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Feed efficiency of lactating Holstein cows is repeatable within diet but less reproducible when changing dietary starch and forage concentrations

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ABSTRACT

Improving feed efficiency has become an important target for dairy farmers to produce more milk with fewer feed resources. With decreasing availability of arable land to produce feeds that are edible for human consumption, it will be important to increase the proportion of feeds in the diets for dairy cattle that are less edible for human consumption. The current research analyzed the ability of lactating dairy cows to maintain their feed efficiency when switching between a high starch diet (**HS** diet**:** 27% starch, 29% NDF, 47.1% forages on a DM basis) and a low starch diet (**LS** diet**:** 13% starch, 37% NDF, 66.4% forages on a DM basis). Sixty-two lactating Holstein cows (137 ± 23 days in milk (**DIM**) at the start of experiment), of which 29 were primiparous cows, were utilized in a crossover design with two 70-d experimental periods, including a 14-d adaption period for each. Feed efficiency was estimated as the individual deviation from the population average intercept in a mixed model predicting DM intake (**DMI**) with net energy in milk, maintenance and BW gain and loss. Repeatability was estimated within each diet by comparing feed efficiency estimated over the first 28-day period and the second 28-day period within each diet, using Pearson's and intraclass correlations, and the estimation of error of repeatability. Similarly, reproducibility was estimated by comparing the second 28-day period of one diet with the first 28-day period of the other diet. Feed efficiency was less reproducible across diets than repeatable within the same diet. This was shown by lower intraclass correlations (0.399) across diets compared to that in the HS diet (0.587) and LS diet (0.806), as well as a lower Pearson's correlation coefficient (0.418) across diets compared to that in the HS diet (0.630) and LS diet (0.809). In addition, the estimation of error of repeatability was higher (0.830 kg DM/d) across diets compared to that in the HS diet (0.761 kg DM/d) and LS diet (0.504 kg DM/d). This means that the feed efficiency of dairy cows is more likely to change after a diet change than over subsequent lactation stages. Other determinants, such as digestive processes, need to be further investigated to determine its effects on estimating feed efficiency.

Implications

Improving feed efficiency is key for dairy farmers to maintain their production while using fewer resources, especially by decreasing feeds that are edible for human consumption. This study analyzed the ability of lactating dairy cows to maintain their feed efficiency when changing the dietary starch concentration. Cows were able to maintain their feed efficiency over time when fed the same diet, but fewer cows maintained their efficiency when the diet was changed. These results suggest that feed efficiency should be considered within the same diet to avoid any misidentification of cows as most or least efficient.

Introduction

A promising way for dairy farmers to be more economically viable is to increase the efficiency of used feed resources while reducing their environmental footprint. With an expected increase in the world population of 26% between 2019 and 2050 (United Nations, 2019), diets for livestock may change to comprise more non-human edible feeds. Wilkinson (2011) assumed that 36% of the concentrate mix fed to dairy cows on a DM basis was edible

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by humans. Assuming that the concentrate mix represents about 40–50% of dairy cows' diet DM and forages are not edible by humans, the proportion of a dairy cow diet that could be directly edible by humans would be between 14 and 18%. Dairy cows are key players of this change in feed ingredient usage because of their ability to digest feeds that are not edible by non-ruminant animals, including humans. Dairy producers will need to improve the conversion of feed to milk while also coping with volatile feed prices and feed availability (HLPE, 2011). Consequently, the diets of dairy cows will likely become more variable in the future, using alternative feedstuffs that are not very digestible by non-ruminant animals. The sensitivity to diet composition of the dairy cow's ranking for efficiency, referred to as the interaction between genetics and environment (Hill and Mackay, 2004), needs to be evaluated in order to determine whether some cows perform better and some worse when changing the composition of the diet. Indeed, if feed efficiency is to be included as a genomic selection trait, then feed efficiency has to be reproducible independently of diet and environment.

Very little research has been published with dairy cows addressing whether feed efficiency is reproducible independently of diet and environment. The few studies that have investigated the sensitivity of feed efficiency to diet composition, defined as reproducibility of feed efficiency when changing the diet, observed that reproducibility of feed efficiency was lower compared to the repeatability within the same diet for steers (r = 0.33 vs 0.42; Durunna et al., 2011) and for dairy cows (r = 0.44–0.64 vs 0.53–0.70; Potts et al., 2015). Consequently, animals will not necessarily rank the same for feed efficiency when changing diet composition. One limitation when analyzing repeatability is that the method requires repeated estimation. For dairy lactating cows, this becomes a limitation when evaluating feed efficiency because the optimal duration to estimate lactation feed efficiency is too short to make repeated estimations of feed efficiency. Indeed, in lactating dairy cows, the correlation of short-term period length with full-lactation feed efficiency increases with later lactation stages (Li et al., 2017; Løvendahl et al., 2018; Connor et al., 2019) and longer measurement periods (Connor et al., 2019). By using shorter measurement periods, or evaluating cows in earlier or later lactation stages, the correlation with full-lactation feed efficiency decreases, resulting in a less reliable feed efficiency estimation. For example, the correlation with full-lactation feed efficiency dropped from 0.90 with the recommended period length of 64–70 days to 0.57–0.86 when using a period length of 28 days (Connor et al., 2019). Their recommended lactation stage is between 150 and 220 days in milk (**DIM**). These results suggest that the optimal duration to measure feed efficiency, and consequently, to estimate its repeatability and reproducibility, is in the middle of the lactation (between 150 and 220 DIM) for a length of 64–70 days. This length limits the number of repetitions that could be measured within a lactation and results in the repeatability and effect of diet on feed efficiency being more difficult to study.

For research and breeding companies, feed efficiency is usually defined with residual feed intake (**RFI**) as the difference between animal's actual and expected intake (Koch et al., 1963). An animal with a positive RFI eats more than expected, and is, consequently, less efficient than expected. Conversely, an animal with a negative RFI is an animal that is more efficient than expected because it eats less than expected. Residual feed intake is defined as the residual of a linear regression estimating actual feed intake from the expected outputs. All energy outputs or inputs explaining differences in DM intake (**DMI**) that are not accounted for in the model contribute to RFI variability. Residual feed intake is often considered a direct indicator of feed efficiency used to analyze the potential of including feed efficiency in genetic selection schemes (Macdonald et al., 2014; Connor, 2015; Pryce et al., 2015) or to understand the biological basis of feed efficiency (Xi et al., 2016; Hardie et al., 2017; Fischer et al., 2018a). However, RFI suffers from its definition as a model residual because its variance also includes model fitting errors, errors of energy intake estimation and measurement errors which represent about 41–49% of RFI variance (Fischer et al., 2018b). To overcome this issue, the part of RFI associated with feed efficiency can be estimated as the random part of RFI, which is supposedly repeatable throughout time and independent from model errors (Fischer et al., 2018b).

Considering the increase of the future human population and the competition of food for humans and feed for dairy cattle, the overall goal for selecting high feed efficiency cows is to select those that are efficient when fed different types of diets, including diets that are less edible for humans. Therefore, the objective of this study was to analyze the effect of dietary starch concentration on the reproducibility of feed efficiency. To do so, this study first estimated the repeatability of feed efficiency when cows were fed within the same diet and then compared this with the reproducibility of feed efficiency before and after the diet change. The main hypothesis was that feed efficiency is repeatable within the same diet, but is less reproducible across different diets.

Material and methods

The experiment was conducted at the U.S. Dairy Forage Research Center Dairy Farm (Prairie du Sac, WI, USA) and initially included 76 lactating Holstein cows. Among those 76 cows, three cows were removed for health reasons and the data of another 11 cows were removed because of technical issues related to accurately estimating their intake. The current study is based on the data of 62 cows (29 primiparous and 33 multiparous cows).

Experimental design

The study was a crossover design starting with a pre-experimental period of 31 days, where all cows were fed the same diet, followed by two experimental periods of 70 days. Within this experimental period, a period of 56 days was used to estimate feed efficiencies within each diet. The remaining 14 days was used for diet transition between periods and was not included to estimate feed efficiency. The cows were assigned to two cohorts based on parity, DMI, milk net energy, BW, body conditional score (**BCS**), BW loss and BW gain over the first 3 weeks of the common diet period. Average DIM was 136 (±23) d for one cohort and 138 (±23) d for the second cohort at the start of the first experimental period. The first cohort started with the HS diet in the first period and then switched over to the LS diet in the second period (cohort **HStoLS**), whereas the second cohort started with LS diet in the first period and then switched over to HS diet in the second period (cohort **LStoHS**, Fig. 1).

The common diet used during the pre-experimental period was formulated to be halfway between both experimental diets and included 27.9% corn silage, 29.0% alfalfa silage, 12.2% high moisture corn, 4.1% roasted soybeans, 5.9% beet pulp, 6.1% soybean hulls, 6.1% canola meal, 6.0% corn distillers grain with soluble and 2.7% minerals and vitamins mix on a DM basis. During the experimental periods, cows were fed either: (1) a diet formulated to be high starch (**HS**) using ingredients commonly used in U.S. dairy cow diets, or (2) a diet formulated to be low starch and high in fiber (**LS**) using ingredients that are less edible for humans (Table 1). The LS diet was formulated to have a lower human edibility potential, focusing on a greater inclusion of forages and fibrous by-products along with the removal of high moisture corn. HS diet had on average a forage-to-concentrate ratio of 47:53, a starch con-

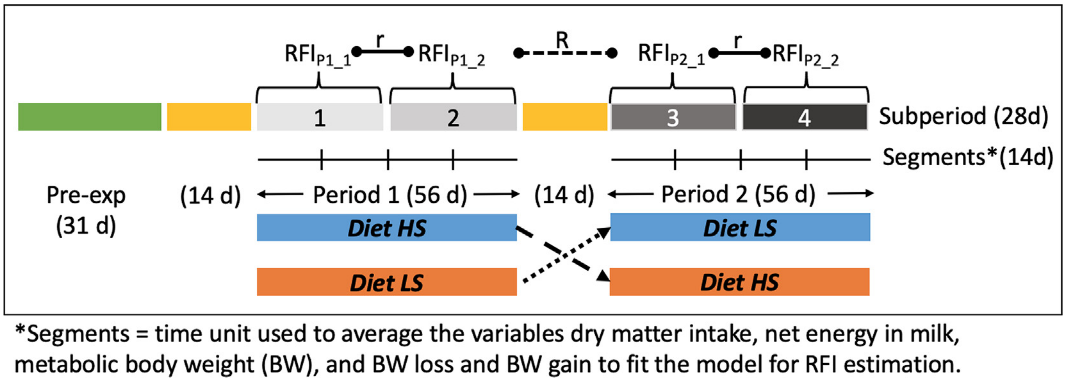

Fig. 1. Diagram of the crossover design used to characterize the repeatability (r) and reproducibility (R) of residual feed intake (RFI) of dairy Holstein cows. Repeatability compares RFI within diet; they are shown with the solid line (●—●). Reproducibility compares RFI across diets; they are shown with the dashed line (●···●). One cohort started with the diet high in starch (HS) and then switched over to the diet low in starch (LS) as shown with the dashed arrow (– – ▶), while the second cohort did the opposite as shown with the dotted arrow (····▶).

Table 1
Composition of both experimental diets (High starch (HS) and low starch (LS)) for both experimental periods (Period 1 and Period 2) and their chemical analysis for dairy Holstein cows.

Items	HS Diet		LS Diet	
	Period 1	Period 2	Period 1	Period 2
Ingredients (% of diet DM ± SD[1])				
Alfalfa silage	24.2 ± 0.66	24.1 ± 0.54	33.9 ± 0.79	33.9 ± 0.66
Corn silage	23.2 ± 0.42	23.0 ± 0.41	32.5 ± 0.59	32.4 ± 0.55
High moisture corn	24.5 ± 0.41	25.0 ± 0.31	0	0
Beet pulp pelleted	2.80 ± 0.04	2.70 ± 0.02	8.90 ± 0.14	8.90 ± 0.11
Canola meal	9.70 ± 0.13	9.80 ± 0.12	2.60 ± 0.05	2.70 ± 0.04
Corn distillers grain	2.70 ± 0.04	2.60 ± 0.03	9.20 ± 0.23	9.20 ± 0.12
Roasted soybean	4.10 ± 0.05	4.00 ± 0.03	4.10 ± 0.06	4.10 ± 0.05
Soybean hulls	6.10 ± 0.08	6.10 ± 0.06	6.10 ± 0.10	6.10 ± 0.09
Mineral and vitamin mix[2]	2.70 ± 0.03	2.70 ± 0.03	2.70 ± 0.04	2.70 ± 0.04
Particle Size (% of diet DM ± SD[1])				
19 mm < size	5.20 ± 1.31	5.10 ± 1.11	10.8 ± 3.25	13.8 ± 0.30
8 < size ≤ 19 mm	42.8 ± 2.70	40.2 ± 0.61	47.2 ± 2.19	49.8 ± 1.22
4 mm < size ≤ 8 mm	14.6 ± 0,27	15.0 ± 0.03	13.7 ± 0.64	13.9 ± 0.26
Size ≤ 4 mm	37.4 ± 1.53	39.7 ± 1.69	28.3 ± 1.22	22.4 ± 1.26
Nutrient composition (% of diet DM ± SD[1])				
DM	50.1 ± 0.51	50.9 ± 0.29	45.1 ± 0.59	45.9 ± 0.39
NDF	29.0 ± 0.29	28.9 ± 0.11	36.9 ± 0.30	36.9 ± 0.12
Forage NDF[3]	61.1 ± 0.50	61.3 ± 0.52	67.2 ± 0.45	67.6 ± 0.40
ADF	21.1 ± 0.14	21.0 ± 0.13	27.5 ± 0.11	27.4 ± 0.16
Lignin	3.0 ± 0.03	3.3 ± 0.12	3.6 ± 0.08	3.9 ± 0.20
Ether extract	4.9 ± 0.22	4.8 ± 0.01	5.1 ± 0.23	5.1 ± 0.06
Ash	5.7 ± 0.10	5.7 ± 0.08	7.4 ± 0.16	7.4 ± 0.16
Starch	26.7 ± 0.29	27.5 ± 0.31	12.8 ± 0.18	13.0 ± 0.27
DEp_4X[4]	2.93 ± 0.01	2.99 ± 0.01	2.87 ± 0.01	2.87 ± 0.01
MEp_4X[4]	2.53 ± 0.01	2.59 ± 0.01	2.47 ± 0.01	2.47 ± 0.01
NE_Lp_4X[4]	1.60 ± 0.01	1.64 ± 0.01	1.56 ± 0.01	1.56 ± 0.004

[1] SDs were calculated using the day-to-day change in offered diet composition.
[2] The mineral and vitamin mix contained (on a DM basis): 16.0% Ca, 5.85% Mg, 0.54% K, 14.8% Na, 6.67% Cl, 0.73% S, 42.5 mg of Co/kg, 519 mg of Cu/kg, 60.2 mg of I/kg, 778 mg of Fe/kg, 2 601 mg of Mn/kg,14.6 mg of Se/kg, 2 808 mg of Zn/kg, 292 kIU of vitamin A/kg, 58.5 kIU of vitamin D/kg, 1.36 kIU of vitamin E/kg, and 0.494 g of monensin/kg (Vita Plus Corporation, Madison, WI).
[3] Forage NDF is reported as a percentage of NDF.
[4] Digestible energy (DEp_4X), metabolizable energy (MEp_4X) and net energy (NE_Lp_4X) at production level were calculated according to NRC (2001) equations, considering that the cows are eating 4 times the maintenance requirements. Those variables were reported in Mcal/kg DM.

centration of 27.1% and NDF concentration of 29.0% on a DM basis. LS Diet had on average a forage-to-concentrate ratio of 66:34, a starch concentration of 12.9% and NDF concentration of 36.9% on a DM basis. All diets were similar for CP and were slightly different in energy content.

Sample collection and analysis

Forages were sampled once a day and concentrates were sampled once a week to measure weekly DM. Feed samples used for DM were dried for 48 h at 55 °C, followed by 24 h at 105 °C. Diets were composited on a DM basis into 4-wk samples for each experimental period. All feed samples were analyzed for nutrient composition according to AOAC (2005) by Dairyland Laboratories Inc. (Arcadia, WI): ash (method 942.05), CP (method 990.03), NDF (method 2002.04), ADF (method 973.18), lignin (method 973.18), ether extract (method 920.39), and starch (method 996.11). Both HS and LS diets were analyzed for particle size using the Penn State Particle Separator with four sieves: 19 mm, 8 mm, 4 mm and the bottom. Each diet was sampled twice per period. The particle size analysis was done twice per sample. Both diets differed in their particle size distribution, with HS diet having fewer long particles and more short particles with 38.6% of particles shorter than 4 mm compared to 25.4% for LS diet, and 5.2% of particles longer than 19 mm compared to 12.3% for LS diet (Table 1).

Cows were housed in tie-stalls and were fed *ad libitum* once a day, adjusting offered feed to allow for 5–10% refusals individually, based on the refusals measured 2 days before. Feed was pushed up into the manger after each milking. Individual as-fed intake was calculated as the difference between offered diet and next morning refusals. Cows were milked three times a day (0400 h, 1030 h and 1800 h), with milk production being recorded at each milking. Milk samples were collected at each milking for two consecutive days per week and analyzed for milk fat, milk protein and lactose with infrared spectroscopy (AgSource, Verona, WI) using a Foss FT6000 instrument (Foss Electric, Hillerød, Denmark) according to methods of AOAC (2005).

Cows were weighed with a scale three consecutive days each week, right after the first morning milking, to be as close as possible to the minimum BW (Peiper et al., 1993), and therefore to the actual empty BW. Body reserve level was monitored once a month with body condition score. Body condition was scored by three trained scorers according to the scale developed by Wildman et al. (1982) going from 1 for an emaciated cow to 5 for a fat cow with a 0.25 unit increment. Scores were averaged per cow and per scoring day.

Data outlier detection

Data quality is essential when estimating feed efficiency. An important step was therefore to identify data outliers. For DMI, days having data associated with technical issues were removed from the dataset. Milk yield and BW data were smoothed with a locally estimated scatterplot (**LOESS**) using the 20% nearest neighbors for BW and 30% closest neighbors for milk yield with the *loess* function in R (R Core Team, 2018). Data were considered as outliers if the value of the day was outside a range of 2 SD for BW and 3 SDs for milk yield of the closest neighbors around the value of the LOESS at this given day. Outlier data were removed from the dataset. Data removed because of technical problems included: one week of BW recorded in period 1 due to scale calibration issues, one week of BW data during period 2 because of scale failure, and 1 day of DMI because of a failure in the automatic data saving process.

Variable calculation to estimate feed efficiency

Estimation of feed efficiency requires DMI data and all energy outputs or inputs to be considered for a lactating dairy cow. Energy outputs include energy in milk, energy required for maintenance, energy gained as adipose tissue and energy required for gestation. Energy input includes body reserve mobilization. DM intake was measured by using the weekly DM value of the diet and multiplying it by the weight of feed intake, corrected by the average weekly DM of refusals of the diet and multiplying the weight of leftover refusals the next morning. Feed intake was measured as the difference between the weight of diet offered and the weight of leftover refusals the next morning.

Milk net energy (**MilkNE**) was calculated according to NRC (2001) equation (2)–(15) below:

$$\text{MilkNE(Mcal of NE\_L/d)} = \text{MProd} \times (0.0929 \times \text{Fat} + 0.0563 \times \text{Protein} + 0.0395 \times \text{Lactose})$$

where MProd is the daily milk production (kg), Fat is the milk fat concentration (%), Protein is the milk true protein concentration (%) and Lactose is the milk lactose concentration (%). Gestation requirements were null if the pregnancy stage was below 190 days and thereafter were estimated according to NRC (2001) equation (2)–(19) with a calf birth weight of 45 kg:

$$\text{gest(Mcal of NE\_L/d)} = \frac{(0.00318 \times \text{day of gestation} - 0.03520)}{0.218}$$

For BW data, we removed the detected outliers from the dataset and smoothed the remaining BW data with a LOESS using the 15% closest neighbors, to better reflect the change in maintenance and not to be sensitive to daily gutfill change. Monthly BCS data were interpolated to get daily BCS using a cubic Spline with the function *smooth.spline* in R using each scoring day as a knot. Maintenance requirements were estimated with the daily metabolic BW (**MBW**), using the smoothed BW data, and calculated as $BW^{0.75}$. Energy gained and energy mobilized as body reserves were estimated as the day-to-day change in smoothed BW, multiplied by the daily BCS. If the BW change was positive, it was attributed to body reserve gain, and body reserve loss was null. Conversely, if the BW change was negative, it was attributed to body reserve mobilization, and body reserve gain was null. Both BW gain and BW loss were constructed to be positive variables. Both BW gain and BW loss were multiplied by daily BCS to account for body reserve differences within a given BW change, resulting in the variables **BWlossBCS** and **BWgainBCS,** respectively.

Estimating feed efficiency

Feed efficiency was estimated as the RFI with the method developed in a previous paper (Fischer et al., 2018b). Instead of being estimated as the residual of the multiple linear regression estimating observed DMI with the main energy outputs and inputs, RFI was defined as the repeatable part of the model's residuals. To do so, each experimental period was subdivided into periods of 14 days, called segments, to have repeated measures for each cow within the experimental period. This model includes a repeated effect of cow over time and a random effect of cow on the intercept. Feed efficiency was then defined according to Fischer et al. (2018b) as the individual deviation from the population average intercept.

In the current study, feed efficiency (**randomRFI**) was defined as the random part of the intercept of the mixed model 1 below, which is μ_{cow}. As the objective of the current paper was to estimate repeatability within the same diet, each period of 56 d has been subdivided into two sub-periods of 28 d each, resulting in four sub-periods in total (two in period 1 and two in period 2). Consequently, the randomRFI was estimated within each sub-period within the same diet. As described by Fischer et al. (2018b), all variables included in the model, daily DMI, smoothed daily BW, daily MilkNE and estimated daily body reserve gain and loss, were averaged per segment of 14 d (Fig. 1). For each sub-period, we fitted the following mixed model 1 (1 model/sub-period/cohort) that includes a repeated effect of cow and a random effect of cow on the intercept:

$$\begin{aligned}\text{DMI}\left(\frac{\text{kg}}{\text{d}}\right) = {} & (\mu + \mu_{cow}) + \text{MilkNE} + \text{MBW} \\ & + \text{BWlossBCS} + \text{BWgainBCS} + \text{gestation} \\ & + \text{parity} + \text{parity} \times \text{MilkNE} + \text{parity} \\ & \times \text{MBW} + \text{parity} \times \text{BWlossBCS} + \text{parity} \\ & \times \text{BWgainBCS} + \text{segment} + \varepsilon \qquad \text{(Model1)}\end{aligned}$$

where segment is the fixed effect of segment, μ is the fixed intercept, μ_{cow} is the random effect of cow on the intercept and ε is the error. Feed efficiency is defined as μ_{cow} in model 1. This model

1 was performed with the Mixed procedure in SAS software (version 9.4 of the SAS System for Linux. 2017. SAS Institute Inc., Cary, NC, USA) with a repeated effect of cow with an unstructured variance-covariance matrix based on the lowest Akaike Information Criterion.

Repeatability and reproducibility of feed efficiency

Repeatability was defined as the capacity of a method to give the same results when using the same sample and repeating measurements in the same experimental conditions (JCGM, 2012). Reproducibility was defined as repeatability while changing one specific characteristic in experimental conditions (temperature, diet, or operator; JCGM, 2012). Applied to feed efficiency, repeatability conditions can be met by comparing efficiency estimated over short periods of lactation when cows are fed the same diet. Comparing feed efficiency estimated within the same experimental conditions but across different diets was referred to as reproducibility. The repeatability compared feed efficiency within the same diet by comparing sub-period 1 with sub-period 2. The reproducibility compared feed efficiency of HS diet with feed efficiency of LS diet by comparing sub-period 2 in period 1 with sub-period 1 in period 2 (Fig. 1). We chose those specific two sub-periods for reproducibility because they were the closest in lactation stage to minimize the difference in time between the two sub-periods, and thus be sure that the major difference between the two sub-periods is the diet.

Repeatability within diet and reproducibility across diets were estimated for feed efficiency using two methods. The first method estimated the standard deviation of repeatability and standard deviation of reproducibility, also known as the standard method, to evaluate repeatability and reproducibility as defined by JCGM (2012). To be comparable with published literature, the second method estimated correlation coefficients using Pearson's correlation coefficient and intraclass correlation coefficient (**ICC**). This is the method used by most published papers evaluating feed efficiency repeatability and reproducibility. The ICC were estimated with the *icc* function of irr package (Gamer et al., 2019) in R. This analysis of variance included cow as a fixed effect and was performed using the *Anova* function of car package (Fox and Weisberg, 2011) in R as follows:

$$\mathrm{randomRFI} = \mu + \mathrm{Cow} + \varepsilon \qquad (\mathrm{Model2})$$

where Cow stands for the fixed effect of cow, μ is the intercept and ε is the error. Standard deviations of repeatability and of reproducibility were defined as the standard deviation of the residuals of model 2.

Statistical test of parameters

The effects of diet and period on animal performance were analyzed by using the *Anova* function in car package in R with the Benjamini-Hochberg correction for multiple comparisons. This analysis of variance was applied on the DMI and animal performance averaged per period and per cow. The least squared means were performed with the *lsmeans* function in lsmeans package (Lenth, 2016) in R. To compare two correlations (ICC and Pearson's), we estimated confidence interval of each coefficient of correlation by using a bootstrap (sampling with replacement method) with 1 000 loops, with each loop estimating both correlations with a random subsample of 20–30 data among the 31 original data per cohort. After estimating the confidence interval of each coefficient of correlation, the *P*-value was selected using the *quantile* function in R for the confidence intervals of the two ICCs or the two Pearson's correlation coefficients that did not overlap between any comparison. Errors of repeatability or reproducibility were compared with an F-test using the *var.test* function in R.

Results and discussion

Diet and period effect on cows' performance

Feed intake changed only for the cohort that changed from LS to HS diet, as shown by the significant interaction between diet and period on DMI ($P < 0.01$, Table 2). This cohort started with an intake of 25.6 kg DM/d in period 1 when fed the LS diet and increased to 28.9 kg DM/d when fed the HS diet in period 2, while cohort **HStoLS**, consumed on average 25.2 kg DM/d (Table 2) for both periods. These observations for DMI of cohort **HStoLS** were similar to previous studies' observations that evaluated diets high in starch and low in fiber compared to diets low in starch and high in fiber (Potts et al., 2015, Boerman et al., 2015, Karlsson et al., 2018).

Cows produced an average of 28.0 Mcal NE_L/d in milk during period 1, which was 2 Mcal NE_L/d more than during period 2 ($P = 0.02$, Table 2). In addition, cows fed HS diet produced 1.8 Mcal NE_L/d more than cows fed LS diet ($P = 0.05$, Table 2). This difference in net energy exported in milk between period and between diet was also observed for milk production (Table 2). Indeed, cows produced 38.3 kg milk/d in period 1, which was reduced by 3.7 kg/d in period 2 ($P < 0.01$) and produced on average 38.1 kg milk/d when fed HS diet, which was 3.3 kg/d higher than when fed LS diet ($P = 0.01$). The higher milk production at the start of the experiment (period 1), compared with the end of the experiment (period 2), was expected because milk production declines with the stage of lactation. Milk protein production also differed between periods and between diets. Cows fed the HS diet averaged 1.24 kg/d of milk protein, 0.16 kg/d more than cows fed the LS diet ($P < 0.01$, Table 2). Greater milk protein production from cows fed the HS diet compared to the LS diet was also observed by Boerman et al. (2015) and Karlsson et al. (2018). For milk fat production, there was no effect of diet ($P = 0.64$), similarly to Karlsson et al. (2018). However, this is not consensual across studies because others have found lower milk fat production from cows fed an HS diet (Boerman et al., 2015). For both milk fat and milk protein, the production results were as expected, with yields that were higher in period 1 compared with period 2 (Table 2). Indeed, milk protein production was 1.18 kg/d in period 1 which was 0.06 kg/d higher than in period 2 ($P = 0.11$), and milk fat production was 1.49 kg/d in period 1, which was 0.10 kg/d more than in period 2 ($P = 0.05$). Milk lactose concentration was neither affected by diet ($P = 0.69$) nor by period ($P = 0.42$) with an average concentration of 49.1 g/kg. Milk lactose production reflected the results observed for milk production with higher production during period 1 compared to period 2 ($P < 0.01$) and a higher production with HS diet compared with LS diet ($P < 0.01$). Overall, this increased performance in milk synthesis for cows fed with the HS diet is often observed in literature (Potts et al., 2015; Boerman et al., 2015, Karlsson et al., 2018), mostly because high starch diets are usually more digestible than low starch diets primarily because low starch diets are higher in fiber. BW and BCS were, as expected with the effect of lactation stage, only affected by period with higher BW and BCS in period 2 compared to period 1 ($P < 0.01$), with averages of MBW (129 $kg^{0.75}$) and 3.2 BCS in period 1, and MBW (135 $kg^{0.75}$) and 3.5 BCS in period 2 (Table 2).

Variables associated with body reserve change, identified as BWloss and BWgain, were affected by diet and period ($P < 0.01$, Table 2). Body reserve loss was greater for cows fed LS diet with an average of 1.50 kg/d compared with cows fed HS diet with an average of 1.12 kg/d (Table 2). Both BW gain and BW loss that accounted for body reserve differences within a given BW change,

Table 2
Population description: number of cows, lactation stage, least square means of intake and performance of the dairy Holstein cows (n = 31/cohort) of both experimental diets (high starch (HS) and low starch (LS)) for both experimental periods (Period 1 and Period 2).

Items	HS Diet		LS Diet		RSD	*P*-value[1]		
	Period 1	Period 2	Period 1	Period 2		D	P	D × P
n (primiparous)	31 (14)	31 (15)	31 (15)	31 (14)				
DMI (kg of DM/d)	25.9[b]	28.9[a]	25.6[b]	24.5[b]	2.91	<0.01	0.09	<0.01
Milk production measures (kg/d)								
Milk production	39.3	36.8	37.3	32.3	7.03	0.01	<0.01	0.32
Milk fat production	1.51	1.39	1.47	1.39	0.28	0.63	0.05	0.74
Milk protein production	1.26	1.21	1.11	1.04	0.21	<0.01	0.11	0.71
Milk lactose production	1.95	1.8	1.82	1.59	0.35	<0.01	<0.01	0.48
Milk component concentration (g/kg)								
Milk fat concentration	38.9[b]	38.2[b]	39.7[b]	43.2[a]	4.82	<0.01	0.12	0.02
Milk protein concentration	32.1	33.0	30.0	32.3	2.36	<0.01	<0.01	0.11
Milk lactose concentration	49.4	48.8	48.9	49.1	1.66	0.69	0.42	0.21
Net energy milk (Mcal of NE_L/d)[2]	28.8	26.9	27.2	25	4.96	0.05	0.02	0.90
MBW ($kg^{0.75}$)[3]	128	136	129	134	11.4	0.85	<0.01	0.45
BCS	3.23	3.53	3.15	3.47	0.36	0.30	<0.01	0.88
BWloss (kg/d)[4]	1.29	0.95	1.53	1.47	0.62	<0.01	0.08	0.24
BWgain (kg/d)[4]	2.41	2.11	1.95	2.02	0.77	0.06	0.42	0.19
BWgainBCS[5]	7.94	7.53	6.19	6.99	2.96	0.04	0.73	0.26
BWlossBCS[5]	4.23	3.37	4.79	5.03	2.22	<0.01	0.45	0.18

Abbreviations: DMI = DM intake; NE_L = net energy of lactation; BCS = body conditional score.
[1] D = effect of diet (HS vs LS); P = effect of period (2 periods of 56 d each); D × P: interaction between diet and period.
[2] Calculated using the equation (2)–(15) adapted for milk true protein in NRC (2001): Milk yield (kg) × [0.0929 × Milk fat (%) + 0.0563 × Milk protein (%) + 0.0395 × Milk lactose (%)].
[3] MBW = $BW^{0.75}$.
[4] BW data were smoothed with a loess function, then the day-to-day change in BW was calculated based on the smoothed data: if the change was positive, it was assigned to the BWgain variable, if it was negative, it was assigned to BWloss variable.
[5] BWgainBCS and BWlossBCS = BW gain and BW loss were multiplied by daily BCS to account for body reserve differences within a given BW change.
[a–b] Treatment means in same row followed by different superscript letters differ significantly ($P < 0.05$).

Table 3
Error (SD) of repeatability and reproducibility, intraclass correlation coefficient (ICC) within diet for repeatability and across diets for reproducibility for feed efficiency (randomRFI) of dairy Holstein cows.

Items	Repeatability[1]		Reproducibility[2]	*P*-value[3]		
	LS Diet	HS Diet		LS vs HS	LS vs Reproducibility	HS vs Reproducibility
SD (kg DM/d)	0.504	0.761	0.830	<0.01	<0.01	0.34
Pearson's correlation coefficient[4]	0.809	0.630	0.418	0.06	<0.01	0.13
ICC[4]	0.806	0.587	0.399	0.03	<0.01	0.13

Abbreviations: randomRFI = residual DM intake defined as the random repeated effect of the model 1; LS = low starch diet; HS = high starch diet.
[1] Repeatability was estimated within diet (LS: low starch and high forage diet; HS: high starch diet), using two repetitions of 28 d within diet (n = 62 cows).
[2] Reproducibility was estimated using two repetitions of 28 d (1 repetition/diet, n = 62 cows).
[3] The SDs of repeatability and reproducibility were tested for significance with an F-test using equality of variances as an alternative hypothesis and the ICC were tested for significance with the estimation of their confidence interval.
[4] Pearson's correlation coefficient and ICC are the averages obtained after a bootstrap of 1 000 loops to get a robust estimation of Pearson's correlation coefficient and ICC.

identified as BWlossBCS and BWgainBCS, were only affected by diet ($P < 0.05$, Table 2). Cows fed HS diet were associated with a smaller body reserve loss and a larger body reserve gain than cows fed LS diet. This higher loss with LS diets is commonly observed in literature (Boerman et al., 2015; Potts et al., 2015). As for milk production, this difference in body reserve mobilization must be due to the lower concentration in starch in LS diet, implying less rapidly fermentable energy in the rumen. Cows mobilized more body reserves in period 1 compared to period 2 with an average of 1.44 kg/d in period 1, which was 0.20 kg/d higher than in period 2. This greater mobilization in period 1 was expected because body reserve mobilization is known to be greater earlier in lactation compared to later in lactation. Body reserve gain was similar in period 1 and period 2 ($P = 0.42$) with an average of 2.12 kg/d was significantly greater when cows were fed the HS diet with an average of 2.26 kg/d than when they were fed the LS diet with an average of 1.99 kg/ (Table 2). This lower body reserve loss and higher body reserve gain with HS diet are compliant with the higher digestibility and net energy value of HS diet compared to LS diet.

Feed efficiency is repeatable within diet

Feed efficiency was more repeatable within LS diet than within HS diet. The Pearson correlation coefficient was 0.630 within HS diet which tended to be lower than the Pearson correlation coefficient of 0.809 within LS diet ($P = 0.06$, Table 3 and Fig. 2). Similarly, the ICC was 0.587 within HS diet which was lower than the ICC of 0.806 within LS diet ($P = 0.03$, Table 3). In the same way, we observed that the error of repeatability within HS diet (0.761 kg DM/d) was higher than the error of repeatability within LS diet (0.504 kg DM/d; $P < 0.01$; Table 3). This significant difference between the repeatability errors of both diets can be explained by a cohort effect. The cohort starting with the HS diet in period 1 had a higher error of repeatability within HS diet compared to the second cohort (error = 0.640 vs 0.424 kg DM/d; data not shown), whereas the errors of repeatability were similar for both cohorts within LS diet (error = 0.369 vs 0.349 kg DM/d; data not shown). In fact, the error of repeatability within LS diet of the cohort starting with LS diet in period 1 (error = 0.349 kg DM/d) was not different from the error of repeatability within HS diet

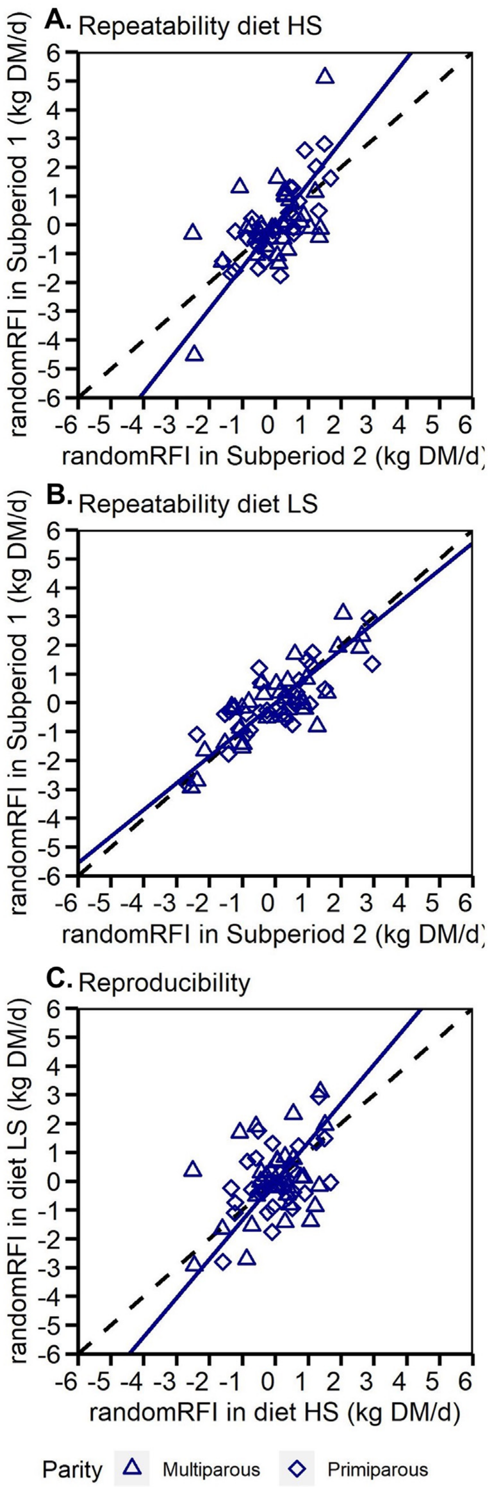

Fig. 2. Relationship between feed efficiency (randomRFI) estimated either within the same diet for repeatability estimation or across diets for reproducibility estimation for the 62 dairy Holstein cows. Primiparous cows are represented with triangles (△), and multiparous cows are represented with diamonds (◇). The dashed black line stands for the first bisector. The least rectangle regression equation within the HS diet (A.) is $\text{randomRFI in sub} - \text{period } 1 = 1.45 \times \text{randomRF in sub} - \text{period } 2$ with an R^2 of 0.40 and RSD of 0.646 kg DM/d. The rectangles regression equation within LS diet (B.) was: $\text{randomRFI in sub} - \text{period } 1 = 0.926 \times \text{randomRF in sub} - \text{period } 2$ with an R^2 of 0.66 and RSD of 0.557 kg DM/d. The regression equation for reproducibility (C.) was: $\text{randomRFI in HS Diet} = 1.351 \times \text{randomRF in LS Diet}$ with an R^2 of 0.179 and RSD of 0.788 kg DM/d.

(error = 0.424 kg DM/d; P = 0.13). The reasons for this diet difference in error of repeatability for the cohort starting with HS diet in period 1 are unknown. It could be due to a difference in the composition of HS diet between the two periods, but HS diet had similar ingredient composition, nutritive composition, and particle size composition over both periods (Table 1). Overall, feed efficiency for a given animal is repeatable across stages of lactation when the diet is consistent. Similar correlations, and consequently conclusions, were found in literature with Pearson's correlation coefficient around 0.70 in dairy cows (Potts et al., 2015; Løvendahl et al., 2018), 0.54–0.70 in heifers and 0.42 in steers (Durunna et al., 2011; Cassady et al., 2016) for feed efficiency.

Feed efficiency is less reproducible when changing diets than repeatable within diet

Here, we compared the repeatability estimation within the same diet with the reproducibility estimation across diets. This means that the repeatability within the same diet which compares RFI of both sub-periods within the same diet was compared with the reproducibility estimation which compares RFI of sub-period 2 in period 1 with RFI of sub-period 1 in period 2. Feed efficiency was less reproducible across diets than repeatable within the same diet, for both error and correlation methods (Table 3, Fig. 2). Pearson's correlation coefficient of reproducibility was 0.418 and was lower than Pearson's correlation coefficient within LS diet (0.809; P < 0.01, Table 3). Similarly, the ICC of reproducibility was 0.399 and was lower than the ICC estimated within LS diet (P < 0.01, Table 3). Error of reproducibility was 0.830 kg DM/d, which was higher than the error of repeatability within LS diet (P < 0.01, Table 3). Reductions in correlation coefficients with diet change were also observed previously with correlations decreasing from 0.65 to 0.56 in dairy cows (Potts et al., 2015), from 0.54–0.70 to 0.40 in heifers and from 0.42 to 0.33 in steers (Durunna et al., 2011, Cassady et al., 2016). Similar correlations were found when changing the nitrogen concentration of the diet in dairy cows with a correlation of 0.51 (Liu and Vandehaar, 2020). This reduction in feed efficiency repeatability when changing diet's composition was also observed when comparing the error of repeatability within diet with the error of reproducibility.

Nevertheless, the observed lower reproducibility of feed efficiency when compared to the repeatability within LS diet was not observed when reproducibility was compared to the repeatability within HS diet (P = 0.34 for the error comparison, 0.13 for both ICC and Pearson's correlation comparison, Table 3). This similarity between repeatability within HS diet and reproducibility is explained by the lower repeatability within HS diet for cohort starting with HS diet in period 1. The repeatability within HS diet was similar to the reproducibility in cohort HStoLS. However, the reproducibility was always lower than the repeatability within HS diet (P < 0.05 for Pearson's and ICC correlation and errors; Table 3) and within LS diet (P < 0.01 for Pearson's and ICC correlation and errors; Table 3) in cohort LStoHS. The error of repeatability within HS diet (0.898 kg DM/d) was similar (P = 0.64) to the error of reproducibility (0.845 kg DM/d), and the repeatability correlations (Pearson's = 0.623 and ICC = 0.567) were similar (P > 0.10) to the reproducibility correlations (Pearson's = 0.417 and ICC = 0.414) for cohort starting with the HS diet in period 1. As previously discussed, this could be explained by a change in HS diet composition and nutritive value, but this was not observed because HS diet was similar in composition, nutritive value and particle size for both periods (Table 1). Except for this specific result for the cohort HStoLS within HS diet, all results show that feed efficiency was less reproducible when diet was changed than within the same diet over subsequent lactation stages.

Overall, both correlations and the errors of repeatability and reproducibility demonstrated that feed efficiency is significantly impacted by a change in dietary starch concentration because it is less repeatable when comparing before and after diet change than within the same diet. This change in feed efficiency when the dietary composition is changed could be explained by the change in digestibility that is induced with the change in dietary starch concentration. Indeed, digestibility is a known determinant of feed efficiency differences, especially when animals are fed with diets that have lower concentrations in starch or in concentrates (Potts et al., 2017 for dairy cows; Oliveira et al., 2016 for beef heifers; Rajaei Sharifabadi et al., 2016 for lambs; Williams et al., 2019 for dairy heifers). This association between feed efficiency and digestibility was not observed when animals were fed a diet that was high in starch (Potts et al., 2017 for dairy cows; Oliveira et al., 2016 for beef heifers). This change in feed efficiency determinants with the change in diet composition was congruent with the change in feed efficiency when the diet changes, as observed in the current study. Altogether, these results combined with results in the literature regarding digestibility as a potential determinant for feed efficiency, suggests that further investigation regarding digestibility as a determinant of feed efficiency is needed. The observed change in feed efficiency when changing dietary starch concentration could be due to the change in digestibility as an effect of diet change. One may wonder if this change in digestibility is the real driver of the change in feed efficiency, of if there is another underlying driver which induces changes in digestibility. These factors may include the level of feed intake or the retention time of feed in the rumen (Volden, 1999, Dias et al., 2011).

In this evaluation, we used intake expressed as DM rather than expressed as net energy. Because individual feed ingredients were consistent in quality throughout the experiment, the net energy value of the diets did not change over time. In the current study, RFI was estimated and modeled within each diet and then compared between diets. If one would estimate RFI of cows fed diets with changing quality over time, then one should use net energy intake instead of DMI to account for quality change over time. This was not observed in the current paper, and we therefore used DMI. The repeatability results for RFI estimated with net energy intake instead of DMI are presented in the Supplementary Tables S1–3.

Conclusion

Feed efficiency was similarly repeatable across time when cows were fed the same diet. However, feed efficiency was less reproducible when changing dietary starch and fiber concentrations than repeatable within diet. This means that the feed efficiency of dairy cows changes more after a diet change than after the lactation stage change. Lactating dairy cows were more able to maintain their feed efficiency when they were fed the same diet than when their diet was changed. This strengthens the position of digestive processes as determinant of feed efficiency and suggests to further investigate the association between digestive processes and feed efficiency.

Supplementary material

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Ethics approval

All animal care and handling procedures were approved by the University of Wisconsin-Madison Institutional Animal Care and Use Committee (Protocol #A005945).

Data and model availability statement

Data are not in an official repository, but are available from the corresponding author upon reasonable request.

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Declaration of interest

None.

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