variable ²	REI groups			SEM	P-value ³	r	P-value ⁴	Select ⁵
	L-REI	Medium	H-REI					
DMI (kg/d)	19.4 ^a	21.7 ^{ab}	23.3 ^b	2.55	0.034	0.25	0.050	NA
NEI (MJ of NE/d)	129 ^a	144 ^{ab}	155 ^b	17.1	0.035	0.25	0.052	NA
REI (MJ of NE/d)	-8 ^a	0 ^b	8 ^c	2.8	0.000	1.00	0.000	NA
Milk yield (kg/d)	28.1	31.1	30.9	4.8	0.379	0.02	0.854	NA
Milk fat yield (g/d)	1,067	1,156	1,156	199	0.581	-0.03	0.827	NA
Milk protein yield (g/d)	879	953	961	136	0.438	0.04	0.776	NA
Primiparous cows (no.)	3	26	1	NA	0.22 ⁶	NA	NA	NA
Potential determinants								
MNE (MJ of NE/d)	86	94	94	14.0	0.438	0.00	1.000	No
Milk lactose (g/kg)	48.1	49.2	48.9	1.7	0.652	0.12	0.375	No
BW (kg)	615	621	645	71	0.703	0.00	0.987	No
BCS	2.24	2.03	2.07	0.31	0.298	-0.08	0.552	No
BCS_loss	0.4	0.4	0.4	0.22	0.992	0.02	0.885	No
BCS_gain	0.8	0.7	0.9	0.31	0.354	-0.01	0.956	No
Nbr_BCSchange	4.8	4.8	3.8	1.56	0.375	-0.30	0.021	Yes
Blood glucose (mg/dL)	79.2	81.0	81.0	3.8	0.580	0.10	0.446	No
Blood NEFA (μmol/L)	212	245	186	78	0.168	-0.07	0.594	No
DM digestibility (kg of DM/kg of DM)	0.73	0.72	0.70	0.020	0.076	-0.26	0.049	Yes
SDTempcor (°C)	0.20 ^a	0.22 ^{ab}	0.24 ^b	0.031	0.042	0.36	0.004	Yes
MeanTempcor (°C)	39.1	39.2	39.2	0.13	0.193	0.21	0.116	No
SDTemp (°C)	1.39	1.47	1.42	0.12	0.561	0.13	0.319	No
MeanTemp (°C)	38.6	38.6	38.6	0.13	0.885	0.01	0.930	No
Time_eating (min/d)	172	148	128	40.2	0.164	-0.39	0.002	Yes
Time_rum (min/d)	529 ^{ab}	528 ^b	485 ^a	33.8	0.016	-0.23	0.083	Yes
Time_other (min/d)	187 ^a	208 ^{ab}	228 ^b	28.3	0.051	0.50	0.000	Yes
Mean_otheract	0.19	0.22	0.24	0.045	0.164	0.36	0.004	Yes
Time_resting (min/d)	443	439	467	35.5	0.202	0.08	0.568	No
Time_overact (min/d)	106	115	130	19.6	0.097	0.33	0.010	No
Mean_overact	0.13	0.14	0.16	0.034	0.448	0.24	0.060	No
Time_stand (min/d)	867	867	881	15.0	0.079	0.30	0.021	No

^{a-c}Means within a row with different superscripts differ ($P < 0.05$).

¹Pearson correlation (r) between each variable and REI and variables selected by partial least squares regression (PLSr) procedure (Select) are also indicated.

²MNE = milk net energy; BCS was scored from 0 for emaciated to 5 for fat cow, with 0.25-unit increments; Nbr_BCSchange = number of inflexion points in BCS kinetic throughout the 238-DIM period; NEFA = blood concentration of nonesterified fatty acids; SDTempcor = SD of the daily corrected rumen temperature; MeanTempcor = average rumen temperature corrected for drinking; Time_eating = time spent eating daily; Time_rum = time spent ruminating daily; Time_resting = time spent resting daily; Time_overact = time spent in overactivity daily; Time_other = time spent doing unidentified activity, different from eating, ruminating, resting, or overactivity; Time_stand = time spent standing daily; Mean_otheract = average score for unidentified activity intensity going from 0 for no activity to 10, with 1-unit increments; Mean_overact = average score for overactivity intensity going from 0 for no activity to 10, with 1-unit increments.

³P-value from ANOVA of REI from the 3-groups comparison.

⁴P-value associated with Pearson correlation between the variable and REI.

⁵NA = not adapted because was either the dependent variable of the PLSr or used to calculate NEI; No = variable not selected in the PLSr; Yes = variable selected in the PLSr.

⁶P-value estimated using a chi-squared test.

Digestibility

Digestibility was negatively correlated ($r = -0.26$, $P = 0.05$; Table 3) with REI, meaning that the higher the DM digestibility, the lower the REI, that is, the higher the feed efficiency. The square of this correlation was 0.068, which means that when digestibility was taken aside to explain REI, it accounted for 6.8% of REI variability. This contribution was constant and slightly

lower than those cited in literature. Potts et al. (2017) estimated that DM digestibility contributed between 9 and 31% to RFI variability among dairy cows, and Richardson et al. (2004) reported a 19% contribution to RFI variability in beef cattle. The 10% most efficient cows in the present study had a 0.03 higher DM digestibility compared with the 10% least efficient cows ($P = 0.08$, Table 3). In lactating dairy cows, Rius et al. (2012) observed that the 8 most efficient cows fed on an

Figure 6. Averaged kinetic of behavior and standing pattern throughout 24 h. Three groups were built: one with the 10% most efficient (▲ = efficient, 6 cows), one with the 10% least efficient (▼ = inefficient, 6 cows), and one with the rest (◆ medium, 48 cows) of the lactating dairy cows. ^{a,b}Groups having different letters for the same hour are significantly different at $P < 0.05$. The asterisks indicate the hours of the variable that were selected by the partial least squares procedure to explain the residual energy intake. The dark gray rectangles are for hours when cows have no access to feed, and the light gray rectangles are for hours when cows are locked at the feed fence. Color version available online.

energy-rich pasture diet had a higher digestibility than the 8 least efficient cows (78.5 vs. 77.3%, $P = 0.07$). In other species, some studies showed similar relationships, with the most efficient animals having a higher DM digestibility (Nkrumah et al., 2006; Krueger et al., 2009, in steers; Mauch et al., 2015, in pigs). However, other studies were not able to prove this relationship (Fitzsimons et al., 2014; McDonnell et al., 2016, in beef; Montagne et al., 2014, in pigs). For a given species, diets and methods used to estimate digestibility were not similar between all studies and may explain why the results diverged. Indeed studies carried out by Mauch et al. (2015) on pigs and Potts et al. (2017) on dairy cows showed that the relationship between feed efficiency and digestibility was more significant for diets that are more difficult for animals to digest, such as high fiber diets in pigs or in dairy cows. When fed on a low starch diet, the most efficient cows had 2-points-higher digestibility than the least efficient cows (64.2 vs. 62.4%, $P < 0.05$), whereas the 1-point-higher digestibility was not significant when animals were fed on a high starch diet (Potts et al., 2017).

The aforementioned contribution to REI variability was weak and fell to almost 0% when all other variables were included in the PLSr to explain REI (Figure 4). When all biological traits associated with behavior and activity were excluded from PLSr, DM digestibility contributed only to 2.8% of REI variability. This contribution increase from 0 to 2.8% suggested apparent confounded effects between DM digestibility and behavior traits, especially with feeding patterns, even if the correlations between DM digestibility and feeding behavior traits were weak (Table 4). This confounding may highlight that the other biological traits measured may either contribute to or be the consequence of DM digestibility, which suggests that digestibility may be involved in REI differences between cows. Numerous studies have also observed a relationship between DM digestibility and feeding patterns in cattle (Shabi et al., 1999; Connor et al., 2012; Fitzsimons et al., 2014), where more frequent meals (Shabi et al., 1999) or lower eating rate (Connor et al., 2012; Fitzsimons et al., 2014) were associated with higher DM digestibility. A hypothesis could be that having lower eating rate or more frequent meals could increase comminution efficiency and thus increase digestibility. Further investigation is needed to better understand the causal relationship between behavior pattern and DM digestibility, especially looking at the effect of meals frequency, intake rate, and comminution efficiency on digestibility and feed efficiency.

The weak contribution of DM digestibility to REI variability observed in the present study in comparison with literature is probably due to use of a method more adapted to identify extreme cows and not adapted

Table 4. Variance and correlation matrix of the measured traits, calculated as averages of the 238 DIM, for the population of 60 Holstein cows¹

Trait ²	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.
1. DM digestibility (%)	0.00042															
2. SDTempcor (°C)	-0.20	0.0011														
3. MeanTempcor (°C)	-0.13	0.51	0.011													
4. Mean_other (min/d)	-0.06	0.13	0.05	0.0021												
5. Mean_overact (min/d)	-0.16	0.26	0.23	0.71	0.0012											
6. Time_eating (min/d)	0.16	-0.34	-0.24	-0.74	-0.75	1.661										
7. Time_rum (min/d)	-0.04	0.01	0.02	0.21	0.30	-0.19	1.272									
8. Time_resting (min/d)	0.09	0.02	-0.03	-0.41	-0.46	0.16	-0.87	1.285								
9. Time_overact (min/d)	-0.20	0.32	0.30	0.56	0.93	-0.77	0.11	-0.27	404							
10. Time_other (min/d)	-0.14	0.21	0.14	0.89	0.60	-0.84	0.03	-0.21	0.57	857						
11. Time_stand (min/d)	-0.11	0.18	0.23	0.15	-0.02	-0.01	-0.37	0.22	0.01	0.19	239					
12. Glucose (mg/dL)	0.26	-0.29	-0.23	0.18	-0.05	-0.03	-0.16	-0.01	-0.05	0.30	0.03	14.2				
13. NEFA (μmol/L)	0.04	0.11	-0.08	0.32	0.21	-0.33	0.38	-0.27	0.10	0.26	-0.20	-0.13	6.275			
14. Nbr_BCSchange	-0.02	0.16	0.13	0.20	0.25	-0.06	0.20	-0.25	0.13	0.07	0.01	0.06	-0.03	2.4		
15. Milk lactose (g/kg)	0.22	-0.07	-0.03	0.17	0.02	-0.06	0.04	-0.21	0.04	0.27	-0.08	0.53	-0.04	0.10	2.8	
16. BW (kg)	-0.10	-0.12	-0.08	-0.32	-0.29	0.27	-0.20	0.38	-0.27	-0.40	0.10	-0.37	-0.26	-0.31	-0.51	4.889

¹The Pearson correlations are below the diagonal and the variances are on the diagonal.

²SDTempcor = SD of the daily rumen temperature; MeanTempcor = average rumen temperature corrected for drinking effect; Mean_other = average score for unidentified activity (score from 0 for no activity to 10 for highest unidentified activity); Mean_overact = average score for overactivity (score from 0 for no activity to 10 for highest unidentified activity); Time_eating = average of daily time spent eating; Time_rum = average of daily time spent ruminating; Time_resting = average of daily time spent resting; Time_overact = average of daily time spent in overactivity; Time_other = average of daily time spent in unidentified activity; Time_stand = average of daily time spent standing; glucose = blood concentration of glucose; NEFA = blood concentration of nonesterified fatty acids; Nbr_BCSchange = number of inflexion points in BCS kinetic throughout the 238-DIM period.

and accurate enough to measure between-cow differences. The strength of the relationship between DM digestibility and RFI was observed in literature to be dependent on diet fiber and starch contents, with a higher correlation when diet is high in fiber and low in starch contents (McDonnell et al., 2016; Potts et al., 2017). Diet fiber and starch contents has therefore to be considered when analyzing DM digestibility differences across animals. Dry matter digestibility differences across animals may explain feed efficiency differences when cows are fed diets with higher fiber and lower starch contents (Potts et al., 2017). The small variability of DM digestibility across cows observed in the current study may therefore be due to high starch and low fiber contents of the diet. Contribution of DM digestibility to REI variability might have been bigger if the diet would have had higher fiber and lower starch contents. In an extra methodological study with 16 cows fed on the same diet as in current experiment, our indirect ytterbium method provided a between-cow coefficient of variation of DM digestibility of 0.04, which was 2.4 times higher than coefficient of variation of the total-feces-collection method (R. Delagarde, A. Fischer, L. Denouel, and P. Faverdin, PEGASE, Agrocampus-Ouest, INRA, Saint-Gilles, France; unpublished data). These results suggest that this indirect method would only be able to identify the 6% highest and 6% lowest digestibilities. Considering the 2.4 higher coefficient of variation for our indirect method, the 0.03 DM digestibility difference between the least and the most efficient cows (Table 3) may in reality only be about 0.013. This digestibility difference is consistent with the 0.01 difference observed by Rius et al. (2012). A second limit of using and interpreting individual DM digestibility data is that measurement repeatability throughout lactation is not well established, even for the total-feces-collection method, especially because the methods are not adapted for frequent measures.

Feeding Behavior and Rumen Temperature

Time spent eating and ruminating accounted for 21.3% of REI variability (Figure 4) with a negative relationship between REI and both of these activities. The more time the cow spent eating ($P = 0.002$, Table 3) and ruminating ($P < 0.1$, Table 3), the more efficient the cow was. The relationship between REI and time spent eating observed in the present study was at odds with results recorded in literature on other species. Indeed most papers in beef cattle (Nkrumah et al., 2006; Fitzsimons et al., 2014; McGee et al., 2014), in pigs (Meunier-Salaün et al., 2014), and in poultry (Xu et al., 2016) reported a positive and strong relationship between RFI and time spent eating. In dairy cows

this relationship is more contested, with some studies showing a strong and positive relationship ($r = 0.58$ in Xi et al., 2016) and others reporting a weak correlation ($r = -0.04$ in Connor et al., 2013). The positive and strong relationship they found in growing animals compared with dairy cows indicated that the more time animals spent eating on a daily basis, the less efficient they were. This relationship suggested that the most efficient animals need less time to eat less feed, especially because for similar energy requirements, the most efficient animals eat less than the least efficient ones. Indeed, this hypothesis is especially valid in growing animals where DM intake and eating duration are positively correlated with each other (Hyun and Ellis, 2001; Do et al., 2013, in pigs and McGee et al., 2014, in beef cattle); DM intake and eating duration are weakly correlated in lactating dairy cows (Rook and Huckle, 1996). In dairy cows the weak relationship between RFI and time spent eating may hide animal differences in eating rate, as suggested by the positive correlation of 0.56 between DM intake and eating rate (Kelly et al., 2010). Because the relationship between eating time and RFI is more contested in dairy cows, it is difficult to draw a conclusion about the relevance of the correlation found in the present study. This variation of relationship observed in literature might also be due to the variation of experimental design, making the results difficult to compare across studies.

The different relationship between REI and eating duration, when comparing the present study with literature or even across literature in dairy cows, may also be explained by the diversity of feeding management. Relationships involving feeding behaviors are highly dependent on feeding management (Jarrige et al., 1995). The particular configuration we had on farm may have forced the cows to eat within the 2.5 h when they were locked in the feeding trough (Figure 6), which may result in individual behavior different from free access to feed, usually reported in literature. All these interpretations assumed that the logger had correctly characterized eating behavior. However, the differing results between the present study and literature studies using video recording for eating behavior suggested that the logger used in the present study may have had difficulty fully characterizing eating behavior. This could explain why the relationship between time spent eating and REI was not the same as in literature. Time spent eating was 149 min daily (Table 5) in the present study, which was lower compared with 300 min in DeVries et al. (2005) using video recording or between 211 min (Connor et al., 2013) and 266 min (Schirrmann et al., 2012) when using automatic devices. Individual feed troughs used in the present study were different from a traditional collective trough that was used for

Table 5. Mean, SD, minimum, and maximum of averaged variables (60 Holstein cows) included in the feed efficiency model (REI model component) and of the potential determinants of feed efficiency (Determinants)

Variable ¹	Mean	SD	Minimum	Maximum
REI model component				
NEI (MJ of NE/d)	143	17.8	111	182
MNE (MJ of NE/d)	93	14.0	71	122
MY (kg/d)	30.7	4.82	23.4	43.4
MFY (g/d)	1,147	197.5	813	1,568
MPY (g/d)	947	135.7	754	1282
BW ^{0.75} (kg ^{0.75})	125	10.4	103	147
BCS_loss	0.4	0.22	0.0	0.9
BCS_gain	0.7	0.31	0.3	2.0
REI (MJ of NE/d)	0	4.5	-11	11
Determinants				
Milk lactose (g/kg)	49.1	1.67	43.2	52.1
Maintenance				
BCS	2.05	0.32	1.44	3.09
Body reserves change				
Nbr_BCSchange	4.7	1.56	1.0	8.0
Blood NEFA (μmol/L)	236	79.2	119	470
Blood glucose (mg/dL)	80.8	3.76	72.4	87.6
Temperature				
MeanTempcor (°C)	39.2	0.10	39.0	39.4
MeanTempraw (°C)	38.6	0.10	38.4	38.8
SDTempraw (°C)	1.42	0.12	1.12	1.68
SDTempcor (°C)	0.22	0.03	0.15	0.31
Digestibility	0.72	0.020	0.65	0.75
Feeding behavior				
Time_eating (min/d)	149	41	46	239
Time_rum (min/d)	524	36	366	573
Time_resting (min/d)	443	36	375	583
Time_overact (min/d)	116	20	72	172
Time_other (min/d)	208	29	152	303
Time_stand (min/d)	868	15	827	907

¹REI = residual energy intake; NEI = net energy intake; MNE = net energy in milk; MY = milk yield; MFY = milk fat yield; MPY = milk protein yield; BCS was scored from 0 for emaciated to 5 for fat cow, with 0.25-unit increments; Nbr_BCSchange = number of inflexion points in BCS kinetic throughout the 238-DIM period; NEFA = blood concentration of nonesterified fatty acids; MeanTempcor = average rumen temperature corrected for drinking; MeanTempraw = average rumen temperature; SDTempraw = SD of the daily raw rumen temperature; SDTempcor = SD of the daily corrected rumen temperature; Time_eating = time spent eating daily; Time_rum = time spent ruminating daily; Time_resting = time spent resting daily; Time_overact = time spent in overactivity daily; Time_other = time spent doing unidentified activity, different from eating, ruminating, resting, or overactivity; Time_stand = time spent standing daily.

validation (Delagarde and Lemonnier, 2015). Because cows had to open and then keep the trough door open to eat, their eating behavior was different from eating behavior in a traditional collective feed trough. The logger may have missed this aspect of eating behavior and may have attributed it as a unidentified activity. Supposing that part of eating behavior was classified as a unidentified activity, then the positive and significant correlation with REI ($r = 0.50$, $P < 0.001$; Table 3) was coherent with previously cited results from literature about eating duration and RFI. However, when trying to characterize relationship between feed efficiency and feeding behavior on a long-term basis, feeding behavior should also be collected on a long-term basis and not just at a given time point. Automatic devices are therefore better adapted than videotaping or observation methods to give a reliable estimation of between-

cow differences in feeding behavior. In opposition, the measured ruminating durations were consistent with literature studies, using either video recording or loggers. Mean ruminating duration was 524 min/d (Table 5) in the present study, which was similar to literature references where cows spent around 550 min/d ruminating (Schirmann et al., 2012; Clément et al., 2014; Delagarde and Lemonnier, 2015).

The most efficient 10% of cows spent 44 min more time ruminating daily than the least efficient 10% (Table 3). Literature poorly documents the relationship between feed efficiency and ruminating behavior. A potential hypothesis could be that higher ruminating time, characterizing the most efficient cows, may contribute to higher digestibility, thanks to higher comminution efficiency. More studies are required to test the relationship between digestibility and rumination.

In any case, these results and results present in literature suggested that feeding behavior differences between cows were associated with feed efficiency differences. To detect whether feeding behavior was confounded with other biological traits measured in the present study, PLSr explaining REI variability was fitted over all biological traits except those associated with behavior and activity. This PLSr showed that behavior traits absorbed variability associated with DM digestibility, body reserves change, and rumen temperature traits because all these traits increased their contribution from near 0% to 27.8% for rumen temperature, 20.7% for body reserves change, and 2.8% for DM digestibility.

The variability of rumen temperature may reflect variability in heat production. The higher the daily variability of corrected rumen temperature, the higher the REI ($r = 0.36$, Table 3). The most efficient 10% of cows had a less variable daily rumen temperature than the least efficient 10% of cows ($P < 0.05$, Table 3). It can therefore be hypothesized that differences between cows in daily variability of corrected rumen temperature may reflect eating rate and meal size differences, with the most variable temperature being associated with a high eating rate and big meals. The higher the daily variability of rumen temperature ($r = -0.34$, $P < 0.05$; Table 4) and the higher the average rumen temperature ($r = -0.24$, $P = 0.11$; Table 4), the lower the time spent eating on a daily basis. This negative relationship combined with the contribution increase occurring when all biological traits associated with behavior were excluded from PLSr suggested that biological traits associated with rumen temperature may reflect feeding patterns. However, when fitting a linear regression to explain the daily variation of rumen temperature with daily behavior durations, eating, unidentified activity, and standing durations explained only 27.4% of the variability of daily rumen temperature variability. Most of the differences between cows in daily rumen temperature variability may thus reflect other processes, which were not recorded in present study, such as rumen size differences or digestive transit rate differences. Further investigations are needed to validate the negative relationship between REI and daily rumen temperature variability and also to better understand the causal relationship between feeding behavior, daily variability in rumen temperature, and feed efficiency. Both, rumen temperature and feeding behavior, could also be health status indicators. Neither the SCC ($r = 0.11$, $P = 0.40$) nor the number of short-term ($r = 0.08$, $P = 0.57$) and long-term rises ($r = 0.14$, $P = 0.29$) of body core temperature had a significant relationship with REI. However, more animals are required to draw conclusions on the relationship between feed efficiency and health status.

Maintenance and Activity

Differences in metabolic BW between cows, which is an indicator of maintenance requirements, contributed to 23.2% of NEI variability (Figure 4) and did not contribute to REI variability, with a correlation of 0 ($P = 0.99$) between BW and REI and of -0.08 ($P = 0.55$) between BCS and REI. The most efficient cows had a slightly higher BCS and lower BW compared with the other groups (Table 3), and this was observed at any stage of the whole experimental period. However, this tendency was not significant ($P = 0.70$ for BW and $P = 0.30$ for BCS) in the current population and would require investigation on a bigger population. The higher number of primiparous cows in the most efficient group compared with the least efficient group could explain the observed tendency. However, BCS was similar between multiparous and primiparous cows.

The population average level of activity, which is inherent to environmental conditions, is usually included in maintenance requirements estimated with national feeding system requirements (Cannas et al., 2010), whereas activity specific to each cow is not included in maintenance requirements. In the present study, physical activity differences between cows appeared positively correlated with REI; the more time the cow spent standing ($r = 0.30$, $P = 0.02$) or in overactivity ($r = 0.24$, $P = 0.06$), the less efficient the cow was (Table 3). In the present study, activity contributed at 26.5% to REI variability (Figure 4). Average standing time per day recorded in the present study was consistent with standing time observed in literature, which claimed for validity of standing time measurement with the logger used in the present study. Time spent standing was 868 min/d (Table 5), which was comparable to the reference time of 780 min/d observed by De Vries et al. (2005) with video recording and around 700 min/d (Schirrmann et al., 2012) and 900 min/d (Hart et al., 2014) when using loggers. The positive correlations found in the present study between activity traits and REI were also found in steers by Richardson et al. (2004) but were not significant in heifers (Lawrence et al., 2012, $P > 0.05$; Hafla et al., 2013, $P = 0.99$). The significance of this correlation between activity and REI is dependent on environmental factors; activity difference between the most and least efficient heifers was higher and significant ($P < 0.05$) under grazing conditions compared with indoors housing and feeding (Lawrence et al., 2012). This interaction between activity significance and environmental conditions claims activity as a determinant of feed efficiency only in high-activity environments, such as grazing. The question of the place of activity in REI definition, either as an independent variable used to estimate REI or as a

potential determinant of feed efficiency, can be raised. If activity is considered as an independent variable used to estimate REI, energy used for activity is considered as a required expense and not as waste, in the same way as milk energy expenditure or maintenance. In opposition, if energy used for activity is considered as a waste of energy, activity should not be used as an independent variable to estimate REI and should be kept as a determinant of feed efficiency. Place of activity in REI definition has therefore to be analyzed considering farm housing and feeding conditions.

Body Reserves Change

Body reserves change explained 4.9% of NEI variability (Figure 4) in model 2, but model 2 residuals (i.e., REI) still included variability associated with body reserves change because the more frequently BCS changed throughout lactation, the more efficient the cow was ($r = -0.30$, $P = 0.02$, Table 3). In cows with a similar amount of mobilized or gained body reserves throughout lactation, the most efficient seemed to be cows having shorter periods of mobilization or accretion, meaning that BCS change occurring for each period might be smaller for the most efficient cows. Interpretation of small changes in BCS is limited because BCS is not adapted to distinguish small changes occurring on a short-time period. Small changes leading to an inflexion point in the BCS curve may therefore not be true changes in body condition but probably BCS measurement errors. Interpretation of the correlation between REI and the number of BCS changes throughout lactation is therefore limited. A more precise method or one at least adapted for high throughput monitoring, such as using 3-dimensioned pictures (Fischer et al., 2015), needs to be used to validate the correlation between the number of inflexion points in the BCS lactation curve and REI. Further investigation is needed to better characterize the relationship between body reserves change and feed efficiency.

An Apparent Confounding Between the Measured Variables

The total contribution of the measured variables to REI variability was slightly different when all variables associated with behavior and activity were excluded from PLSr. PLSr without behavior and activity variables explained 51.3% of REI variability, with 27.8% for rumen temperature, 20.7% for body reserves change, and 2.8% for digestibility. Rumen temperature was also correlated with digestibility and unidentified activity; the more variable the daily rumen temperature is, the more time the cow spends in unidentified activity ($r =$

0.21, $P = 0.12$, Table 4) and the lower the digestibility ($r = -0.20$, $P = 0.12$, Table 4). These results highlighted apparent confounding effects between activity traits, rumen temperature, and digestibility. However, PLSr excluding behavior and activity traits had a worse cross-validation with a RMSEP of 4.2 MJ of NE/d and a coefficient of determination of 0.10, whereas PLSr including all traits had a RMSEP of 3.6 MJ of NE/d and a coefficient of determination of 0.35. These cross-validation results suggest that PLSr including behavior and activity traits is more reliable than PLSr excluding behavior and activity traits. Apparent confounding effects observed among behavior, activity, rumen temperature, and digestibility make it difficult to make conclusions about the causal relationship between these traits and thus to identify which are determinant of feed efficiency and which are just consequences of other traits. To better characterize the relationship between these traits, the effect of each trait on efficiency should be tested while measuring the other traits. Moreover, all of these results need to be validated on an external population and are only valid with the model used to estimate REI. Indeed, if additional variables were included in the model used to estimate REI, they could no more be considered as potential determinant of REI, because as independent variable in the model, they can no longer explain differences in model residuals (i.e., in REI).

Relevance of Estimated Contributions of Milk Net Energy, Metabolic BW, and Body Reserves Change to NEI Variability

The observed contribution of 23.2% of maintenance to NEI variability using the coefficients of the current study was slightly higher than the contribution of 14.5% calculated using the reference coefficient published in the French feeding system requirements (INRA, 2010). Milk net energy contributed to 65.5% of NEI variability in our study when using our model (Figure 4) and to 70.6% when using INRA (2010) reference coefficients. Body reserves change contributed to 4.9% of NEI variability in our study when using our model (Figure 4) and to 6.8% when using INRA (2010) reference coefficients. These results showed that the estimated contributions of MNE, metabolic BW, and body reserves change to NEI variability were relevant and comparable to the contributions estimated with the reference coefficients in INRA (2010). However, current coefficients estimated a higher contribution of metabolic BW and smaller contribution of MNE to NEI variability than the contributions estimated with the reference coefficients in INRA (2010). This difference highlights that the coefficients estimated in the

current study assigned a higher part of NEI variability to metabolic BW and a smaller to MNE than the INRA (2010) reference coefficients.

CONCLUSIONS

This study measured the individual variability of feed efficiency for lactating dairy cows using REI, which was calculated as NEI corrected for net energy in milk, metabolic BW, and body condition gain and loss. A PLSr was used to explain REI variability with all measured traits. Of all measured traits, feeding patterns, activity, rumen temperature, body reserves change, and digestibility explained 58.9% of REI phenotypic variability, equivalent to 3.8% of NEI phenotypic variability. These 58.9% were mainly explained by activity (26.5%) and feeding behavior (21.3%). However, a confounding effect was observed among behavior, activity, rumen temperature, and digestibility traits. The present results were therefore not sufficient to draw definitive conclusions on the biological determinants of feed efficiency. Further investigation is needed to better characterize the causal relationship between feed efficiency and feeding behavior, digestibility, body reserves change, activity, and rumen temperature. Most of the variables used in the present study were built as whole experimental period averages. However, the high-throughput monitoring used in the present study could also be used to better understand lactation dynamic. Analysis of lactation kinetics of all measured phenotypes is therefore an interesting next step to better understand feed efficiency differences in lactating cows.

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