Three-breed rotational crossbreds of Montbéliarde, Viking Red, and Holstein compared with Holstein cows for feed efficiency, income over feed cost, and residual feed intake

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ABSTRACT

Rotational 3-breed crossbred cows of Montbéliarde, Viking Red, and Holstein (CB) were compared with Holstein (HO) cows for alternative measures of feed efficiency as well as income over feed cost (IOFC) and residual feed intake (RFI) during the first 150 d of first, second, and third lactations. Primiparous and multiparous CB ($n = 63$ and $n = 43$, respectively) and HO ($n = 60$ and $n = 37$, respectively) cows were fed the same total mixed ration twice daily with refusals weighed once daily. Feed was analyzed for dry matter content, net energy for lactation, and crude protein content. Body weight (BW) was recorded twice weekly. Daily production of milk, fat, and protein were estimated from monthly test days with best prediction. Measures of efficiency from 4 to 150 d in milk (DIM) were feed conversion efficiency (FCE), defined as fat plus protein production (kg) per kilogram of dry matter intake (DMI); ECM/DMI, defined as kilograms of energy-corrected milk (ECM) per kilogram of DMI; net energy for lactation efficiency (NE_{LE}), defined as ECM (kg) per megacalorie of net energy for lactation intake; crude protein efficiency (CPE), defined as true protein production (kg) per kilogram of crude protein intake; and DMI/BW, defined as DMI (kg) per kilogram of BW. The IOFC was defined as revenue from fat plus protein production minus feed cost. The RFI from 4 to 150 DIM for each lactation was the residual error remaining from regression of DMI on milk energy output (Mcal), metabolic BW, and energy required for change in BW (Mcal). Statistical analysis of measures of feed efficiency and RFI for primiparous cows included the fixed effects of year of calving and breed group. For multiparous cows, statistical analysis included breed as a fixed effect and cow as a repeated effect nested within breed group. Primiparous CB cows had higher means for FCE (+5.5%), ECM/DMI (+4.0%), NE_{LE}

(+4.0%), and CPE (+5.2%) and a lower mean DMI/BW (−5.3%) than primiparous HO cows. Primiparous CB cows (\$875) also had higher mean IOFC than primiparous HO cows (\$825). In addition, mean RFI from 4 to 150 DIM was significantly lower (more desirable) for primiparous CB cows than HO cows. Likewise, multiparous CB cows had higher means for FCE (+8.2%), ECM/DMI (+5.9%), NE_{LE} (+5.8%), and CPE (+8.1%) and a lower mean for DMI/BW (−4.8%) than multiparous HO cows. Multiparous CB cows (\$1,296) also had a higher mean for IOFC than multiparous HO cows (\$1,208) and a lower mean for RFI from 4 to 150 DIM than HO cows.

Key words: crossbreeding, feed efficiency

INTRODUCTION

The efficient utilization of feed consumed by dairy cows has grown in interest as an area of research in recent years because of heightened emphasis on agriculture sustainability. More than 50% of the expenses of dairy operations in the United States are feed cost (USDA-ERS, 2018); therefore, feed efficiency (FE) of dairy cows is economically important. The definition of FE is the ability of an animal to convert feed to product (Connor, 2015). Modern dairy cows have higher FE than their ancestors because of increased milk production per cow resulting from genetic selection, improved nutrition, and enhanced herd management. Today's cows partition a higher percentage of feed to production instead of maintenance (VandeHaar et al., 2016); however, much of the potential gain in FE from increased production has already been exploited, so other approaches are needed to further increase production per unit of feed (VandeHaar et al., 2016).

The number of crossbred dairy cows in the United States has risen over the past decade because of the decline in fertility, health, and survival and the increase of average inbreeding of Holstein (HO) cows (Council on Dairy Cattle Breeding, 2018a,b). In addition, most milk pricing systems in the United States favor high fat and protein solids production rather than milk volume,

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and crossbreds usually have higher fat and protein content in their milk than HO cows (López-Villalobos et al., 2000; USDA-AMS, 2018b). Many studies have reported favorable results of crossbred cows compared with HO cows for production, fertility, health, and survival (López-Villalobos et al., 2000; Heins et al., 2012; Hazel et al., 2017a,b), but little research has been conducted on the FE of crossbred compared with HO cows. In order for dairy producers to make more judicious decisions on the breed composition of their cows, the FE of crossbred cows needs to be investigated. However, data on FE are costly to acquire because of the specialized labor and equipment to collect feed intake (**FI**) for individual cows.

Universal agreement on the optimum measure of FE for dairy cattle has not been achieved (Coleman et al., 2010; Hurley et al., 2016), and this adds to the complexity of assessing FE. For example, Hurley et al. (2016) reported relationships among 14 alternative definitions of energy efficiency. Ratio traits that compare output (production) to input (intake) are common, but they do not adequately account for differences in cows for energy partitioning toward milk production, body maintenance, or mobilization of body tissue (Veerkamp and Emmans, 1995; Berry and Crowley, 2013). Many of the ratio measures of FE in the study by Hurley et al. (2016) were not correlated, which suggested alternative measures of FE might describe different aspects of FE.

Residual feed intake (**RFI**) has become a common measure of FE for dairy cows, especially for genetic evaluation. The RFI is the difference between the predicted and actual FI required for production and body maintenance and is often estimated as the residual from the regression of DMI on energy sinks, such as production, BW, and change in BW for individual cows (Berry and Crowley, 2013; Connor, 2015). An advantage of deriving RFI from multiple regression is RFI becomes independent of the energy sinks, which allows for comparison of cows across production levels (Coleman et al., 2010). A negative RFI indicates a cow had less FI than predicted based on her energy sinks and, thus, is more efficient. The regression variables used to estimate RFI also differ among studies (Hurley et al., 2016); therefore, comparison of RFI across studies is somewhat difficult.

The beef cattle industry in the United States has taken advantage of the benefits of crossbreeding (breed complementarity and heterosis) for more than 40 yr to enhance productivity through increased growth rates and female longevity, which, in turn, has resulted in improved FE (Gregory and Cundiff, 1980). Historical estimates of heterosis for FE of beef cattle have generally been positive, but usually <5%; however, hetero-

sis varied depending on the breed composition of the crossbred cattle and differences in herd management (Gregory et al., 1966; Urick et al., 1984). Capitalizing on heterosis from crossbreeding has been a major contributor to the commercial pig industry for more than 60 yr in the United States, as heterosis is substantial for litter size and rate of gain and these traits have a large effect on FE (Young et al., 1976; Johnson, 1981). However, heterosis for FE has not been a focus of research in recent years for either beef or dairy cattle (Berry and Crowley, 2013).

Most recent research on FE has explored the genetic control of FE for pure HO cows rather than comparing breeds of cows for FE. Research on FE of crossbred cows has mostly focused on Jersey × HO crossbreds, and the results have been mixed. Schwager-Suter et al. (2001) reported Jersey × HO crossbreds in a confinement system had more FE than pure HO cows because of a higher ratio of ECM to net energy intake. Prendi-ville et al. (2009) found Jersey × HO crossbreds had a higher ratio of milk solids to DMI over a total lactation in a pasture system. In contrast, Heins et al. (2008) reported Jersey × HO crossbreds were not different than HO cows for the ratio of ECM to DMI through 150 DIM. Olson et al. (2010) found neither Jersey × HO nor HO × Jersey crossbreds were different from HO for FE defined as the ratio of energy required for milk production to total energy consumed. Buckley et al. (2007) reported MO × HO crossbreds were not different from HO for milk solids production per unit of DMI or for DMI per unit of BW.

Rotational crossbreeding, usually with 3 distinct breeds, has grown in global popularity over the past decade. In particular, the 3-breed rotation of the HO, Montbéliarde (**MO**), and Viking Red (**VR**) breeds has broad interest for dairying in temperate climates and is marketed internationally as ProCROSS by Coopex Montbeliarde (Roulans, France) and Viking Genetics (Randers, Denmark). The MO breed was developed in France and has based selection on traits related to production, functionality, and conformation, the latter of which includes the trait of muscularity that indirectly places a favorable weight on body condition, unlike most other breeds of dairy cattle (Montbéliarde, 2018). The VR breed includes the subpopulations of Swedish Red, Finnish Ayrshire, and Danish Red, and VR cows tend to have lower milk volume but higher fat and protein content of milk than HO cows (Jönsson, 2015). Furthermore, the VR breed has been selected for health and fertility for over 30 yr (Pryce et al., 2014). The objective of our study was to compare 3-breed rotational crossbred cows of the HO, MO, and VR breeds (**CB**) to pure HO for alternative measures of FE.

MATERIALS AND METHODS

Experimental Units

Research with crossbreeding at the University of Minnesota began in the early 2000s. The initial crossbreds were Jersey $\times$ HO and MO $\times$ HO and, subsequently, 3-breed crossbreds of those breeds. The Jersey breed was later replaced with the VR breed for an ongoing 3-breed rotational system of HO, MO, and VR. A description of the crossbreeding design and genetic level of cows in this study was reviewed in Shonka-Martin et al. (2019).

Cows were housed at the Dairy Cattle Teaching and Research Facility of the University of Minnesota, St. Paul, and animal use was approved by the Institutional Animal Care and Use Committee of the University of Minnesota (#1408-31736A). The CB and HO cows were paired before first calving according to age (mo) and expected calving date. The cows that calved for the first time from September 2014 to May 2015 (yr 1) had the opportunity for 2 subsequent lactations to be included in the study. Cows that calved for the first time from September 2015 to April 2016 (yr 2) had the opportunity for 1 subsequent lactation to be included in the study. The cows that calved for the first time from August 2016 to April 2017 (yr 3) had the opportunity for only a first lactation to be included in the study.

Some cows were involuntarily culled, and cows that left the herd before 150 DIM were eliminated from the study for only the terminal lactation (Shonka-Martin et al., 2019). Less than 9% of the lactations of cows were eliminated for cows that left the herd before 150 DIM. In total, 63 CB and 60 HO cows were available for analysis. Of the 63 primiparous CB cows, 14 had a HO sire, 29 had a MO sire, and 20 had a VR sire. The multiparous analysis had 43 lactations (15 with a HO sire, 15 with a MO sire, and 13 with a VR sire) of CB cows and 37 lactations of HO cows. More details about the cows in this study were reviewed by Shonka-Martin et al. (2019).

Data Collection

A TMR was delivered twice daily to cows housed in the tiestall barn for the duration of study period. The amount fed to each cow had a target of at least a 5% daily refusal rate and was adjusted daily. Missing or aberrant observations were removed, but they accounted for a small proportion (2.6%) of daily FI data. Missing daily FI were estimated by extrapolation using the mean from 2 d before and 2 d after the missing daily FI observation. The DM content of the TMR was determined from weekly samples and the

NE_L and CP density of the TMR was determined from monthly samples. The TMR had a mean DM of 54.6%, a mean NE_L of 1.62 Mcal per kilogram of DM, and a mean CP of 16.6% on a DM basis. The daily DMI (kg) was daily FI multiplied by the respective weekly DM content of the TMR, the daily NE_L intake (NEI) was daily DMI multiplied by the respective monthly NE_L density of the diet, and the daily CP intake (CPI) was DMI multiplied by the respective monthly CP content of the diet.

The BW was recorded twice weekly with a digital scale at the time cows exited the milking parlor. The BCS was evaluated on all cows once per week by a single trained evaluator and was scored on a 5-point scale with 0.25 increments, where 1 = thin and 5 = obese (Wildman et al., 1982). Additional details about the FI, BW, and BCS of individual cows, as well as the ingredients and nutritional composition of the diet, are presented in Shonka-Martin et al. (2019).

Cows were milked twice daily at 0400 and 1600 h. Milk volume and fat, protein, and lactose percentages from monthly DHI (Minnesota DHIA, Buffalo, MN) were used to estimate production for complete lactations with best prediction (BP). Edits applied to test-day observations for milk volume and fat and protein percentages were described in Shonka-Martin et al. (2019). Daily lactose production could not be estimated with BP; therefore, percentage of lactose was assigned for each DIM from 4 to 150 d based on the test day closest to that DIM for each cow.

Measures of FE

Measures of FE were chosen based on historically common measures in FE literature and those that represented multiple ways to quantify production (Coleman et al., 2010; Vallimont et al., 2011; Potts et al., 2017). Measures were also chosen to represent relevant economic efficiencies in the dairy industry.

Ratio Measures. Both FI and production were the sums of daily observations from 4 to 150 DIM. The FI was quantified as DMI (kg), NEI (Mcal), or CPI (kg). Production was quantified as fat plus protein production (kg), true protein production (kg), or ECM (kg) calculated with the equation of Tyrrell and Reid (1965):

$$\text{ECM} = 0.327 \times \text{milk (kg)} + 12.95 \times \text{fat (kg)} \\ + 7.20 \times \text{protein (kg)},$$

with daily milk, fat, and protein of a cow estimated by BP. The BW was the mean BW from 4 to 150 DIM. The FE for 4 to 150 DIM was defined as

- 1) Feed conversion efficiency (**FCE**) = fat plus protein production (kg)/DMI (kg);
- 2) ECM per unit of DMI (**ECM/DMI**) = ECM (kg)/DMI (kg);
- 3) Net energy for lactation efficiency (**NE_LE**) = ECM (kg)/NEI (Mcal);
- 4) Crude protein efficiency (**CPE**) = true protein production (kg)/CPI (kg); and
- 5) DMI per unit of BW (**DMI/BW**) = DMI (kg)/BW (kg).

Income Over Feed Cost. Feed cost was estimated as \$0.2936/kg of DM reported by FINBIN (Center for Farm Financial Management, 2017), which summarizes financial data from dairy producers in the Upper Midwest region of the United States. Feed cost per cow from 4 to 150 d of lactation was calculated by multiplying the feed cost per kilogram (\$0.2936) by the total DMI (kg) consumed. The value of fat and protein production was derived from Federal Milk Marketing Order component prices (USDA-AMS, 2018a) from September 2014 to December 2017 and resulted in a mean price of fat of \$5.3471/kg and a mean price of protein of \$4.8674/kg. Income from fat and protein production was obtained by multiplying the fat and protein produced by a cow by the respective fat and protein price and summing the 2 components. Income over feed cost (**IOFC**) was then calculated as revenue (\$) from fat plus protein production minus feed cost (\$) from 4 to 150 DIM.

RFI from 4 to 150 DIM. Fat, protein, and lactose production, as well as BW and BCS, were used to assess the major energy sinks of cows. The energy sinks were chosen based on those commonly found in the literature (Hardie et al., 2015; Tempelman et al., 2015; Potts et al., 2017) and based on practicality in accounting for feed intake. Energy expended in milk (**MilKE**) was calculated according to the NRC (2001) with the use of true protein as

$$\text{MilKE} = 9.29 \times \text{fat (kg)} + 5.63 \times \text{true protein (kg)} \\ + 3.95 \times \text{lactose (kg)},$$

with fat, protein, and lactose production of each cow from 4 to 150 DIM. Metabolic BW (**MBW**) was used to estimate maintenance requirements of each cow as $\text{BW}^{0.75}$ from mean BW from 4 to 150 DIM. The BW change (**BWC**) from 4 to 150 DIM was estimated by regressing BW on week of observation within each lactation of a cow. Energy gained or lost for BWC (**BWCE**) from 4 to 150 DIM when BW increased was

$$\text{BWCE (Mcal/d)} = \text{BWC (kg/d)} \\ \times (2.88 + 1.026 \times \text{BCS}) \times 0.85,$$

and when BW decreased was

$$\text{BWCE (Mcal/d)} = \text{BWC (kg/d)} \times (2.88 + 1.026 \\ \times \text{BCS}) \times 0.82 \text{ (NRC, 2001; Hardie et al., 2015)}.$$

In both situations, BCS was the mean BCS recorded from 4 to 150 DIM. Energy required for physical activity was not taken into consideration because cows were housed in a tiestall barn for the duration of the study. In addition, energy required for pregnancy was considered negligible because none of the cows in the study had reached 100 d of gestation by 150 DIM (NRC, 2001).

The RFI was explored separately for the primiparous and multiparous cows because their lactation curves differed substantially for DMI, BW, and production (Shonka-Martin et al., 2019). Consequently, the phenotypic RFI for the *i*th cow was defined as the error term (ε_i) from the regression model for primiparous cows:

$$\text{DMI}_i = \beta_0 + \beta_1 \times \text{MilKE}_i + \beta_2 \times \text{MBW}_i \\ + \beta_3 \times \text{BWCE}_i + \text{year}_i + \varepsilon_i,$$

where DMI_i is the total DMI from 4 to 150 DIM for the *i*th cow; β_0 is the intercept; β_1 , β_2 , and β_3 are the partial regression coefficients associated with the MilKE, MBW, and BWCE from 4 to 150 DIM, respectively; and year_i is year of study (1, 2, or 3) to reflect differences in heifer rearing for the 3 yr. For multiparous cows, the phenotypic RFI for the *i*th cow was defined as the error term (ε_i) from the regression model:

$$\text{DMI}_i = \beta_0 + \beta_1 \times \text{MilKE}_i + \beta_2 \times \text{MBW}_i \\ + \beta_3 \times \text{BWCE}_i + \text{cow}_i + \varepsilon_i,$$

where all variables are defined the same as for primiparous cows and cow_i is the repeated effect for cows with both second and third lactations.

RFI for 28-d Intervals. Previous research has suggested DMI and RFI may be regulated by different genes during alternative stages of lactation (Tetens et al., 2014; Li et al., 2017). In addition, research has suggested the partial regression coefficients of DMI on the various energy sinks may differ by stage of lactation, especially in early lactation, when body condition is mobilized and large changes in BW are most likely to occur (Li et al., 2017). Therefore, RFI was estimated separately for 5 stages of lactation (28-d intervals) to compare CB and HO cows from 11 to 150 DIM, and primiparous and multiparous cows were again analyzed separately within each 28-d interval. The energy sinks were again based on the mean MilKE, MBW, and BCS, but only within each 28-d interval for each cow. The BWC within each 28-d interval was estimated using a

regression coefficient from weekly BW observations and converted to BWCE. The RFI for 28-d intervals were estimated with the same model that was previously used for estimation of RFI from 4 to 150 DIM.

Statistical Analysis

Variables Contributing to Measures of FE and RFI. Least squares means of breed groups for DMI, fat plus protein production, and BW of cows in this study were previously reported (Shonka-Martin et al., 2019). The other variables contributing to measures of FE (NEI, CPI, ECM, and true protein production) and to RFI (Milke, MBW, and BWCE) were also analyzed to assess breed group differences. For primiparous cows, year of calving (1, 2, or 3) and breed group (CB or HO) were the fixed effects for the statistical analysis for all variables contributing to FE and RFI, and the MIXED procedure of SAS (release 9.4, SAS Institute Inc., Cary, NC) was used to conduct the ANOVA and obtain solutions. For multiparous cows, breed group (CB or HO) was a fixed effect and cow nested within breed group was a repeated effect because some cows had both second and third lactations included in the study. The MIXED procedure of SAS was used to conduct the ANOVA and obtain solutions for the multiparous analyses.

Ratio Measures of FE and IOFC. For primiparous cows, independent variables for the statistical analysis of FCE, ECM/DMI, NE_LE, CPE, DMI/BW, and IOFC included the fixed effects of year of calving (1, 2, or 3) and breed group (CB or HO), and the MIXED procedure of SAS was used to conduct the ANOVA and obtain solutions. For multiparous cows, the independent variables for the analysis of all of the ratio measures of FE, as well as IOFC, were breed group (CB or HO) and repeated cow within breed group to account for cows that had both second and third lactations. The MIXED procedure of SAS was used for analysis of multiparous cows to conduct the ANOVA and obtain solutions.

RFI from 4 to 150 DIM. For primiparous cows, breed group (CB or HO) was the only independent variable, and the MIXED procedure of SAS was used for the analysis of RFI to conduct the ANOVA and obtain solutions. For multiparous cows, effects were breed group (CB or HO) and repeated cow within breed group, and the MIXED procedure of SAS was used for the analysis of RFI from 4 to 150 DIM to conduct the ANOVA and obtain solutions.

RFI for 28-d Intervals. Ten separate analyses of RFI were conducted because each 28-d interval was analyzed separately by parity group (primiparous and multiparous). As for RFI from 4 to 150 DIM, breed group (CB or HO) was the only fixed effect for the

analysis of RFI for 28-d intervals for the primiparous cows, and the MIXED procedure of SAS was used to conduct the ANOVA and obtain solutions. Breed group (CB or HO) and repeated cow within breed group were the effects in the statistical model to analyze RFI for 28-d interval for the multiparous cows, and the MIXED procedure of SAS was used to conduct the ANOVA and obtain solutions.

RESULTS AND DISCUSSION

The least squares means and standard errors of means for the variables contributing to ratio measures of FE from 4 to 150 DIM are summarized in Table 1. Both the primiparous and multiparous CB cows had lower ($P < 0.05$) means for DMI, NEI, and CPI than HO cows, but were not different from HO cows for all measures of production (mean fat plus protein production, mean ECM, and mean true protein production). Furthermore, both primiparous and multiparous CB cows were not different from HO cows for mean BW.

FCE and ECM/DMI

Year of calving significantly ($P < 0.01$) explained variation of both FCE and ECM/DMI for primiparous cows. Primiparous CB cows had higher ($P < 0.01$) mean FCE than HO cows (Table 2), and this was likely because CB cows consumed significantly less DMI than HO cows but were not different from HO cows for fat plus protein production (Shonka-Martin et al., 2019). Likewise, multiparous CB cows had higher ($P < 0.01$) mean FCE than multiparous HO cows (Table 2). The estimates of mean FCE for HO cows in our study were slightly higher than the FCE of 0.09 reported for HO cows in the same herd as our study from 4 to 150 DIM (Heins et al., 2008) and for North American HO cows in Irish grazing systems from 21 to 288 DIM (Coleman et al., 2010); the departure is likely a reflection of differences in diet, management, genetic selection, or a combination of these factors. Contrary to the results for CB and HO cows from our study, Buckley et al. (2007) reported MO $\times$ HO crossbreds (0.142) and HO cows (0.146) did not differ for FCE in the first 8 wk of lactation in a grazing environment, likely because the breed groups did not differ for either fat plus protein production or DMI.

Both primiparous and multiparous CB cows had higher ($P < 0.05$) ECM/DMI than HO cows (Table 2). The higher ECM/DMI for the CB cows was not surprising because the CB and HO cows were not different for ECM, but CB cows had lower DMI than HO cows (Table 1). The ECM/DMI for both primiparous and multiparous HO cows in our study was higher than

Table 1. Least squares means and SEM for the variables contributing to the ratio measures of feed efficiency from 4 to 150 DIM by parity group and breed group¹

Variable	Primiparous				Multiparous			
	Holstein (n = 60)		3-breed crossbred ² (n = 63)		Holstein (n = 37)		3-breed crossbred ² (n = 43)	
	LSM	SEM	LSM	SEM	LSM	SEM	LSM	SEM
DMI ³ (kg)	2,948	36.9	2,807**	36.3	3,592	68.1	3,360*	63.1
NEI ⁴ (Mcal)	4,790	61.9	4,563**	60.7	5,867	108.9	5,487*	101.0
CPI ⁵ (kg)	491	6.6	467*	6.5	605	11.2	565*	10.4
Fat + protein ³ (kg)	329	3.3	331	3.2	441	7.0	445	6.5
ECM (kg)	4,985	48.9	4,939	48.0	6,759	105.9	6,676	98.2
Protein (kg)	146	1.4	146	1.3	194	2.9	196	2.7
BW ³ (kg)	556	7.1	562	7.0	644	10.2	636	9.4

¹Means are for feed intake (DMI, NEI, and CPI), production (fat + protein, ECM, protein) and mean BW from 4 to 150 DIM.

²Three-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows.

³From Shonka-Martin et al. (2019).

⁴NEI = net energy of lactation intake.

⁵CPI = crude protein intake.

** $P < 0.01$, * $P < 0.05$ for differences from Holstein within parity group.

the estimates of 1.43 to 1.66 for HO cows with mixed parities and diets (Heins et al., 2008; Potts et al., 2017).

NE_LE and CPE

Year of calving significantly ($P < 0.01$) explained variation of both NE_LE and CPE for primiparous cows. Primiparous ($P = 0.02$) and multiparous ($P = 0.02$) CB cows both had higher NE_LE than HO cows (Table 2). Vallimont et al. (2011) reported a mean 305-d lactational NE_LE (using FCM instead ECM) of 0.98 for HO cows housed in commercial tiestall barns, and this was slightly lower than the estimates of 1.05 and 1.16 for HO cows from 4 to 150 DIM in our study. As for FCE and ECM/DMI, NE_LE was anticipated to be superior

for both the primiparous and multiparous CB cows than the HO cows because CB cows consumed less NEI ($P < 0.01$) than HO cows but were not different from HO cows for ECM (Table 1).

Primiparous CB cows had higher ($P < 0.01$) CPE than HO cows (Table 2), likely because CB cows had less ($P = 0.01$) CPI than HO cows but did not differ from HO cows for true protein production. Likewise, multiparous CB cows had higher ($P < 0.01$) CPE than HO cows. Again, this was likely because multiparous CB cows had less ($P = 0.01$) CPI than HO cows but did not differ from HO cows for true protein production (Table 1). The CPE of HO cows in our study was comparable to the 305-d lactational CPE of 0.32 reported by Vallimont et al. (2011). Protein is often an expensive

Table 2. Least squares means and SEM for ratio measures of feed efficiency from 4 to 150 DIM by parity group and breed group

Ratio	Primiparous				Multiparous			
	Holstein (n = 60)		3-breed crossbred ¹ (n = 63)		Holstein (n = 37)		3-breed crossbred ¹ (n = 43)	
	LSM	SEM	LSM	SEM	LSM	SEM	LSM	SEM
FCE ²	0.113	0.001	0.119**	0.001	0.124	0.002	0.134**	0.002
ECM/DMI	1.704	0.020	1.773*	0.019	1.894	0.034	2.006*	0.032
NE _L E ³	1.048	0.013	1.091*	0.013	1.159	0.020	1.226*	0.019
CPE ⁴	0.300	0.004	0.322**	0.004	0.324	0.006	0.350**	0.005
DMI/BW	5.314	0.069	5.035**	0.068	5.574	0.090	5.306*	0.083

¹Three-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows.

²FCE = feed conversion efficiency.

³NE_LE = net energy for lactation efficiency.

⁴CPE = crude protein efficiency.

** $P < 0.01$, * $P < 0.05$ for differences from Holstein within parity group.

component of TMR diets, so efficient use of protein is economically important for milk production.

DMI/BW

For primiparous cows, both year of calving and breed group significantly ($P < 0.01$) explained variation for DMI/BW, and CB cows had lower ($P < 0.01$) mean DMI/BW than HO cows (Table 2). Multiparous CB cows also had a lower ($P = 0.03$) mean DMI/BW than multiparous HO cows (Table 2). The HO cows in our study had a mean daily DMI/BW of 0.036 and 0.038 for primiparous and multiparous cows, respectively. The DMI/BW for HO cows in our study was comparable to the estimates reported by Coleman et al. (2010), ranging from 0.030 to 0.034 daily DMI/kg of BW for alternative strains of HO cows in grazing systems. Buckley et al. (2007) reported MO $\times$ HO and HO cows did not differ for DMI per 100 kg of BW because the 2 breed groups did not differ for either DMI or BW. The lower DMI, but equivalent BW, of CB cows compared with HO cows in our study (Table 1) resulted in CB cows having a lower DMI/BW than HO cows.

In a review paper, Grainger and Goddard (2004) suggested higher FCE could be achieved, all other things being equal, if cows had a higher DMI/BW, especially in grazing systems. However, contrary to the suggestion of Grainger and Goddard (2004), CB cows had a higher mean FCE despite a lower DMI/BW than HO cows. In addition, Grainger and Goddard (2004) reviewed studies that indicated Jersey cows have a higher DMI/BW and a higher mass to the digestive system per unit of BW and, therefore, have more capacity for intake per unit BW than HO cows. Furthermore, Grainger and Goddard (2004) reviewed studies that indicated Jerseys have a higher rate of passage of feed, and Colucci et al. (1982) reported higher passage rates are associated with less digestion of feed compared with lower passage rates. The lower DMI/BW of CB cows than HO cows in our study may suggest CB cows have enhanced ability to extract nutrients from the diet.

Measures of FE that included some measure of both production and intake (FCE, ECM/DMI, NE_L E, and CPE) were highly and positively correlated for both primiparous (>0.83) and multiparous (>0.70) cows of both breed groups. High correlations were anticipated because each measure was a different method for quantifying production per unit of intake. The correlation between DMI/BW and FCE, ECM/DMI, NE_L E, and CPE were moderate and negative for primiparous (-0.45 to -0.48) and multiparous (-0.34 to -0.39) cows, indicating cows that had a lower DMI/BW were more efficient at converting feed to product.

IOFC

For primiparous cows, year of study significantly ($P < 0.01$) explained variation for IOFC. Primiparous CB cows ($\$875 \pm 13$) had higher ($P < 0.01$) IOFC from 4 to 150 DIM than primiparous HO cows ($\$825 \pm 14$). The \$50 advantage of primiparous CB cows over HO cows is the equivalent of \$0.34/d, with \$0.06/d from more fat plus protein production and \$0.28/d from lower feed costs than HO cows. Multiparous CB cows ($\$1,296 \pm 29$) also had higher ($P = 0.04$) IOFC than multiparous HO cows ($\$1,208 \pm 31$). The \$88 difference is the equivalent of \$0.60/d, with \$0.14/d from more fat plus protein production and \$0.46/d from lower feed cost than HO cows.

Fat plus protein production was chosen as the measure of income in our study because most milk in the United States is priced based on the fat and protein solids in milk rather than on the fluid volume of milk. As with ratio measures of FE, higher IOFC of CB cows than HO cows was anticipated because both primiparous and multiparous CB cows had lower DMI than HO cows but were not different from HO cows for fat plus protein production (Shonka-Martin et al., 2019). The IOFC is an informative measure of profit (Heins et al., 2012), but IOFC ignores longevity, fertility, and health of cows. Crossbred livestock usually have an advantage over purebreds for fertility and health because of heterosis (Falconer and Mackay, 1996), and lower cost for fertility and health disorders of crossbred dairy cows would be in addition to their advantage for IOFC.

RFI

RFI from 4 to 150 DIM. The least squares means and standard errors of means for variables used to estimate RFI from 4 to 150 DIM are in Table 3. The CB and HO cows were not different for MilkE, MBW, and BWCE in either parity group.

For primiparous cows, partial regression coefficients of DMI on MilkE, mean MBW, and BWCE from 4 to 150 DIM were 0.75, 8.45, and 0.62, respectively, and all significantly ($P < 0.01$) explained variation for DMI. For multiparous cows, the partial regression coefficients were 0.51, 23.2, and 0.40, respectively, for DMI on MilkE, mean MBW, and BWCE from 4 to 150 DIM, and all of the partial regression coefficients were significant ($P < 0.05$). The positive regression coefficients were intuitive, because a cow is expected to require more DMI as production, maintenance, or BWCE increases.

Primiparous CB cows (-65.5 kg) had significantly lower ($P < 0.01$) mean RFI from 4 to 150 DIM than HO cows ($+68.8$ kg); however, the breed groups overlapped substantially for RFI (Figure 1). Most of the lowest

Table 3. Least squares means and SEM for variables in addition to DMI used to estimate residual feed intake (RFI) from 4 to 150 DIM by parity group and breed group¹

Variable	Primiparous				Multiparous			
	Holstein (n = 60)		3-breed crossbred ² (n = 63)		Holstein (n = 37)		3-breed crossbred ² (n = 43)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
MilkE (Mcal)	3,460	34.2	3,431	33.6	4,656	73.1	4,606	67.8
MBW (kg ^{0.75})	114	1.1	115	1.1	128	1.5	126	1.4
BWCE (Mcal)	302	24.1	316	23.7	131	35.4	41	32.8

¹Means are for total milk energy output (MilkE), mean metabolic BW (MBW), and change in body weight energy (BWCE) from 4 to 150 DIM.
²Three-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows.

10% (most favorable) of primiparous cows for RFI were CB (7 of 12 cows), and most of the highest 10% (least favorable) of primiparous cows for RFI were HO (10 of 12 cows). Multiparous CB cows (−64.5 kg) had significantly lower ($P = 0.02$) mean RFI from 4 to 150 DIM than HO cows (+75.0 kg). As with primiparous cows, significant overlap of the breed groups existed for the multiparous cows (Figure 1). Again, for multiparous cows, most of the lowest 10% (most favorable) of cows for RFI were CB (7 of 8 cows), and most of the top 10% (least favorable) of cows for RFI were HO (5 of 8 cows).

The CB cows in our study had lower mean RFI than HO cows but did not differ from HO cows for MilkE, mean MBW, and BWCE, and the CB cows had higher ECM/DMI than HO cows. In addition, CB cows consumed less DMI, had higher FCE, and had lower DMI/BW than HO cows. Potts et al. (2017) reported MilkE, MBW, and BWCE were not different for HO cows stratified by high or low RFI at approximately 120 DIM. In addition, the low-RFI cows had significantly lower DMI and higher ECM/DMI than the high-RFI cows (Potts et al., 2017). Coleman et al. (2010) provided

Figure 1. Residual feed intake (RFI) plotted against predicted DMI from 4 to 150 DIM for primiparous and multiparous cows by breed group. The solid black line references mean RFI (0 kg); the dotted-dashed line in each panel represents the mean RFI of primiparous (68.8 kg) and multiparous (75.0 kg) Holstein cows, and the dotted-dashed ovals represent 95% prediction ellipses for Holstein cows. The dashed line in each panel represents the mean of primiparous (− 65.5 kg) and multiparous (−64.5 kg) 3-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows, whereas the dashed ovals represent 95% prediction ellipses for the crossbred cows.

associations between RFI and various measures of FE for different strains of HO cows in a grazing system. The cows with low (more efficient) RFI consumed less DMI, had higher FCE, and had lower DMI/BW than cows with high RFI from 21 to 288 DIM (Coleman et al., 2010). Heterosis for RFI of crossbred dairy cows has not been well documented (Berry and Crowley, 2013), but the cumulative effects of heterosis for the variables contributing to RFI could explain some of the differences in RFI in our study for the breed groups.

By definition, RFI should be independent of model effects; therefore, inclusion of breed group in the model for RFI would have resulted in no breed group difference for RFI. Li et al. (2016) suggested breed differences for the partial regression coefficients of DMI on energy sinks may exist when estimating RFI, because of potential differences of breeds in partitioning of energy. Therefore, partial regression coefficients for RFI from 4 to 150 DIM were calculated for CB and HO cows separately by parity group. A simple *z*-test was used to compare breed groups for specific partial regression coefficients, as described by Tempelman et al. (2015); for primiparous cows, we found no differences between the 2 breed groups for the partial regression coefficients of DMI on MilkE or BWCE (Figure 2). On the other hand, the partial regression coefficient of DMI on MBW was significantly ($P = 0.02$) lower for CB cows than HO cows (Figure 2), so DMI for primiparous HO cows increased more per unit increase of MBW than DMI for primiparous CB cows. However, partial regression coefficients for multiparous cows were not different for any of the 3 energy sinks (Figure 2).

The mean BCS of cows was initially included in the analysis as an energy sink in the estimation of RFI from 4 to 150 DIM. However, when RFI was estimated with the primiparous CB and HO cows combined, the partial regression coefficient for BCS was significant ($P = 0.02$) and negative, which was illogical and counter to biological expectation. Likewise, when RFI was estimated separately for primiparous CB and HO cows, the partial regression coefficients for DMI on BCS were nearly equal in magnitude but opposite in direction (negative for CB cows and positive for HO cows) and not significant. The multiparous cows behaved in a similar fashion to the primiparous cows for relationship of DMI and BCS. Collinearity between BCS, MilkE, MBW, and BWCE did not exist, which was likely because of low to moderate correlations between BCS and the other traits. A reasonable assumption could be that BCS and BW are highly correlated, but in our data the Pearson correlation between them was 0.47 for primiparous cows and 0.32 for multiparous cows. The Pearson correlations between BCS and BWCE were even lower (0.30 for primiparous cows, but not significantly dif-

Figure 2. Partial regression coefficients from estimation of residual feed intake (RFI) from 4 to 150 DIM for Holstein (white bars), 3-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows (diagonal striped bars), and breed groups combined (gray bars). Coefficients are from the regression of DMI on milk energy output (MilkE), mean metabolic BW (MBW), and change in body weight energy (BWCE). Error bars represent SE of the partial regression coefficients.

Table 4. Unadjusted means and SD for the variables contributing to the estimation of residual feed intake (RFI) for 28-d intervals from 11 to 150 DIM by parity group and breed group¹

Variable and interval ²	Primiparous				Multiparous			
	Holstein (n = 60)		3-breed crossbred ³ (n = 63)		Holstein (n = 37)		3-breed crossbred ³ (n = 43)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
DMI (kg/d)								
1	17.6	1.8	16.9	1.9	21.6	3.1	20.5	3.0
2	20.0	2.4	19.1	2.4	24.9	3.2	23.3	3.3
3	20.7	2.9	19.7	2.8	26.1	3.2	23.8	3.5
4	21.3	2.8	20.2	2.8	26.1	3.2	24.3	3.5
5	22.0	2.6	20.6	2.6	25.3	3.6	24.0	3.3
MilKE (Mcal/d)								
1	21.7	1.8	21.4	2.1	31.8	4.5	31.6	3.8
2	23.8	1.8	23.5	2.1	32.9	3.7	32.7	3.2
3	24.4	1.9	24.2	2.0	32.6	3.2	32.1	2.9
4	24.5	2.0	24.3	2.1	31.6	3.0	31.1	2.9
5	24.3	2.0	24.1	2.2	30.2	3.0	29.8	3.2
MBW (kg ^{0.75})								
1	111	7.8	111	9.2	126	8.1	126	10.9
2	112	7.5	113	9.4	126	7.7	125	10.7
3	115	7.6	115	9.5	128	7.4	126	10.6
4	116	7.2	117	10.0	129	7.3	127	10.4
5	118	7.4	119	10.2	130	7.3	127	10.6
BWCE (Mcal/d)								
1	0.9	3.7	0.7	4.2	−2.9	4.1	−3.0	4.1
2	2.5	2.3	2.4	3.1	2.5	4.6	−0.3	3.6
3	2.1	2.7	2.1	2.6	2.0	2.9	0.9	3.6
4	2.0	3.2	2.1	3.1	0.3	3.5	0.8	4.3
5	2.7	2.5	2.5	3.0	1.3	2.8	0.9	3.1

¹Means are for DMI, milk energy output (MilKE), metabolic BW (MBW), and change in body weight energy (BWCE) for each interval.

²Intervals correspond to DIM: 1 (11–38), 2 (39–66), 3 (67–94), 4 (95–122), and 5 (123–150).

³Three-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows.

ferent from 0 for multiparous cows). The outcome of an illogical partial regression coefficient for DMI on BCS may have occurred because CB cows in our study consumed significantly less DMI than HO cows but had significantly higher BCS than HO cows (Shonka-Martin et al., 2019). Because of the incongruous relationship of DMI and BCS for the breed groups, the model for RFI did not include BCS for either primiparous or multiparous cows. However, inclusion of BWCE rather than BWC permitted BCS to be indirectly taken into account, because BCS contributed to the calculation of BWCE for cows.

RFI for 28-d Intervals. Unadjusted means and standard deviations for the variables contributing to the estimation of RFI in each 28-d interval are in Table 4. Primiparous cows had their highest numerical DMI in interval 5 (123–150 DIM). The MilKE increased numerically with time until intervals 3 to 5, and the MBW increased numerically in intervals 1 to 5 (Table 4). The BWCE of primiparous cows was lowest in interval 1 (11–38 DIM). Typically, cows lose BW after calving and slowly regain BW as lactation progresses. For multiparous cows, DMI was numerically highest in interval 4 (95–122 DIM) and MilKE was numerically

highest in interval 2 (39–66 DIM). As with primiparous cows, BWCE of multiparous cows was lowest in interval 1 and was negative, which indicated cows lost BW.

The partial regression coefficients for DMI on MilKE and MBW were all positive and significant in each interval ($P < 0.01$) for primiparous cows (Figure 3). The partial regression coefficient for DMI on BWCE was positive for all intervals and was significant ($P < 0.05$) in intervals 1, 2, and 4 and not significant in intervals 3 and 5 for primiparous cows (Figure 3). The partial regression coefficients for DMI on MilKE and MBW were positive and significant ($P < 0.01$) for all intervals for multiparous cows (Figure 3), and the partial regression coefficient of DMI on BWCE was positive for all intervals and significant ($P < 0.05$) in intervals 1, 2, 3, and 5.

Estimated partial regression coefficients of DMI on MilKE for both primiparous and multiparous cows were lowest in interval 1, followed by an increase and then a plateau (Figure 3). This pattern was akin to that reported by Li et al. (2017) for primiparous Danish HO for entire lactations, although ECM was used as the measure of production instead of MilKE in that study. In general, the partial regression coefficients of DMI

Figure 3. Partial regression coefficients from the regression of DMI on mean milk energy output (MilkE), mean metabolic BW (MBW), and change in body weight energy (BWCE) for estimates of residual feed intake (RFI) by 28-d interval and parity group. The RFI was estimated separately for each interval and parity group. Symbols above partial regression coefficients represent energy sinks that were significant in explaining variation in DMI (* $P < 0.05$ and ** $P < 0.01$). Intervals correspond to DIM: 1 (11–38), 2 (39–66), 3 (67–94), 4 (95–122), and 5 (123–150). Error bars represent SE of the partial regression coefficients.

on MilkE by 28-d interval in our study were higher than those estimated in recent studies with comparable DIM (Tempelman et al., 2015; Li et al., 2017; Potts et al., 2017). The partial regression coefficients for DMI on MBW were comparable to those reported by Tempelman et al. (2015), Li et al. (2017), and Potts et al. (2017). On the other hand, the partial regression coefficients for DMI on BWCE were similar to those reported by Tempelman et al. (2015), but they were lower than those of Li et al. (2017) for DMI on BWC and higher than those of Potts et al. (2017) for DMI on BWCE. Partial regression coefficients often differ between locations and between trials within a single location (Davis et al., 2014; Tempelman et al., 2015), so comparison of coefficients across studies is difficult.

Primiparous CB cows had significantly lower ($P < 0.05$) RFI in each 28-d interval than primiparous HO cows (Table 5) and, for both breed groups, RFI became larger in magnitude from interval 1 to 5. Multiparous CB cows had significantly lower ($P < 0.05$) RFI than HO cows in intervals 1, 3, and 4; however, the CB cows were not different from HO cows for RFI in intervals 2 and 5 (Table 5). Conclusions about RFI after 150 DIM cannot be made from our study, and further investigation is needed to compare CB and HO cows during the remainder of lactation and during the dry period.

Limitations for Measures of FE for Cross-bred Versus HO Cows. Ratio measures of FE are easy to calculate and are readily interpreted. However, Berry and Crowley (2013) pointed out ratios are often strongly correlated with either the numerator or denominator and do not take into account the partitioning of energy from FI. Furthermore, most measures of FE are narrow in scope and measure only input and output without accounting for additional factors, such as pregnancy status (Hazel et al., 2013). Previously, CB cows were documented to have superior fertility to HO cows (Malchiodi et al., 2014); therefore, measures of FE in our study were conservative from a comprehensive perspective.

Coleman et al. (2010) suggested RFI may not be an appropriate measure of FE because accounting for BWC is challenging. The BWC is often included as an energy sink in RFI models but does not adequately explain how energy is partitioned. More energy is required to deposit fat than protein or water, but protein requires more energy to maintain than fat (DiCostanzo et al., 1990). Differences of CB and HO cows for percentages and location of muscle versus fat in the body were not investigated in this or other studies, but could explain some of the differences for FE found in our study. Coleman et al. (2010) also suggested separate regression coefficients for BW gain versus BW loss might be necessary to estimate RFI, because the energy generated

Table 5. Least squares means and SEM of residual feed intake (RFI; kg/d) for 28-d intervals by breed group and parity group

Interval ¹	Primiparous				Multiparous			
	Holstein (n = 60)		3-breed crossbred ² (n = 63)		Holstein (n = 37)		3-breed crossbred ² (n = 43)	
	LSM	SEM	LSM	SEM	LSM	SEM	LSM	SEM
1	0.34	0.18	-0.33**	0.18	0.51	0.34	-0.44*	0.32
2	0.42	0.21	-0.40**	0.20	0.47	0.38	-0.41	0.35
3	0.43	0.25	-0.41*	0.24	0.75	0.38	-0.65**	0.36
4	0.53	0.24	-0.50**	0.24	0.63	0.37	-0.54*	0.34
5	0.70	0.23	-0.66**	0.23	0.33	0.39	-0.28	0.36

¹Intervals correspond to DIM: 1 (11–38), 2 (39–66), 3 (67–94), 4 (95–122), and 5 (123–150).

²Three-breed (Montbéliarde, Viking Red, and Holstein) rotational crossbred cows.

* $P < 0.05$, ** $P < 0.01$ for differences from Holstein within parity group.

from BW loss is less than the energy required for BW gain. Furthermore, prediction equations for DMI used for RFI are often based on HO cows and may not be appropriate for application to cows of other breeds or crossbreds.

CONCLUSIONS

A growing number of dairy producers globally are implementing crossbreeding systems; therefore, the FE of crossbred versus purebred cows requires investigation. The CB cows in this study had higher mean FE for every measure of production per unit of intake (FCE, ECM/DMI, NE_LE, and CPE) than the HO cows, and the CB cows also had lower mean DMI/BW than the HO cows. Furthermore, the CB cows had higher mean IOFC than HO cows. The mean RFI of CB cows was lower (more favorable) than the mean RFI of HO cows. Consequently, this study suggests CB cows should have greater profitability than HO cows because of enhanced FE without loss of fat plus protein production. Furthermore, the measures of FE reported in this study may be conservative because they do not account for the gain in FE from the enhanced fertility and longevity of CB cows.

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