ABSTRACT

Selection for feed efficiency, the ratio of output (e.g., milk yield) to feed intake, has traditionally been limited on commercial dairy farms by the necessity for detailed individual animal intake and performance data within large animal populations. The objective of the experiment was to evaluate the effects of individual animal characteristics (animal breed, genetic potential, milk production, body weight (BW), daily total dry matter intake (TDMI), and energy balance) on a cost-effective production efficiency parameter calculated as the annual fat and protein (milk solids) production per unit of mid-lactation BW (MSperBWlact). A total of 1,788 individual animal intake records measured at various stages of lactation (early, mid, and late lactation) from 207 Holstein-Friesian and 200 Jersey × Holstein-Friesian cows were used. The derived efficiency traits included daily kilograms of milk solids produced per 100 kg of BW (dMSperBWint) and daily kilograms of milk solids produced per kilogram of TDMI (dMSperTDMI). The TDMI per 100 kg of BW was also calculated (TDMI/BWint) at each stage of lactation. Animals were subsequently either ranked as the top 25% (Heff) or bottom 25% (Leff) based on their lactation production efficiency (MSperBWlact). Dairy cow breed significantly affected animal characteristics over the entire lactation and during specific periods of intake measurements. Jersey crossbred animals produced more milk, based on a lower TDMI, and achieved an increased intake per kilogram of BW. Similarly, Heff produced more milk over longer lactations, weighed less, were older, and achieved a higher TDMI compared with the Leff animals. Both Jersey × Holstein-Friesian and Heff cows achieved superior production efficiency due to lower maintenance energy requirements, and consequentially increased milk solids production per kilogram of BW and per kilogram of TDMI at all stages of lactation.

Indeed, within breed, Heff animals weighed 20 kg less and produced 15% more milk solids over the total lactation than Leff. In addition, Heff achieved increased daily milk solids yield (+0.16 kg) and milk solids yield per kilogram of TDMI (+ 0.23 kg/kg DM) during intake measurement periods. Moreover, the strong and consistently positive correlations between MSperBWlact and detailed production efficiency traits (dMSperBWint, dMSperTDMI) reported here demonstrate that MSperBWlact is a robust measure that can be applied within commercial grazing dairy systems to increase the selection intensity for highly efficient animals.

Key words: feed efficiency, animal intake, dairy cow

INTRODUCTION

Sustainable and efficient conversion of feed to milk has been an important determinant of farm productivity within all dairy production systems due to the prominent effect of feed costs on total milk production costs (Dillon et al., 2008; EU, 2019). More recently, the importance of feed efficiency (FE) has taken on even greater prominence due to its considerable additional effects on both the environmental efficiency and resilience of dairy production systems (de Haas et al., 2017; Hurley et al., 2017). The underlying principle of most FE evaluations is to improve the balance between output (production) and input (feed intake) characteristics (Martin et al., 2021a). On that basis, recent reviews of dairy cattle improvement programs have concluded that the inclusion of other production efficiency parameters as estimates of FE in selection indices worldwide can further accelerate the rate of improvement in animal traits influencing both productivity and environmental sustainability (Cole and VanRaden, 2018).

Although evaluations of production efficiency are commonplace within various dairy production systems within the literature, efforts to achieve consensus on agreed parameters which to incorporate within breeding programs have yielded limited success (Tempelman and Lu, 2020). Considerable challenges remain regarding the genetic evaluation due to the diverse array of
feed and production efficiency traits evaluated (Berry and McCarthy, 2021) and the frequency of measures both within and between lactations (Pryce et al., 2015; Fischer et al., 2020). While many discrete methodologies have been proposed (Berry and Crowley, 2013), residual feed intake (RFI) is most commonly used to determine FE in dairy cattle as the difference between the actual feed intake of an animal and its predicted feed intake necessary to meet animal requirements primarily for production, maintenance, and reproduction (Martin et al., 2021a). However, these breeding values are generally derived indoors on high supplementary grain diets, which may not be applicable to studies within a grazing system, where the majority of an animal’s lifetime dietary intake originates from fresh pasture (Lahart et al., 2020).

The opportunities to improve overall animal efficiency within grazing systems are limited because the possibility to increase pasture allowance to allow higher levels of animal intake and performance is inefficient, as it results in higher refusals and reduced utilization of pasture and subsequently impaired feed quality (Pérez-Prieto and Delagarde, 2013; Delaby and Horan, 2017; Fischer et al., 2020). Moreover, dairy cattle within pasture-based production systems are exposed to limiting and fluctuating grazing conditions (Delaby et al., 2018) and are able to express their genetic potential only partially (Mendes et al., 2021). Although a plethora of studies have evaluated cow production efficiency within controlled grazing experiments using detailed methodologies, which are not available on commercial farms (Prendiville et al., 2009; Coffey et al., 2017; O’Sullivan et al., 2019), Evers et al. (2021a) recently reported significant variation in the lactation production efficiency [total lactation milk fat plus protein production (milk solids) per unit of mid-lactation BW] within a large data set of Irish commercial pasture-based dairy farms consisting of over 20,000 records. Estimating production efficiency indirectly based on farm level parameters is interesting, especially if we are able to identify an indicator, which does not require individual daily total DMI (TDMI) measurements and is accessible on the farm. In that study, highly efficient dairy cattle were characterized by high levels of milk solids production and a lower BW. Although large variability in production efficiency was observed by Evers et al. (2021a) on commercial farms, little is known of the specific genetic and phenotypic characteristics of dairy cattle that exhibit increased lactation production efficiency. Thus, the objectives of this study were to outline specific animal characteristics that underlie the feed and production efficiency of dairy cows and evaluate the relationships between cost-effective and traditional measures of animal efficiency within lactation on which to more accurately define individual animal traits that support increased production efficiency within grazing systems. Additionally, the correlations among various detailed feed and production efficiency traits and measurement timings are evaluated as the basis for more accurate and intensive selection on dairy cow efficiency in the future.

**Materials and Methods**

Because no human or animal subjects were used, this analysis did not require approval by an Institutional Animal Care and Use Committee or Institutional Review Board. Previous studies’ license numbers and approvals have been previously published in the relevant studies (McClearn et al., 2014; Coffey et al., 2017; Evers et al., 2021b; McClearn et al., 2021).

**Data**

Records from 2 experimental research farms (Clonakilty and Curtins Research Farm) from the national research organization Teagasc, located in the south of Ireland, were available. In total, 1,788 animal TDMI measurements, BW, BCS, and milk recording data were used from 9 treatments over multiple years (2014–2019, inclusive). The 407 cows that were selected for the current study originated from several controlled experiments that evaluated alternative grazing strategies, stocking rates, breeds, and sward characteristics (McCarthy et al., 2014; Coffey et al., 2017; Evers et al., 2021b; McClearn et al., 2021). A seasonal spring-calving system is predominantly found on Irish dairy farms and the mean calving date across the years was February 14. All animals had full-time access to pasture postcalving, and thus the TDMI primarily consisted of fresh pasture with 0 or up to 3.6 kg of DM of concentrates included during periods of pasture deficits or inclement weather conditions. On average, cows were fed 1.7, 0.4, and 2.1 kg of DM of concentrate in early, mid, and late lactation. Animal intake data were collected for 6 d in late March or the start of April (53 ± 16 DIM) for the early lactation period; mid-lactation data were collected between mid-June and mid-August (100 ± 24 DIM), and late lactation measurements were conducted at the end of September or the start of October (211 ± 23 DIM).

Both herds included Holstein-Friesian (HF) as well as Jersey × Holstein-Friesian (JFX) crossbred dairy cattle which were thereby classified into these 2 breeds (BR): where the BR proportion of the animal was ≥75% Holstein-Friesian, these animals will be referred to as HF; where the BR proportion was ≥25% Jersey, and to a lesser proportion other BR, the animal was
considered JFX. There were 23, 22, 19, 15, and 21% of the animals from the study in parity 1, 2, 3, 4, and ≥5.

**Animal Measurements**

Cows were milked twice a day at 0700 and 1500 h and the individual milk yield was recorded, each time throughout the year, using electronic milk meters (Dairymaster, Causeway Co.). Milk fat, protein, and lactose concentrations were determined via weekly sample collection from successive evening and morning milkings and were thereafter analyzed using a MilkoScan 203 instrument (DK-3400, Foss Electric). The full-lactation milk profile (milk and milk solids) per cow was derived from these measurements and was used for analysis. The standard annual milk yield (Std-MY) was calculated according to the fat and protein content following the equation below (INRA, 2018):

\[
\text{StdMY} = \text{annual milk yield} \times \left(0.0055 \times (\text{fat content (g/kg)} - 40) + 0.0033 \times (\text{protein content (g/kg)} - 31) + 0.44\right) / 0.44.
\]

Body weight and BCS were recorded biweekly. All cows were weighed with the Winweigh software package (Tru-Test Limited) after morning milking. The BW included in the study were taken in the first week of June for the mid-lactation BW (BW\text{lact}) and at every DMI measurement in early, mid, and late lactation (BW\text{int}). The BW change during the intake measurement periods was calculated as the difference between the BW before the week of measurement plus the following 2 weeks, divided by 14 d (Buckley et al., 2000). Body condition score was measured by an experienced evaluator on each farm on a scale of 1 to 5 (with 1 being emaciated and 5 being obese) with increments of 0.25, similar to the scoring outlined by Edmonson et al. (1989).

Data for individual cow TDMI was obtained by using the n-alkane technique (Mayes et al., 1986), as modified by Dillon and Stakelum. (1989), on multiple occasions throughout the stage of lactation (S) across 6 yr (2014–2019, inclusive). The intake measurements periods were classified as early, mid, and late lactation. In line with the seasonal spring-calving system in Ireland, intake data in early lactation were collected in late March or at the start of April (53 ± 16 DIM); mid-lactation data were collected between mid-June and mid-August (100 ± 24 DIM); and late-lactation measurements were conducted at the end of September or the start of October (211 ± 23 DIM). Twice a day for 12 consecutive days, cows were dosed after milking with paper bungs containing 500 mg of C32-alkane (n-dotriacontane). For each measurement period, fecal grab samples were collected from each cow for 6 d from d 7 to 12 and initially stored in a freezer. Once thawed, these samples were subsequently bulked and prepared for analysis. On the same days, selected herbage samples were also taken. The ratio of herbage C33-alkane (tritriacontane) to dosed C32-alkane was used to estimate TDMI, and the n-alkane concentration was determined as described by Dillon (1993). Concentrate allocations differed between year and treatments depending on herbage availability.

Observations for individual daily TDMI in this study were collected between 13 and 251 DIM, averaging at 16.0, 17.0, and 17.7 kg of DM during early, mid, and late lactation, respectively.

**Cow Efficiency Parameters**

The energy values of the herbage and concentrates were determined at each intake measurement, based on the French net energy system: 1 Unité Fourragère Lait (UFL) is defined as the net energy content of 1 kg of standard barley, which is equivalent to 1,760 kcal (INRA, 2018). The sum of the net energy content of the herbage and concentrate consumed were then used to determine the total net energy intake (NEI) of the animal.

The NE\text{L} was calculated as follows (INRA, 2018):

\[
\text{NE}_L = \text{daily milk yield (kg)} \times (0.0055 \times (\text{fat content (g/kg)} - 40) + 0.0033 \times (\text{protein content (g/kg)} - 31) + 0.44).
\]

Net energy requirements for maintenance (NE\text{M}) and growth (NE\text{G}) were calculated using the following formulas (INRA, 2018):

\[
\text{NE}_M = 0.041 \times \text{BW}^{0.75} \times 1.2,
\]

where BW\text{0.75} is the metabolic BW of the animal; and

\[
\text{NE}_G = 3.25 - 0.08 \times \text{age}, \text{if age is <40 mo.}
\]

The measures of milk production efficiency calculated have previously been published in various studies (Prendiville et al., 2009; Hurley et al., 2016; Coffey et al., 2017) and included

\[
\text{MSperBW_{lact}} = \text{total kilogram of milk solids produced per kilogram of mid-lactation BW;}
\]
dMSperBW
\text{int} = \text{daily kilogram of milk solids produced per 100 kg of BW at the time of intake;}

dMSperTDMI = \text{daily kilogram of milk solids produced per kilogram of total DMI (TDMI)}.

The standard annual milk yield per kilogram of mid-lactation BW was StdMYperBW
\text{int}.

Energy balance (EB; in UFL) was also calculated for individual animals as the difference between total energy intake (NEI) and estimated energy requirement as the sum of net energy requirement for lactation, maintenance, and growth, as described by Horan et al. (2006):

\[ EB = \text{NEI} - (\text{NEL} + \text{NEM} + \text{NEG}). \]

Energetic calculations were based on daily milk production, BW, and estimated TDMI during the intake measurement periods, as the energy (UFL) available to produce 1 kg of standard (4.0% fat and 3.1% protein content) milk production after accounting for NEM and NEG as described by Prendiville et al. (2009) and was calculated as

\[ \text{UFLforMY: } (\text{NEI} - \text{NEM} - \text{NEG})/\text{kg dStdMY}. \]

The residual energy intake (REI), where the total predicted UFL intake according to the model including parity, metabolic BW, BCS and daily standard milk production (4.0% fat and 3.1% protein content) is subtracted from the calculated total UFL requirement (NEL + NEM + NEG) as described by Prendiville et al. (2009) and was calculated as

\[ \text{REI} = \text{calculated UFL requirement} - \text{predicted UFL intake}. \]

**Data Edits**

Obvious data errors or missing data and outliers of the data of the population for daily and full-lactation production traits (i.e., milk yield, fat yield, and protein yield), BW, and BCS were discarded. Following edits, the final data set contained 1,788 records from 407 individual animals across the 6-y study period and a detailed breakdown of the records used for analysis and the respective breeds are presented in Table 1. To avoid the influence of the animal’s own performance on its genetic evaluation, the Economic Breeding Index (EBI) was either the animal’s previous EBI obtained from the 2013 national genetic evaluation (i.e., before data collection) or the animal’s calculated parental average EBI for primiparous animals (Table 2).

**Statistical Analysis**

All statistical analyses were carried out using SAS (version 9.4, 2010; SAS Institute Inc.). The analyses were divided into 3 sections. First, the annual full-lactation performance of milk and milk solids yield, mid-lactation BW, and the overall production efficiency parameter MSperBW
\text{act} were analyzed using mixed models (PROC MIXED). Year (2014 to 2019, inclusive), BR (HF and JFX), parity (1, 2, 3, 4, ≥ 5), farm (1 or 2), and treatment (1 to 9) were included as fixed effects, whereas total DIM (for milk production traits) or calving day of the year (for BW and MSperBW
\text{act}), and genetic merit (EBI subindices) were included as continuous effects. Animal was included as a random effect in the model.

Second, milk and milk solids production, BW and BCS, and various production efficiency parameters at each intake measurement were analyzed using mixed models (PROC MIXED). Year (2014 to 2019, inclusive), BR (HF and JFX), parity (1, 2, 3, 4, ≥ 5), and stage of lactation (early, mid, and late) were included in the model.

**Table 1.** Number of lactations, cows, and mean parity (SD in parentheses) for both breeds\(^1\) available for the present study

<table>
<thead>
<tr>
<th>Breed</th>
<th>Lactation</th>
<th>Cow (n)</th>
<th>Parity</th>
</tr>
</thead>
<tbody>
<tr>
<td>HF</td>
<td>879</td>
<td>207</td>
<td>3.2 (1.88)</td>
</tr>
<tr>
<td>JFX</td>
<td>909</td>
<td>200</td>
<td>2.9 (1.66)</td>
</tr>
</tbody>
</table>

\(^1\)Breed: HF = Holstein-Friesian, where ≥75% of the breed proportion was Holstein-Friesian; JFX = Jersey × Holstein-Friesian crossbreds, where ≥25% of the breed proportion was Jersey.

**Table 2.** The mean and SD of the Economic Breeding Index (EBI), EBI subindices, and PTA for milk production traits for both breeds\(^1\)

<table>
<thead>
<tr>
<th>Trait</th>
<th>HF</th>
<th></th>
<th></th>
<th>JFX</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>EBI (€)</td>
<td>151</td>
<td>51.6</td>
<td>156</td>
<td>46.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subindex (€)</td>
<td>Milk</td>
<td>48</td>
<td>18.9</td>
<td>58</td>
<td>24.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maintenance</td>
<td>14</td>
<td>10.7</td>
<td>32</td>
<td>9.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fertility</td>
<td>66</td>
<td>44.7</td>
<td>53</td>
<td>38.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Beef</td>
<td>−13</td>
<td>10.7</td>
<td>−31</td>
<td>10.1</td>
<td></td>
</tr>
<tr>
<td>PTA (kg)</td>
<td>Milk yield</td>
<td>53</td>
<td>153.1</td>
<td>−85</td>
<td>137.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fat yield</td>
<td>8.83</td>
<td>4.892</td>
<td>11.57</td>
<td>5.423</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protein yield</td>
<td>5.85</td>
<td>3.723</td>
<td>4.46</td>
<td>3.837</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fat (%)</td>
<td>0.12</td>
<td>0.125</td>
<td>0.26</td>
<td>0.111</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protein (%)</td>
<td>0.07</td>
<td>0.056</td>
<td>0.13</td>
<td>0.054</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Breed: HF = Holstein-Friesian, where ≥75% of the breed proportion was Holstein-Friesian; JFX = Jersey × Holstein-Friesian crossbreds, where ≥25% of the breed proportion was Jersey.
as fixed effects, whereas genetic merit (EBI subindices) was included as a continuous effect. Animal was included as a random effect in the model.

Third, 2 efficiency groups were established based on the production efficiency level for MSperBW\textsubscript{act}. For this, the bottom 25% (Leff) and top 25% (Heff) animals within each breed group were identified and the annual and daily milk and milk solids production, BW, BCS, MSperBW\textsubscript{act}, and various FE parameters at each intake measurement were analyzed using mixed models (PROC MIXED). Year (2014 to 2019, inclusive), BR (HF and JFX), parity (1, 2, 3, 4, ≥5), stage of lactation (early, mid, and late), and production efficiency level (Leff or Heff), and their respective interactions were included in the model as fixed effects, whereas genetic merit (EBI subindices) was included as a continuous effect, while animal was included as a random effect in the model.

The relationship between MSperBW\textsubscript{act}, annual and daily milk solids yield, BW\textsubscript{act}, TDMI, various production efficiency traits, EB, and REI was computed using partial Spearman’s rank correlations adjusted for year, BR, parity, and calving day of the year.

**RESULTS**

**Milk Production, Body Weight, Animal Intake, and Production Efficiency**

Breed had a significant effect on milk production characteristics (Table 3). Although annual milk yield was significantly \(P < 0.001\) higher for HF (+286 kg) compared with JFX (5,648 kg), JFX animals had a higher milk solids yield (+8 kg; \(P < 0.01\)). In mid-lactation, HF animals were 52 kg heavier than JFX (477 kg; \(P < 0.001\)). Thus, MSperBW\textsubscript{act} was significantly \(P < 0.001\) greater for JFX (+0.12 kg/kg) compared with HF (0.95 kg/kg). Whereas HF animals achieved a higher \(P < 0.001\) daily milk yield (+1.3 kg) compared with JFX (24.5 kg), the daily milk solids yield had no difference (2.10 kg), despite a higher fat and protein content (+0.13 and +0.08%, respectively) for JFX, compared with HF contemporaries (4.72 and 3.85% for milk fat and protein content, respectively). Body weight differed significantly at the time of intake measurement between breeds \(P < 0.001\), yet BCS was similar (2.95 units). Breed also had a significant effect on TDMI and various measures of production efficiency. Despite TDMI being higher for HF (17.1 vs. 16.7 kg of DM; \(P < 0.001\)), JFX had a significantly higher TDMI per 100 kg of BW (+0.25 kg of DM/100 kg) and a higher \(P < 0.001\) daily milk solids yield per kilogram of BW at the time of intake measurement (+0.05 kg/100 kg; MSperBW\textsubscript{int}). Similarly, daily milk solids production per kilogram of TDMI (dMSperTDMI) was also higher (+0.005 kg/kg DM) for JFX than HF \(P < 0.001\) during each intake measurement. However, BR had no effect \(P > 0.05\) on either EB (0.42 UFL/d), UFL\textsubscript{forMY} (0.47 UFL/d), or REI (0.20 UFL).

**Characteristics of Animals Partitioned on MSperBW\textsubscript{act}**

The least squares means for MSperBW\textsubscript{act}, StdMYperBW\textsubscript{act}, annual milk and milk solids yields, mid-lactation BW\textsubscript{act} and BCS\textsubscript{act}, lactation number, total DIM, and genetic merit of animals differing in production efficiency level from both BR are described in Table 4. By construction, the MSperBW\textsubscript{act} and StdMYperBW\textsubscript{act} were significantly greater \(P < 0.001\) for Heff (+0.26 and +3.4 kg/kg for HF and +0.30 and +3.8 kg/kg for JFX, respectively) compared with Leff (0.80 and 10.9 kg/kg for HF and 0.91 and 12.2 kg/kg for JFX, respectively). Similarly, annual milk yield for HF decreased by 751 kg for the Leff animals, whereas Leff JFX animals had 557 kg less milk across lactation. Differences in annual milk solids yield between Leff and Heff were 73 and 70 kg for HF and JFX, respectively. Additionally, both breeds exhibited a lower BW\textsubscript{act} and BCS\textsubscript{act} with increasing efficiency.

Greater production efficiency level (Heff) was associated with more mature animals in both BR (+0.2 and +1.0 lactations for HF and JFX, respectively) and a longer lactation length (total DIM) of +22 and +25 d for HF and JFX, respectively. Moreover, an increased Milk subindex (SI; +€19 and +€24 for HF and JFX, respectively) and an increased Maintenance SI (+14 and +€12 for HF and JFX, respectively) were also characteristics of the most efficient animals. Conversely, both Fertility SI and Beef SI decreased for both BR for Heff. Finally, the Heff animals from both BR had a greater TDMI and TDMI/BW\textsubscript{int} during the measurement periods. A significant BR × production efficiency level interaction for MSperBW\textsubscript{act}; StdMYperBW\textsubscript{act}; annual milk yield, mid-lactation BW\textsubscript{act}, and lactation number implied a greater increase in efficiency for Heff JFX.

**Stage of Lactation**

Table 5 shows the effect of lactation stage and efficiency group (in terms of level of MSperBW\textsubscript{act}) on individual animal performance, TDMI, and production efficiency traits. Mean DIM for measurements in early, mid, and late lactation were 45 (±11), 97 (±23), and 211 (±23) days, respectively. Stage of lactation had a significant effect on all milk production, BW\textsubscript{int}, and production efficiency parameters estimated except for BCS\textsubscript{int}, where it approached significance \(P =\)
Equally, milk production, BW<sub>int</sub>, and efficiency parameters differed significantly between production efficiency groups at various stages of lactation. Daily milk and milk solids yield were consistently higher for Heff animals (<i>P</i> < 0.001) and although Heff cows had a higher daily milk production in early (+1.3 kg) and...
mid-lactation (+3.3 kg), low and high efficiency groups had no difference in late lactation (18.1 kg). In contrast, Heff achieved a higher \( (P < 0.001) \) daily milk solids yield than Leff in early (+0.16 kg) and mid-lactation (+0.38), which they subsequently maintained (2.26 kg) before the daily milk solids yield reduced to 1.74 (+0.15 kg compared with Leff) in late lactation. Contrary to this, Leff had a lower daily milk solids yield (−0.16 kg) in mid-lactation than in early lactation (2.04 kg). We observed no difference in BW\textsubscript{int} between high and low ranked animals \( (P = 0.37) \) in early or mid-lactation, but we observed a significant difference in late lactation, when Heff were 10 kg heavier \( (P < 0.05) \) than Leff contemporaries. In contrast, and although BCS\textsubscript{int} did not change until late lactation, Heff were thinner \( (P < 0.05) \) in early and mid-lactation, but obtained similar BCS\textsubscript{int} to Leff in late lactation when all animals had a BCS\textsubscript{int} of 2.90 units. The Heff animals reached peak TDMI in mid-lactation (17.4 kg of DM) and maintained it thereafter (17.3 kg of DM), whereas, Leff had a similar TDMI in early and mid-lactation (15.8 kg of DM) and only reached peak TDMI in late lactation when it was similar to the intake level of Heff (17.0 kg of DM). Whereas the TDMI/BW\textsubscript{int} did not change across lactation for Leff (3.17 kg of DM/100 kg), Heff had a consistently greater \( (P < 0.001) \) TDMI/BW\textsubscript{int} throughout lactation, reaching a peak of 3.63 kg of DM/100 kg in mid-lactation and dropping back to 3.15 kg of DM/100 kg by late lactation.

Although dMSperBW\textsubscript{int} was consistently greater for Heff, the differential decreased in late lactation. Energy balance was negative in early (−2.28 UFL/d) and mid-lactation (−0.54 UFL/d) for both efficiency groups and positive in late lactation, although higher for Leff (1.57 vs. 0.86 UFL/d). The energy available for standard milk yield after accounting for maintenance and growth (UFLavail\textsubscript{MY}) did not differ between low and high efficiency animals until late lactation, when more energy was available for Leff (+0.05 UFL/kg). Finally, albeit unaffected in early lactation, REI was significantly lower for Leff in mid and late lactation \( (P < 0.05) \).

**Correlation Coefficient Between Efficiency Parameters**

The correlation between various animal performance and efficiency variables across both breed groups are presented in Table 6. The MSperBW\textsubscript{ lact} was positively associated with daily milk solids yield, TDMI, TDMI/BW\textsubscript{int}, dMSperBW\textsubscript{int}, dMSperTDMI, and REI. However, a negative association was evident between MSperBW\textsubscript{ lact} and BW\textsubscript{ lact}, EB, and UFLavail\textsubscript{MY}. Annual and daily milk and milk solids yield were posi-
tively associated with BW\textsubscript{lact}, TDMI, TDMI/BW\textsubscript{lact}, dMSperBW\textsubscript{int}, dMSperTDMI, and REI, but negatively associated with EB and UFL\textsubscript{availMY}. We observed a moderate positive correlation between BW\textsubscript{lact} and TDMI. A strong positive correlation was found between TDMI and EB, UFL\textsubscript{availMY} and REI. The TDMI/BW\textsubscript{lact} was positively associated with dMSperBW\textsubscript{int} and all energetic efficiency parameters, but negatively associated with BW\textsubscript{lact} and dMSperTDMI. Additionally, strong positive correlations were observed between dMSperBW\textsubscript{int} and dMSperTDMI, whereas strong negative correlations were found between dMSperTDMI and EB, UFL\textsubscript{availMY} and REI. Energy balance and UFL\textsubscript{availMY} and REI were also strongly correlated, similar to UFL\textsubscript{availMY} and REI.

The relationship between MSperBW\textsubscript{lact} and MSper BW\textsubscript{int} at the different stages of lactation from this study are illustrated in Figure 1. The strongest relationship was found in mid-lactation (R\textsuperscript{2} = 0.39), whereas the weakest relationship occurred in late lactation (R\textsuperscript{2} = 0.20). Although not significantly different in early and mid-lactation (Table 5), Heff animals exhibited a greater recovery from negative EB than Leff as lactation progressed (Figure 2). In late lactation (≥150 DIM), however, Heff animals reduced their EB faster again.

**DISCUSSION**

Within grazing systems, productivity is dependent on achieving a balance between the competing objectives of a high daily DMI to optimize milk production per cow and also achieving high feed conversion efficiency, which necessitates excellent pasture management and quality over the entire lactation. However, enhancing production efficiency within grazing systems is a multidimensional continuum beginning at the farm and system level (compact calving, high genetic potential cows with increased longevity, high quality pasture utilization) and ending with refined improvements at the animal level (Delaby and Horan, 2017; Fischer et al., 2020). Even though previous studies often evaluated the effects of management strategies on animal intake (i.e., stocking rates, pasture management), few studies have focused on the evaluation of specific animal characteristics that enhance cow efficiency on farms (Grainger and Goddard, 2004; Prendiville et al., 2011; McCarthy et al., 2013). Thus, this study focused on the latter part of the continuum, and aimed to compare both lactation wide data that is easily accessible by farmers and specific detailed production efficiency data measured within controlled environments to describe the specific characteristics of highly efficient animals within grazing systems. We concluded that MSperBW\textsubscript{lact} is a widely accessible measure as a proxy for production efficiency.
Figure 1. Relationship between annual milk solids production per kilogram of mid-lactation BW (MSperBW_{int}) and daily milk solids production per kilogram of BW at the time of intake (MSperBW_{lact}) in (a) early, (b) mid, and (c) late lactation.
Figure 2. Relationship between DIM and energy balance at intake measurement in (a) early, and (b) mid, and (c) late lactation for low (○) and high (●) production efficiency level based on annual milk solids production per kilogram of mid-lactation BW (MSPerBW_{mid}). UFL = unité fourragère lait.
for commercial farms, including the full-lactation performance (milk solids yield) and a mid-lactation BW, and can be a robust and effective parameter to evaluate overall cow efficiency on the farm, while also showing consistent correlations to other efficiency traits across lactation. The objective of this study was to also outline more specific characteristics of high efficiency animals across lactation and across years.

The results from this experiment give further credence to previous (inter)national research that points to the superior compatibility of JFX cows both within controlled experiments (Lopez-Villalobos et al., 2000; Grainger and Goddard, 2004; Prendiville et al., 2009; Coffey et al., 2017) and commercial pasture-based dairy farms (Coffey et al., 2016; Evers et al., 2021a). Prendiville et al. (2009) described similar differences in daily TDMI between HF and JFX cows (16.9 and 16.2 kg of DM, respectively) within Irish grazing systems at similar SR to the present experiment, while Coffey et al. (2017) reported similar differences in terms of TDMI/BWint between breeds (3.30 and 3.55 kg of DM/100 kg for HF and JFX, respectively). The analyses of this study also accentuate the high production efficiency attainable with crossbred cows reported elsewhere (Prendiville et al., 2009; Coffey et al., 2017; Evers et al., 2021a). The JFX cows achieved a higher total milk solids yield driven by higher fat and protein composition from a reduced milk volume, a lower BWlact, and a high feed intake per kilogram of BWint. Jersey crossbred animals showed a higher daily milk solids production both per kilogram of TDMI and per kilogram of BWint, while achieving similar overall EB, which has been consistently reported in many previous studies and can be associated with a greater dilution of maintenance requirements (Grainger and Goddard, 2004; Prendiville et al., 2009; Coffey et al., 2017).

The overall level of TDMI/BWint, dMSperBWint, and dMSperTDMI within the experiment (3.37 kg of DM/100 kg, 0.39 kg/100 kg, and 0.112 kg/kg DM, respectively) compare favorably with previous comparable grazing studies (Mackle et al., 1996; Prendiville et al., 2009; Beecher et al., 2014) and is indicative of highly efficient intensive grass-based systems. Within BR group, the current study also shows large variation in cow efficiency among pasture-fed animals. At an overall level, Heff animals within both breeds are characterized as older animals, achieving increased milk solids production over longer lactations, and with a lower mid-lactation BW than Leff contemporaries. The overall level of production efficiency in terms of available energy to produce 1 kg of standard milk achieved by Heff and Leff in this study (UFLavailMY = 0.43 UFL/kg) is similar to the theoretical potential (0.44 UFL/kg; INRA, 2018). Similar to previous studies, Heff had increased daily TDMI both per cow and per 100 kg of BW, resulting in increased milk solids production per unit intake (Martin et al., 2021b).

Evaluating FE in dairy cows is more challenging than in growing animals because catabolic and anabolic processes vary during lactation (Roche et al., 2009; Berry and Crowley, 2013). Different biological processes are involved at the different lactation stages, in particular body reserve mobilization in early lactation and therefore, RFI components are likely to vary when taken at different times throughout lactation (Li et al., 2017). In the present study, the evaluation of detailed intake and FE parameters during various stages of lactation reveal important differences between Heff and Leff animals. The significant interaction between stage of lactation and production efficiency level provides for important differences in terms of both intake and feed utilization between the most and least efficient animals. The least efficient animals showed a steady decline in daily milk and milk solids production as lactation progressed (similar to Prendiville et al., 2011) and did not display an increase in daily TDMI from early to mid-lactation (15.5 kg of DM). In contrast, Heff animals maintained high levels of milk production into mid-lactation, which appears to be supported by the increased TDMI (17.3 kg of DM) compared with early lactation (15.7 kg of DM). While Heff achieved greater dMSperTDMI at all stages of lactation, the overall efficiency superiority of Heff animals is particularly evident in mid-lactation when the combined benefits of increased TDMI and increased dMSperTDMI are accumulated. Although Heff displayed a more pronounced and severe reduction in BCSint in early and mid-lactation in this study, the EB was not affected during this period (Table 5), which contrasts the findings from both Seymour et al. (2020) and Becker et al. (2021). Despite having a lower BCSint in early and mid-lactation, Heff animals managed to compensate BCSint and gain more BWint than Leff contemporaries by late lactation. Furthermore, the results of the present study indicate that Heff animals increase EB more rapidly in early and mid-lactation compared with Leff (Figure 2). Nonetheless, selection for more efficient animals is cautioned (Martin et al., 2021b; Berry and McCarthy, 2021) as increased mobilization of body reserves during early lactation among Heff has also been associated with reduced reproductive capacity and ability to re-calf and remain in the herd (Delaby and Horan, 2017; Mendes et al., 2021).

Estimating production efficiency indirectly based on farm level data is interesting, as it reduces the requirement for individual feed intake measures and permits increased selection for overall cow efficiency based on commercial farm performance. Previous studies have indicated weaker phenotypic correlations for efficiency
parameters across lactation, which can result in re-ranking of cows depending on stage of lactation and diet (Coleman et al., 2010; Berry and Crowley, 2013; Hurley et al., 2018). The moderate positive correlation between TDMI and EB documented herein (0.64) and the negative correlation between daily milk solids yield and EB (−0.50) highlight the importance of a rapid increase in TDMI in early lactation to combat negative EB and to maintain peak production into mid-lactation. In fact, the strong positive correlations between MSperBWlact and detailed efficiency traits (dMSperBWint, dMSperTDMI) across lactation indicate that MSperBWlact is a relatively robust measure to identify Heff animals within the herd. At the same time, genetic improvement in production efficiency is contingent on the compatibility with other key attributes of pasture-based dairy systems such as calving interval and longevity (Delaby and Horan, 2017). On that basis, further investigation is needed to characterize the relationship between MSperBWlact and such attributes as reproductive performance (Schuster et al., 2020; Martin et al., 2021b) and the beef merit of male progeny from the dairy herd (Berry and McCarthy, 2021).

CONCLUSIONS

Within intensive pasture-based systems, this study demonstrates that Heff animals produced more kilograms of milk solids over a longer lactation, were older, weighed less, achieved a higher DMI throughout lactation, were consistently more efficient in terms of animal intake (TDMI/BWint) and various efficiency traits (dMSperBWint, dMSperTDMI) measured at multiple time points during lactation. Hence, this study proposes a new and compelling efficiency measure, which is cost-effective and easily measurable, as it is based on the full-lactation milk solids production and a mid-lactation BW (MSperBWlact) as key determinants. This methodology provides an opportunity to increase the selection intensity for production efficiency within commercial grazing dairy systems to further enhance overall farm sustainability and profitability. Nonetheless, lactation parameters such as lactation number and the lactation duration merit further evaluation.

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