Estimates of genetic parameters for feeding behavior traits and their associations with feed efficiency in Holstein cows

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ABSTRACT

Residual feed intake (RFI) is commonly used to measure feed efficiency but individual intake recording systems are needed. Feeding behavior may be used as an indicator trait for feed efficiency using less expensive precision livestock farming technologies. Our goal was to estimate genetic parameters for feeding behavior and the genetic correlations with feed efficiency in Holstein cows. Data consisted of 75,877 daily feeding behavior records of 1,328 mid-lactation Holstein cows in 31 experiments conducted from 2009 to 2020 with an automated intake recording system. Feeding behavior traits included number of feeder visits per day, number of meals per day, duration of each feeder visit, duration of each meal, total duration of feeder visits, intake per visit, intake per meal [kg of dry matter (DM)], feeding rate per visit, and feeding rate per meal (kg of DM per min). The meal criterion was estimated as 26.4 min, which means that any pair of feeder visits separated by less than 26.4 min were considered part of the same meal. The statistical model included lactation and days in milk as fixed effects, and experiment-treatment, animal, and permanent environment as random effects. Genetic parameters for feeding behavior traits were estimated using daily records and weekly averages. Estimates of heritability for daily feeding behavior traits ranged from 0.09 ± 0.02 (number of meals; mean ± standard error) to 0.23 ± 0.03 (feeding rate per meal), with repeatability estimates ranging from 0.23 ± 0.01 (number of meals) to 0.52 ± 0.02 (number of feeder visits). Estimates of heritability for weekly averages of feeding behavior traits ranged from 0.19 ± 0.04 (number of meals) to 0.32 ± 0.04 (feeding rate per visit), with repeatability estimates ranging from 0.46 ± 0.02 (duration of each meal) to 0.62 ± 0.02 (feeding rate per visit and per meal). Most of the feeding behavior measures were strongly genetically correlated, showing that with more visits or meals per day, cows spend less time in each feeder visit or meal with lower intake per visit or meal. Weekly averages for feeding behavior traits were analyzed jointly with RFI and its components. Number of meals was genetically correlated with milk energy (0.48), metabolic body weight (−0.27), and RFI (0.19). Duration of each feeder visit and meal were genetically correlated with milk energy (0.43 and 0.44, respectively). Total duration of feeder visits per day was genetically correlated with DM intake (0.29), milk energy (0.62), metabolic body weight (−0.37), and RFI (0.20). Intake per visit and meal were genetically correlated with DM intake (0.63 and 0.87), milk energy (0.47 and 0.69), metabolic body weight (0.47 and 0.68), and RFI (0.31 and 0.65). Feeding rate was genetically correlated with DM intake (0.69), metabolic body weight (0.67), RFI (0.47), and milk energy (0.21). We conclude that measures of feeding behavior could be useful indicators of dairy cow feed efficiency, and individual cows that eat at a slower rate may be more feed efficient.

Key words: feeding rate, genetic correlation, heritability, meal, residual feed intake

INTRODUCTION

Genetic selection is a powerful tool to improve livestock production, given that genetic gains are cumulative and permanent. Genomic technologies allow important economic traits that are difficult to measure to be included into breeding programs through the application of genomic selection (Pryce et al., 2014; Wiggans et al., 2017; Li et al., 2020). Automated feeders, for example, enable the evaluation of feed efficiency for an individual animal using daily DMI data. Residual feed intake (RFI) is commonly used to measure feed efficiency, and in lactating dairy cattle it is typically calculated as the difference between actual DMI observations and predictions from regression on known energy sinks (e.g., metabolic BW, BW change, and secreted milk energy). Although this is a reliable system,
it is too expensive for commercial farms, which limits the measurement of phenotypes and leads to low reliabilities of genomic breeding values for RFI (Li et al., 2020).

Interestingly, automated feeding system technology also provides information about the feeding behavior of the animals, which can be associated with feed efficiency. Feeding behavior can be analyzed using traits such as number of feeder visits or meals per day, duration and intake per visit or meal, and feeding rate. Indeed, evidence indicates that variation in feeding behavior explains part of the variation observed in RFI in dairy cattle (Connor et al., 2013; Green et al., 2013; Lin et al., 2013). However, little is known about the genetic variation of feeding behavior traits and their genetic correlations with feed efficiency traits in lactating dairy cows, as most studies have been reported in beef cattle and pigs, and studies involving dairy cattle have been limited. Studies in meat animals have shown high heritability estimates for feeding behavior traits, ranging from 0.17 to 0.61 (Kavlak and Uimari, 2019; Benfica et al., 2020; Herrera-Cáceres et al., 2020; Kelly et al., 2021; Olson et al., 2021), as well as strong genetic correlations between feeding behavior and feed efficiency. Therefore, feeding behavior may be used as an indicator trait for feed efficiency, using less expensive wearable sensors or computer vision systems that do not require measurement of individual intake and could be implemented on commercial farms to generate a greater number of phenotypic records.

Thus, due to the lack of feeding behavior genetic studies in lactating dairy cattle and the potential for using these traits as indicators of feed efficiency, the objective of this study was to estimate genetic parameters for feeding behavior traits using daily records, as well as estimate genetic correlations of feeding behavior with milk energy (MilkE), metabolic BW (mBW), change in BW (ΔBW), DMI, and RFI, using weekly averages.

MATERIALS AND METHODS

Cows, Housing, and Feeding System

Animal handling and sampling procedures were approved by the University of Wisconsin-Madison College of Agricultural and Life Sciences Animal Care and Use Committee.

Data consisted of 75,877 daily feeding behavior records of 1,328 Holstein cows in 31 experiments conducted from 2009 to 2020 in a freestall facility at the University of Wisconsin-Madison Emmons Blaine Dairy Cattle Research Center (Arlington, WI) with a roughage intake control system (RIC; Hokofarm Group). The RIC system permits one animal to access the feeder at a given time and records the start and end time of each visit to the feeder and the weight of feed consumed during each visit. Cows (n = 64 maximum in the pen) typically had access to all 32 feeders, but in some specific experiments with dietary treatments, an individual cow may have had access to 8 or 16 randomly assigned feeders, depending on the number of diets. The raw data generated by this system consisted of more than 4 million feeder visits and included date, time entered the feeder, time exited the feeder, duration of visit, weight of feed at entry, weight of feed at exit, weight of feed consumed, and identification number of responder, cow, and feeder. For cows used in more than one experiment, only data from the first experiment were retained. Data from cows with less than 28 d on experiment, feeder visits with as-fed intake ≤0 or >20 kg or visit duration <5 s or >3,000 s were removed; these edits removed approximately 16% of feeder visits in the data set.

Feeding Behavior Traits

Using the data generated by the feeding system, the following feeding behavior traits were calculated: number of feeder visits per day, number of meals per day, duration of each feeder visit, duration of each meal, total duration of feeder visits per day, intake per visit (kg of DM), intake per meal (kg of DM), feeding rate per visit (kg of DM/min), and feeding rate per meal (kg of DM/min). To define a meal, we determined the meal criterion by fitting a mixture model of the log10 frequency distribution of the interval between feeder visits using maximum likelihood (DeVries et al., 2003; Horvath and Miller-Cushon, 2019). Any pair of feeder visits separated by less than the meal criterion was defined as a single meal. The meal criterion derived from this data set was 26.4 min. Note that feeding behavior traits were analyzed using daily records and weekly averages. Descriptive statistics for daily records of feeding behavior traits are shown in Table 1. Descriptive statistics for feeding behavior traits summarized on a weekly basis are shown in Table 2.

Feed Efficiency Traits

The following feed efficiency traits were considered: DMI, the 3 primary energy sinks in lactating dairy cows—MilkE, mBW, and ΔBW—and RFI.

Descriptive statistics for DMI on a daily and weekly basis are shown in Tables 1 and 2, respectively. Milk samples were obtained weekly for determination of milk composition. Milk energy was calculated using the following equation:
MilkE = (0.0929 × fat % + 0.0563 × protein % + 0.0395 × lactose %) × milk yield.

Body weights were obtained on 3 consecutive days at the beginning, middle, and end of the experimental period, with a total of 11,325 recorded BW (mean ± SD equal to 678.9 ± 76.1 kg). We used linear regression to estimate weekly BW, given that the experiment lasted just a few weeks. Metabolic BW was calculated as the weekly average BW^{0.75}, and ΔBW was calculated as the difference in BW at the end and beginning of each week.

Weekly DMI records were regressed on the 3 main energy sinks to calculate weekly RFI values using a linear mixed model as follows:

\[ \text{DMI} = \text{DIM} + \text{Lact} + b_1\text{MilkE} + b_2\text{mBW} + b_3\DeltaBW + \text{block} + \text{week} + e, \]

where DIM represents the effect of days in milk with 9 levels (grouped by 19 d), Lact represents the effect of lactation number with 4 levels (1, 2, 3, and 4+), MilkE is milk energy with partial regression coefficient \( b_1 \), mBW is metabolic BW with partial regression coefficient \( b_2 \), and \( b_3 \) is the change in BW with partial regression coefficient \( b_3 \). ΔBW is change in BW with partial regression coefficient \( b_3 \). block represents the random effect of experiment-treatment, week represents the random effect of the week of the experiment, and e is the random residual of the model, representing RFI. Random effects were assumed to follow a multivariate normal distribution, as described below:

\[
\begin{bmatrix}
\text{block} \\
\text{week} \\
e
\end{bmatrix}
\sim N
\begin{bmatrix}
0 \\
0 \\
0
\end{bmatrix}
\begin{bmatrix}
\sigma_{\text{block}}^2 & 0 & 0 \\
0 & \sigma_{\text{week}}^2 & 0 \\
0 & 0 & \sigma_e^2
\end{bmatrix},
\]

where \( \sigma_{\text{block}}^2 \), \( \sigma_{\text{week}}^2 \), and \( \sigma_e^2 \) are the block, week, and residual variances, respectively, and \( I \) is the identity matrix.

Descriptive statistics for feed efficiency traits are shown in Table 2. Milk energy had fewer records because of some missing data, and outliers were removed as described by Tempelman et al. (2015).

**Univariate Analyses**

Estimates of heritability and repeatability for daily and weekly feeding behavior traits, daily and weekly

### Table 1. Descriptive statistics for daily feeding behavior and feed DMI in lactating Holstein cows

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of records</th>
<th>No. of cows</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of feeder visits per day</td>
<td>75,877</td>
<td>1,328</td>
<td>35.7</td>
<td>15.6</td>
<td>0.00</td>
<td>169</td>
</tr>
<tr>
<td>No. of meals per day</td>
<td>75,877</td>
<td>1,328</td>
<td>7.48</td>
<td>1.70</td>
<td>0.00</td>
<td>17.0</td>
</tr>
<tr>
<td>Duration of each feeder visit (min)</td>
<td>75,877</td>
<td>1,328</td>
<td>0.008</td>
<td>0.447</td>
<td>0.44</td>
<td>6.51</td>
</tr>
<tr>
<td>Intake per visit (kg of DM)</td>
<td>75,877</td>
<td>1,328</td>
<td>3.81</td>
<td>1.13</td>
<td>0.04</td>
<td>4.07</td>
</tr>
<tr>
<td>Feeding rate per visit (kg of DM/min)</td>
<td>75,877</td>
<td>1,328</td>
<td>0.150</td>
<td>0.058</td>
<td>0.043</td>
<td>1.07</td>
</tr>
<tr>
<td>Feeding rate per meal (kg of DM/min)</td>
<td>75,877</td>
<td>1,328</td>
<td>0.137</td>
<td>0.040</td>
<td>0.042</td>
<td>0.677</td>
</tr>
<tr>
<td>DMI (kg/d)</td>
<td>75,095</td>
<td>1,328</td>
<td>21.9</td>
<td>4.98</td>
<td>0.751</td>
<td>54.9</td>
</tr>
</tbody>
</table>

### Table 2. Descriptive statistics for weekly averages of feeding behavior and feed efficiency traits in lactating Holstein cows

<table>
<thead>
<tr>
<th>Trait</th>
<th>No. of records</th>
<th>No. of cows</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of feeder visits per day</td>
<td>12,317</td>
<td>1,326</td>
<td>35.7</td>
<td>14.0</td>
<td>0.00</td>
<td>146</td>
</tr>
<tr>
<td>No. of meals per day</td>
<td>12,317</td>
<td>1,326</td>
<td>7.50</td>
<td>1.14</td>
<td>0.00</td>
<td>14.0</td>
</tr>
<tr>
<td>Duration of each feeder visit (min)</td>
<td>12,317</td>
<td>1,326</td>
<td>6.80</td>
<td>2.34</td>
<td>1.02</td>
<td>20.6</td>
</tr>
<tr>
<td>Duration of each meal (min)</td>
<td>12,317</td>
<td>1,326</td>
<td>29.4</td>
<td>7.10</td>
<td>10.3</td>
<td>110</td>
</tr>
<tr>
<td>Total duration of feeder visits per day (min)</td>
<td>12,317</td>
<td>1,326</td>
<td>213</td>
<td>48.0</td>
<td>22.0</td>
<td>677</td>
</tr>
<tr>
<td>Intake per visit (kg of DM)</td>
<td>12,317</td>
<td>1,326</td>
<td>0.905</td>
<td>0.401</td>
<td>0.174</td>
<td>3.55</td>
</tr>
<tr>
<td>Intake per meal (kg of DM)</td>
<td>12,317</td>
<td>1,326</td>
<td>3.79</td>
<td>0.898</td>
<td>1.56</td>
<td>10.6</td>
</tr>
<tr>
<td>Feeding rate per visit (kg of DM/min)</td>
<td>12,317</td>
<td>1,326</td>
<td>0.133</td>
<td>0.035</td>
<td>0.052</td>
<td>0.320</td>
</tr>
<tr>
<td>Feeding rate per meal (kg of DM/min)</td>
<td>12,317</td>
<td>1,326</td>
<td>0.133</td>
<td>0.035</td>
<td>0.051</td>
<td>0.320</td>
</tr>
<tr>
<td>DMI</td>
<td>12,317</td>
<td>1,326</td>
<td>26.9</td>
<td>4.17</td>
<td>9.93</td>
<td>47.0</td>
</tr>
<tr>
<td>Milk energy (Mcal)</td>
<td>9,805</td>
<td>1,325</td>
<td>31.1</td>
<td>5.97</td>
<td>3.46</td>
<td>54.2</td>
</tr>
<tr>
<td>Metabolic BW (kg^{0.75})</td>
<td>12,296</td>
<td>1,324</td>
<td>11.1</td>
<td>86.4</td>
<td>192.5</td>
<td>129.5</td>
</tr>
<tr>
<td>Change in BW (kg)</td>
<td>12,294</td>
<td>1,324</td>
<td>2.54</td>
<td>3.95</td>
<td>-47.63</td>
<td>55.56</td>
</tr>
<tr>
<td>Residual feed intake (kg)</td>
<td>9,782</td>
<td>1,324</td>
<td>0</td>
<td>1.99</td>
<td>-11.8</td>
<td>13.8</td>
</tr>
</tbody>
</table>
DMI records, and weekly records of MilkE, mBW, and ΔBW were obtained using the following repeatability animal model:

\[ y = X\beta + Z_1b + Z_2u + Wpe + e, \]

where \( y \) is a vector of phenotypic records, \( \beta \) is a vector of fixed effects, \( b \) is a vector of random block effects of experiment-treatment (60 levels), \( u \) is a vector of random additive genetic effects, \( pe \) is a vector of random permanent environmental effects, and \( e \) is the vector of random residual effects. Fixed effects included lactation number with 4 levels (1 to 4+) and DIM with 9 levels (grouped by 19 d). \( X, Z_1, Z_2, \) and \( W \) are incidence matrices relating \( y \) to \( \beta, b, u, \) and \( pe \), respectively. Random effects were assumed to follow a multivariate normal distribution:

\[
\begin{bmatrix}
  b \\
  u \\
  pe \\
  e
\end{bmatrix} 
\sim N
\begin{bmatrix}
0 \\
0 \\
0 \\
0
\end{bmatrix} \begin{bmatrix}
\sigma_b^2 & 0 & 0 & 0 \\
0 & \sigma_a^2 & 0 & 0 \\
0 & 0 & \sigma_{pe}^2 & 0 \\
0 & 0 & 0 & \sigma_e^2
\end{bmatrix}.
\]

where \( \sigma_b^2, \sigma_a^2, \sigma_{pe}^2, \) and \( \sigma_e^2 \) are the block, additive genetic, permanent environmental, and residual variances, respectively; \( I \) is the identity matrix; and \( A \) is the matrix of additive relationships between animals in the pedigree using the last 3 generations.

Estimates of heritability and repeatability for weekly RFI values were obtained using the following repeatability animal model:

\[ y = m + Zu + Wpe + e, \]

where \( y \) is a vector of RFI records, \( m \) represents a general intercept, \( u \) is a vector of random additive genetic effects, \( pe \) is a vector of random permanent environmental effects, and \( e \) is the vector of random residual effects. Matrices \( Z \) and \( W \) are incidence matrices relating \( y \) to \( u \) and \( pe \), respectively. Random effects were assumed to follow a multivariate normal distribution:

\[
\begin{bmatrix}
  u \\
  pe \\
  e
\end{bmatrix} 
\sim N
\begin{bmatrix}
0 \\
0 \\
0
\end{bmatrix} \begin{bmatrix}
\sigma_u^2 & 0 & 0 \\
0 & \sigma_{pe}^2 & 0 \\
0 & 0 & \sigma_e^2
\end{bmatrix}.
\]

where \( \sigma_u^2, \sigma_{pe}^2, \) and \( \sigma_e^2 \) are the additive genetic, permanent environmental, and residual variances, respectively; \( I \) is the identity matrix; and \( A \) is the matrix of additive relationships between animals in the pedigree using the last 3 generations.

Estimates were obtained using the REML method with the AIREMLF90 software (Aguilar et al., 2018).

**Bivariate Analyses Using Daily Records**

Estimates of genetic correlations between daily feeding behavior traits and daily DMI records were performed in bivariate analyses using the following model:

\[ y = X\beta + Z_1b + Z_2u + Wpe + e, \]

where \( y \) is a vector of daily phenotypic records, \( \beta \) is a vector of fixed effects, \( b \) is a vector of random block effects of experiment-treatment (60 levels), \( u \) is a vector of random additive genetic effects, \( pe \) is a vector of random permanent environmental effects, and \( e \) is the vector of random residual effects. Fixed effects included lactation number with 4 levels (1 to 4+) and DIM with 9 levels (grouped by 19 d). \( X, Z_1, Z_2, \) and \( W \) are incidence matrices relating \( y \) to \( \beta, b, u, \) and \( pe \), respectively. Random effects were assumed to follow a multivariate normal distribution:

\[
\begin{bmatrix}
  b \\
  u \\
  pe \\
  e
\end{bmatrix} 
\sim N
\begin{bmatrix}
0 \\
0 \\
0 \\
0
\end{bmatrix} \begin{bmatrix}
\sigma_b^2 & 0 & 0 & 0 \\
0 & \sigma_a^2 & 0 & 0 \\
0 & 0 & \sigma_{pe}^2 & 0 \\
0 & 0 & 0 & \sigma_e^2
\end{bmatrix}.
\]

where \( \sigma_b^2, \sigma_a^2, \sigma_{pe}^2, \) and \( \sigma_e^2 \) are the block, additive genetic, permanent environmental, and residual variances, respectively; \( I \) is the identity matrix; and \( A \) is the matrix of additive relationships between animals in the pedigree using the last 3 generations.

Estimates were obtained using the REML method through the AIREMLF90 software (Aguilar et al., 2018).

**Bivariate Analyses Using Weekly Records**

Estimates of genetic correlations between weekly feeding behavior traits and weekly feed efficiency traits were performed in bivariate analyses using the following model:

\[ y = X\beta + Z_1b + Z_2u + Wpe + e, \]

where \( y \) is a vector of weekly phenotypic records, \( \beta \) is a vector of fixed effects, \( b \) is a vector of random
block effects of experiment-treatment (60 levels), \( \mathbf{u} \) is a vector of random additive genetic effects, \( \mathbf{pe} \) is a vector of random permanent environmental effects, and \( \mathbf{e} \) is the vector of random residual effects. Fixed effects included lactation number with 4 levels (1 to 4+) and DIM with 9 levels (grouped by 19 d). \( \mathbf{X}, \mathbf{Z}_1, \mathbf{Z}_2, \) and \( \mathbf{W} \) are incidence matrices relating \( y \) to \( \mathbf{b}, \mathbf{b}, \mathbf{u}, \) and \( \mathbf{pe} \), respectively. Random effects were assumed to follow a multivariate normal distribution:

\[
\begin{bmatrix}
\mathbf{b} \\
\mathbf{u} \\
\mathbf{pe} \\
\mathbf{e}
\end{bmatrix} ~ N
\begin{bmatrix}
0 \\
0 \\
0 \\
0
\end{bmatrix}
\begin{bmatrix}
\mathbf{B}_0 \otimes \mathbf{I} & 0 & 0 & 0 \\
0 & \mathbf{G}_0 \otimes \mathbf{A} & 0 & 0 \\
0 & 0 & \mathbf{P}_0 \otimes \mathbf{I} & 0 \\
0 & 0 & 0 & \mathbf{R}_0 \otimes \mathbf{I}
\end{bmatrix}
\]

where \( \mathbf{B}_0, \mathbf{G}_0, \) and \( \mathbf{P}_0 \) are the \( 2 \times 2 \) block, additive genetic direct, and environmental permanent effects (co)variance matrices, respectively; \( \mathbf{A} \) is the matrix of additive relationships between animals in the pedigree of the last 3 generations; \( \mathbf{R}_0 \) is the \( 2 \times 2 \) residual (co)variance matrix; and \( \mathbf{I} \) is an identity matrix with suitable dimensions. For RFI, only the random additive genetic effects and the random permanent environmental effects were considered.

Estimates were obtained using the REML method through the AIREMLF90 software (Aguilar et al., 2018).

### RESULTS AND DISCUSSION

#### Genetic Parameters for Feeding Behavior Traits

Variance components, heritability, and repeatability estimates for 9 feeding behavior traits measured daily, as well as for daily DMI, are shown in Table 3. Estimates of heritability for feeding behavior traits ranged from 0.09 ± 0.02 (number of meals per day) to 0.23 ± 0.03 (feeding rate per meal), indicating that a significant proportion of phenotypic variance is explained by additive genetic effects, such that feeding behavior could be incorporated into genetic selection schemes. Moreover, most traits were highly repeatable across days, with repeatability estimates ranging from 0.23 ± 0.01 (number of meals per day) to 0.52 ± 0.02 (number of feeder visits per day). Interestingly, all feeding behavior traits determined on a meal basis, except for feeding rate per meal, had lower heritability and repeatability estimates compared with those traits generated using feeder visits. No studies have been published in dairy cattle involving genetic parameters for feeding behavior defined as a meal concept. However, Kelly et al. (2021) used a similar approach in crossbred growing cattle, and they also observed greater heritability estimates for direct measures of feeding behavior traits than those defined using a meal criterion. Despite the lack of a commonly agreed upon meal definition, the approach considered in the present study has been used in nutrition, management, and welfare studies in lactating dairy cows, with a meal criterion ranging from 20 to 35 min (Tolkamp and Kyriazakis, 1999; DeVries et al., 2003; DeVries and Chevaux, 2014).

To our knowledge, Lin et al. (2013) is the only published genetic study of feeding behavior in dairy cattle; these authors reported heritability estimates of 0.45 to 0.50 for number of visits, feeding duration, feeding rate, and intake per visit in dairy heifers. Moderate to high heritability estimates have also been reported for feeding behavior in beef cattle (Nkrumah et al., 2007; Chen et al., 2014; Benfica et al., 2020; Kelly et al., 2021) and pigs (Lu et al., 2017; Kavlak and Ümari, 2019; Herrera-Cáceres et al., 2020). For example, Benfica et al. (2020) reported heritability estimates from 0.27 to 0.35 for frequency of bunk visits, DMI per visit, feeding rate, and duration of each feeding event in Nellore cattle. In pigs, Herrera-Cáceres et al. (2020) reported heritability estimates ranging from 0.23 (average daily time at the feeder) to 0.48 (average daily feeding frequency). Dif-

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**Table 3. Variance component estimates and genetic parameters (± SE)² for daily feeding behavior and DMI in lactating Holstein cows**

<table>
<thead>
<tr>
<th>Trait</th>
<th>( \sigma^2_v )</th>
<th>( \sigma^2_{pe} )</th>
<th>( \sigma^2_e )</th>
<th>( \sigma^2_b )</th>
<th>( h^2 )</th>
<th>( \rho )</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of feeder visits per day</td>
<td>35.03 ± 7.82</td>
<td>78.63 ± 6.85</td>
<td>12.49 ± 3.98</td>
<td>93.32 ± 0.48</td>
<td>0.16 ± 0.03</td>
<td>0.52 ± 0.02</td>
</tr>
<tr>
<td>No. of meals per day</td>
<td>0.25 ± 0.05</td>
<td>0.41 ± 0.04</td>
<td>0.08 ± 0.03</td>
<td>2.09 ± 0.01</td>
<td>0.09 ± 0.02</td>
<td>0.23 ± 0.01</td>
</tr>
<tr>
<td>Duration of each feeder visit (min)</td>
<td>1.15 ± 0.24</td>
<td>2.13 ± 0.20</td>
<td>0.69 ± 0.19</td>
<td>3.00 ± 0.02</td>
<td>0.16 ± 0.03</td>
<td>0.47 ± 0.02</td>
</tr>
<tr>
<td>Duration of each meal (min)</td>
<td>10.83 ± 1.78</td>
<td>13.24 ± 1.41</td>
<td>5.87 ± 1.48</td>
<td>47.80 ± 0.25</td>
<td>0.14 ± 0.02</td>
<td>0.31 ± 0.01</td>
</tr>
<tr>
<td>Total duration of feeder visits per day</td>
<td>452.14 ± 75.65</td>
<td>623.66 ± 61.22</td>
<td>336.41 ± 83.65</td>
<td>1,446.20 ± 7.49</td>
<td>0.16 ± 0.03</td>
<td>0.38 ± 0.02</td>
</tr>
<tr>
<td>Intake per visit (kg of DM)</td>
<td>0.026 ± 0.005</td>
<td>0.051 ± 0.005</td>
<td>0.015 ± 0.004</td>
<td>0.065 ± 0.000</td>
<td>0.16 ± 0.03</td>
<td>0.49 ± 0.02</td>
</tr>
<tr>
<td>Intake per meal (kg of DM)</td>
<td>0.14 ± 0.02</td>
<td>0.15 ± 0.02</td>
<td>0.05 ± 0.01</td>
<td>0.70 ± 0.004</td>
<td>0.13 ± 0.02</td>
<td>0.28 ± 0.01</td>
</tr>
<tr>
<td>Feeding rate per meal (kg of DM/min)</td>
<td>0.0003 ± 0.00</td>
<td>0.0006 ± 0.00</td>
<td>0.0006 ± 0.00</td>
<td>0.0012 ± 0.00</td>
<td>0.11 ± 0.02</td>
<td>0.32 ± 0.02</td>
</tr>
<tr>
<td>Feeding rate per meal (kg of DM/min)</td>
<td>0.0003 ± 0.00</td>
<td>0.0003 ± 0.00</td>
<td>0.0002 ± 0.00</td>
<td>0.0004 ± 0.00</td>
<td>0.23 ± 0.03</td>
<td>0.49 ± 0.02</td>
</tr>
<tr>
<td>DMI (kg/d)</td>
<td>2.11 ± 0.42</td>
<td>3.42 ± 0.34</td>
<td>1.68 ± 0.42</td>
<td>10.47 ± 0.05</td>
<td>0.12 ± 0.02</td>
<td>0.31 ± 0.01</td>
</tr>
</tbody>
</table>

²\( \sigma^2_v \) is additive genetic variance; \( \sigma^2_{pe} \) = permanent environmental variance; \( \sigma^2_e \) = block of experiment-treatment variance; \( \sigma^2_r \) = residual variance; \( h^2 \) = heritability; \( \rho \) = repeatability.
ferences between estimated heritability parameters in the aforementioned studies and those reported herein can be explained by the fact that, although those studies used data recorded over a 24-h period, they averaged these data over the entire test period to generate a single phenotype per animal for each feeding behavior trait, whereas we analyzed the daily records directly. Indeed, after aggregating our feeding behavior data into weekly averages, we observed higher heritability estimates (mean ± SE; 0.19 ± 0.04 to 0.32 ± 0.04) than for daily records, especially for traits based on the meal (Table 4). Repeatability estimates were also higher for weekly averages (0.46 ± 0.02 to 0.62 ± 0.03), demonstrating strong consistency in feeding behavior traits over time. The main reason for higher heritability and repeatability estimates obtained for weekly averages is the lower residual variances (Table 3 and Table 4), showing that weekly records can decrease the noise of daily records, thus reducing the residual variance. Similar heritability estimates were obtained for most of the feeding behavior traits in our study, with the exception of feeding rate, which appears to be more highly heritable.

Genetic and Phenotypic Correlations Among Feeding Behavior Traits

Genetic and phenotypic correlations among daily feeding behavior traits and daily DMI, milk energy, metabolic BW, change in BW, and residual feed intake in lactating Holstein cows

<table>
<thead>
<tr>
<th>Trait</th>
<th>$\sigma^2_u$</th>
<th>$\sigma^2_{pe}$</th>
<th>$\sigma^2_b$</th>
<th>$\sigma^2_e$</th>
<th>$h^2$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of feeder visits per day</td>
<td>35.43 ± 7.67</td>
<td>71.10 ± 6.66</td>
<td>13.54 ± 1.18</td>
<td>53.29 ± 0.72</td>
<td>0.20 ± 0.04</td>
<td>0.61 ± 0.02</td>
</tr>
<tr>
<td>No. of meals per day</td>
<td>0.25 ± 0.05</td>
<td>0.41 ± 0.04</td>
<td>0.10 ± 0.03</td>
<td>0.54 ± 0.01</td>
<td>0.19 ± 0.04</td>
<td>0.51 ± 0.02</td>
</tr>
<tr>
<td>Duration of each feeder visit (min)</td>
<td>1.12 ± 0.23</td>
<td>2.01 ± 0.20</td>
<td>0.68 ± 0.19</td>
<td>1.27 ± 0.02</td>
<td>0.22 ± 0.04</td>
<td>0.61 ± 0.03</td>
</tr>
<tr>
<td>Duration of each meal (min)</td>
<td>10.85 ± 1.78</td>
<td>11.92 ± 1.41</td>
<td>5.32 ± 1.37</td>
<td>20.84 ± 0.28</td>
<td>0.22 ± 0.03</td>
<td>0.46 ± 0.02</td>
</tr>
<tr>
<td>Total duration of feeder visits per day (min)</td>
<td>455.34 ± 76.02</td>
<td>565.28 ± 61.45</td>
<td>283.93 ± 72.89</td>
<td>756.90 ± 10.21</td>
<td>0.22 ± 0.03</td>
<td>0.49 ± 0.02</td>
</tr>
<tr>
<td>Intake per visit (kg of DM)</td>
<td>0.025 ± 0.005</td>
<td>0.047 ± 0.004</td>
<td>0.016 ± 0.005</td>
<td>0.029 ± 0.000</td>
<td>0.21 ± 0.02</td>
<td>0.61 ± 0.03</td>
</tr>
<tr>
<td>Intake per meal (kg of DM)</td>
<td>0.18 ± 0.03</td>
<td>0.27 ± 0.03</td>
<td>0.13 ± 0.03</td>
<td>0.26 ± 0.003</td>
<td>0.21 ± 0.04</td>
<td>0.54 ± 0.02</td>
</tr>
<tr>
<td>Feeding rate per visit (kg of DM/min)</td>
<td>0.0003 ± 0.000</td>
<td>0.0003 ± 0.000</td>
<td>0.0002 ± 0.000</td>
<td>0.0001 ± 0.000</td>
<td>0.32 ± 0.04</td>
<td>0.62 ± 0.03</td>
</tr>
<tr>
<td>Feeding rate per meal (kg of DM/min)</td>
<td>0.0004 ± 0.000</td>
<td>0.0004 ± 0.000</td>
<td>0.0003 ± 0.000</td>
<td>0.0001 ± 0.000</td>
<td>0.28 ± 0.04</td>
<td>0.62 ± 0.04</td>
</tr>
<tr>
<td>DMI (kg)</td>
<td>2.08 ± 0.41</td>
<td>3.24 ± 0.34</td>
<td>1.53 ± 0.39</td>
<td>3.32 ± 0.04</td>
<td>0.20 ± 0.04</td>
<td>0.52 ± 0.02</td>
</tr>
<tr>
<td>Milk energy (Mcal)</td>
<td>2.75 ± 0.88</td>
<td>9.82 ± 0.83</td>
<td>4.72 ± 1.14</td>
<td>5.97 ± 0.09</td>
<td>0.12 ± 0.04</td>
<td>0.54 ± 0.03</td>
</tr>
<tr>
<td>Metabolic BW (kg$^{0.75}$)</td>
<td>37.62 ± 4.71</td>
<td>23.43 ± 3.25</td>
<td>3.98 ± 1.42</td>
<td>6.11 ± 0.08</td>
<td>0.53 ± 0.05</td>
<td>0.86 ± 0.02</td>
</tr>
<tr>
<td>Change in BW (kg)</td>
<td>19.96 ± 2.57</td>
<td>7.39 ± 1.67</td>
<td>224.45 ± 42.79</td>
<td>4.49 ± 0.06</td>
<td>0.08 ± 0.08</td>
<td>0.11 ± 0.02</td>
</tr>
<tr>
<td>Residual feed intake (kg)</td>
<td>0.65 ± 0.15</td>
<td>1.40 ± 0.14</td>
<td>—</td>
<td>1.95 ± 0.03</td>
<td>0.16 ± 0.04</td>
<td>0.51 ± 0.01</td>
</tr>
</tbody>
</table>

$\sigma^2_u$ = additive genetic variance; $\sigma^2_{pe}$ = permanent environmental variance; $\sigma^2_b$ = block of experiment-treatment variance; $\sigma^2_e$ = residual variance; $h^2$ = heritability; $r^2$ = repeatability.

Table 4. Variance component estimates and genetic parameters (± SE) for weekly averages of feeding behavior, DMI, milk energy, metabolic BW, change in BW, and residual feed intake in lactating Holstein cows.

Comparing the same feeding behavior traits using the visit and meal concepts, we found little association between number of visits and number of meals (genetic and phenotypic correlations of 0.15 and 0.10), a weak association between duration of each visit and duration of each meal (genetic and phenotypic correlations of 0.30 and 0.09), and a moderate association between intake per visit and intake per meal (genetic and phenotypic correlations of 0.36 and 0.32). In beef cattle, Kelly et al. (2021) also reported a very low genetic correlations of 0.06 between duration of a feeding event and a meal. In contrast, the respective genetic and phenotypic correlations between feeding rate per visit and per meal (0.99 and 0.82; Figure 1) showed that the different feeding behavior definitions using either meals or visits potentially have little influence on defining feeding rate.

Estimated genetic and phenotypic correlations between DMI and daily feeding behavior traits were possible because of our access to daily records of DMI.
Dry matter intake had strong positive genetic correlations with feeding rate per visit and meal (0.71 and 0.68) and intake per visit and per meal (0.66 and 0.88). This implies that selection for higher DMI would favor animals that eat more rapidly and with a greater DMI per visit or per meal; this may lead to an unfavorable trend in feed efficiency. Despite similar phenotypic correlations, Lin et al. (2013) reported a low genetic correlation (0.11) between feeding rate and DMI in Holstein-Friesian heifers; however, they reported a moderate genetic correlation (0.48) between DMI and feeding duration. These differences can be explained by the population (lactating cows vs. heifers), as well as a difference in feeding rate calculation (kg of DMI divided by feeding duration per day). In beef cattle, results have varied between studies, such as a high genetic correlation between DMI and feeding rate in Angus and Charolais finishing steers (Chen et

![Figure 1](https://example.com/figure1.png)

**Figure 1.** Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among daily feeding behavior traits and daily DMI in lactating Holstein cows.
al., 2014), but no association between these 2 traits in a Nellore population (Benfica et al., 2020).

**Genetic and Phenotypic Correlations Between Feeding Behavior and Feed Efficiency Traits**

Genetic and phenotypic correlations between feeding behavior traits and MilkE, mBW, ΔBW, DMI, and RFI, measured as weekly averages, are depicted in Figure 2. Standard errors of estimates ranged from 0.03 to 0.14 (Supplemental Table S1). Heritability and repeatability estimates for feeding efficiency traits are shown in Table 4. Our results support that some feeding behavior traits were strongly genetically correlated with RFI and the energy sinks used in its calculation. Only ΔBW was not significantly associated, phenotypically or genetically, with feeding behavior.

Number of feeder visits had a weak genetic correlation with mBW (−0.13) and RFI (0.15); however, number of meals had a higher genetic correlation with mBW (−0.27) and with RFI (0.15). In addition, number of meals was positively genetically correlated with secreted MilkE (0.38). Despite the moderate genetic correlation, selection for animals that eat fewer meals per day may favor greater mBW and less MilkE. Similar genetic correlations between number of visits and RFI (0.14 and 0.18) were reported in beef cattle (Chen et al., 2014; Olson et al., 2021). Also, Kelly et al. (2021) observed a genetic correlations of 0.19 between residual energy intake and meals per day in crossbred growing cattle.

Total duration of feeder visits per day had greater genetic correlation estimates with feed efficiency traits than with duration of individual visits, although they generally followed the same pattern. Duration of each feeder visit, duration of each meal, and total duration of feeder visits per day were positively genetically correlated with DMI (0.20, 0.18, and 0.29, respectively) and MilkE (0.43, 0.44, and 0.62, respectively), and negatively genetically correlated with mBW (−0.10, −0.17, and −0.37, respectively). Only total duration of feeder visits per day showed a significant genetic correlation with RFI (0.20). Therefore, cows that spend more time at the feeder per day tend to be less efficient. This genetic association is consistent with results reported in beef cattle (Chen et al., 2014), and a similar genetic correlation between total feeding duration and RFI (0.27) was reported in Holstein-Friesian heifers (Kelly et al., 2021).

Intakes per visit and meal were genetically associated with all feed efficiency traits except ΔBW. Therefore, cows with greater DMI per visit or meal tend to be less efficient genetically with greater DMI per day and greater mBW that was not fully compensated by greater MilkE, hence also greater RFI. Intake per meal showed higher genetic correlation estimates with feed efficiency traits compared with those obtained for intake per visit; this was expected because one meal can capture a greater proportion of DMI per day than one feeder visit. Positive genetic correlations of different magnitudes (0.04 to 0.56) between feed intake per visit and RFI have been reported in several pig breeds (Lu et al., 2017; Kavlak and Uimari, 2019; Homma et al., 2021).

Strong genetic correlation estimates were observed between RFI and both visit and meal feeding rate (0.47 and 0.43), suggesting that selection of animals that eat at a slower rate will favor efficient animals with lower breeding values for RFI. Feeding rate also had a strong genetic association with DMI (0.69) and mBW (0.67). Lin et al. (2013) observed a negligible genetic correlation between feeding rate and RFI in dairy heifers. However, Connor et al. (2013) concluded that efficiency may be associated with feeding rate, as they observed a positive phenotypic association between feeding rate and RFI. In addition, weak estimated genetic correlations between feeding rate and RFI and residual energy intake (0.10 to 0.13) were found in beef cattle, although feeding rate was highly genetic correlated with DMI, ME intake, and mBW (Chen et al., 2014; Kelly et al., 2021). Some studies in pigs reported genetic correlation estimates from 0.21 to 0.47 between feeding rate and RFI (Lu et al., 2017; Homma et al., 2021).

The vast majority of phenotypic correlations between feeding behavior traits and feed efficiency traits followed the same direction as genetic correlations for the corresponding traits, but with lower magnitude. Despite being limited in number, studies in dairy cattle nutrition have reported differences between feeding behavior in groups of animals classified as high or low RFI (Williams et al., 2011; Ben Meir et al., 2019). In support of our data, slower feeding rate and shorter daily feeding duration have been reported in efficient animals (Green et al., 2013; Xi et al., 2016).

Overall, the genetic correlations between feeding behavior and feed efficiency estimated in the present study suggest that selecting dairy cows with slower feeding rates and with less intake per visit or meal may favor animals with lower RFI that are genetically more feed efficient. In addition to that, feeding behavior traits had higher heritability estimates compared with RFI. Therefore, feeding behavior traits could be used in genetic selection programs as indicators of feed efficiency, which would increase selection accuracy for RFI due to the possibility of substantially increasing the number of phenotypes compared with measuring individual daily intakes.
Figure 2. Genetic correlations (A) and phenotypic correlations (B) between weekly feeding behavior traits and weekly feed efficiency traits in lactating Holstein cows.

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Implications

Genetic selection for feed efficiency is challenging due to the difficulty of measuring individual feed intakes on a large number of cows. However, genomic selection has enabled the inclusion of feed efficiency traits, such as RFI and Feed Saved, in national genetic evaluations for dairy cattle (Pryce et al., 2015; VanRaden et al., 2018, 2021). Although genomic selection allows genetic improvement in feed efficiency, the reliabilities of genomic breeding values for RFI are low (Li et al., 2020). In addition, these systems depend on continued collection of phenotypic measurements to calculate RFI. Traits that are easier to measure, less expensive, generate a greater number of records, and are correlated with feed efficiency traits can be used as indicator traits for feed efficiency. Our results demonstrate that feeding behavior could be a potential indicator of dairy cow feed efficiency. The feeding behavior traits proposed in this study are heritable, and some were genetically correlated with feed efficiency traits. Feeding rate seems to be the most promising indicator of feed efficiency, because it showed a strong genetic correlation with RFI. Although feed intake is part of feeding rate calculation (kg of DM/min), feeding rate can be obtained using a different system that does not involve expensive automated feeders. Feeding rate could be measured, or approximated, using wearable sensors or computer vision systems, enabling implementation on commercial farms and generating enormous quantities of data (Bloch et al., 2021). This would increase the reliabilities of genetic evaluations for feed efficiency and accelerate genetic progress. Although measuring feeding rate is feasible, its implementation in commercial farms is still under study. Thus, for an immediate and easier implementation, total duration of visits could be an interesting alternative.

CONCLUSIONS

In this study, we investigated the genetic portions of different feeding behavior traits and their genetic associations with feed efficiency traits in lactating US Holstein cows. Feeding behavior traits were heritable and repeatable across days and weeks, indicating that a significant proportion of phenotypic variance is explained by additive genetic effects, such that feeding behavior could be incorporated into genetic selection programs. Interestingly, some feeding behavior traits were strongly genetically correlated with feed efficiency; in particular, feeding rate showed a strong positive genetic correlation with DMI, mBW, and RFI. Overall, our results suggest that measures of feeding behavior could be useful indicators of dairy cow feed efficiency and that individual cows that eat at a slower rate may be more feed efficient.

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