Inter-relationships among alternative definitions of feed efficiency in grazing lactating dairy cows

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ABSTRACT

International interest in feed efficiency, and in particular energy intake and residual energy intake (REI), is intensifying due to a greater global demand for animal-derived protein and energy sources. Feed efficiency is a trait of economic importance, and yet is overlooked in national dairy cow breeding goals. This is due primarily to a lack of accurate data on commercial animals, but also a lack of clarity on the most appropriate definition of the feed intake and utilization complex. The objective of the present study was to derive alternative definitions of energetic efficiency in grazing lactating dairy cows and to quantify the inter-relationships among these alternative definitions. Net energy intake (NEI) from pasture and concentrate intake was estimated up to 8 times per lactation for 2,693 lactations from 1,412 Holstein-Friesian cows. Energy values of feed were based on the French Net Energy system where 1 UFL is the net energy requirements for lactation equivalent of 1 kg of air-dry barley. A total of 8,183 individual feed intake measurements were available. Energy balance was defined as the difference between NEI and energy expenditure. Efficiency traits were either ratio-based or residual-based; the latter were derived from least squares regression models. Residual energy intake was defined as NEI minus predicted energy to fulfill the requirements for the various energy sinks. The energy sinks (e.g., NE_L, metabolic live weight) and additional contributors to energy kinetics (e.g., live weight loss) combined, explained 59% of the variation in NEI, implying that REI represented 41% of the variance in total NEI. The most efficient 10% of test-day records, as defined by REI (n = 709), on average were associated with a 7.59 UFL/d less NEI (average NEI of the entire population was 16.23 UFL/d) than the least efficient 10% of test-day records based on REI (n = 709).

Additionally, the most efficient 10% of test-day records, as defined by REI, were associated with superior energy conversion efficiency (ECE, i.e., NE_L divided by NEI; ECE = 0.55) compared with the least efficient 10% of test-day records (ECE = 0.33). Moreover, REI was positively correlated with energy balance, implying that more negative REI animals (i.e., deemed more efficient) are expected to be, on average, in greater negative energy balance. Many of the correlations among the 14 defined efficiency traits differed from unity, implying that each trait is measuring a different aspect of efficiency.
Key words: feed efficiency, dairy, residual energy intake, energy balance, feed conversion

INTRODUCTION

The expanding world human population (FAO, 2009) is contributing to increased global demand for animal-derived energy and protein sources. International interest in sustainable resource use efficiency is therefore intensifying. Although global, national, and even herd resource use efficiency is multi-factorial, affected by animal characteristics such as reproductive performance, longevity, and per lactation energy produced (Berry et al., 2015), individual animal feed intake recording as well as the appropriate definitions of efficiency are also fundamental to achieving the necessary gains in efficiency.

The definition of alternative measures of feed efficiency and their respective utility is the subject of extensive discussion. Since the 1960s, more than 2 dozen definitions of feed efficiency have been presented in the scientific literature (Archer et al., 1999). Feed conversion ratio and feed conversion efficiency are the traditional measures of feed efficiency in growing and lactating animals, respectively. Residual feed intake, used predominately in growing animals as a measure of feed efficiency (Berry and Crowley, 2013), is now also being used in lactating dairy cow populations (Coleman et al., 2010; McParland et al., 2014; Pryce

et al., 2014). The definition of residual energy intake (**REI**) in lactating cows does, however, differ among studies (Coleman et al., 2010; McParland et al., 2014; Pryce et al., 2014). Consequently, the applications and benefits of these definitions are different. A plethora of other definitions of feed efficiency also exist in both growing and lactating animals, all with their respective advantages and disadvantages (for review, see Berry and Crowley, 2013). Irrespective of the definition, estimates of feed efficiency in dairy cows must account for different functions involved in energy usage and supply over the entire lactation, for example, lipid and protein body mass changes (Berry et al., 2006). Some currently used definitions of feed efficiency in lactating cows (e.g., feed conversion efficiency) do not fully account for body tissue mobilization patterns. Moreover, the inter-relationships among the alternative definitions of feed efficiency traits have not been fully elucidated.

The objectives of the present study were (1) to derive alternative definitions of energetic efficiency in lactating Holstein-Friesian dairy cows, and (2) to quantify the inter-relationships among these alternative definitions. Results from this study may be useful in determining the most appropriate definition of energy efficiency in lactating dairy cows, although one definition is unlikely to meet the requirements of all potential stakeholders.

MATERIALS AND METHODS

Data

Data were available from the Teagasc, Animal & Grassland Research and Innovation Centre, Moorepark, Fermoy, Co. Cork, Ireland (50°7′N; 8°16′W) from the years 1988 to 2009, inclusive. All studies were undertaken on 2 adjacent research farms, namely, Curtin's Research Farm and Moorepark Research Farm. Cows originated from studies which evaluated alternative grazing strategies, nutritional strategies, or strain of Holstein-Friesian animals; see O'Neill et al. (2013) for a description of the database. Animals were fed a basal diet of grazed grass. Swards consisted primarily of perennial ryegrass (*Lolium perenne*) and were managed under a rotational grazing system similar to that described by Dillon et al. (1995). Some animals were supplemented sporadically with concentrates, varying from 0.89 to 3.9 kg of DM per cow daily, offered in equal feeds during each milking. All cows were milked twice daily.

Individual cow milk yield was recorded daily; milk fat and protein concentration was determined from successive morning and evening milk samples once per week using mid-infrared spectroscopy (Fos-let instrument, AS/N Foss Electric, Hillerød, Denmark). Net energy

requirement for lactation was calculated as (Agabriel, 2007)

$$NE_L = (0.054 \times FC + 0.031 \times PC + 0.028 \times LC - 0.015) \times \text{milk kg},$$

where FC is fat concentration expressed in grams per kilogram, PC is protein concentration expressed in grams per kilogram, and LC is lactose concentration expressed in grams per kilogram.

Individual animal live weight was recorded weekly upon exiting the milking parlor using an electronic scale (Tru-Test Limited, Auckland, New Zealand). Animal BCS (scale 1 = emaciated, 5 = obese) was recorded every 2 to 3 wk in increments of 0.25 (Edmonson et al., 1989). Cubic splines with 6 knot points at 20, 70, 120, 170, 220, and 270 DIM, with a covariance structure fitted among knot points, were fitted through individual live weight and BCS test-day records. Live weight and BCS at each DIM were interpolated from the fitted splines. Forward differencing was used to estimate daily live weight and BCS change for each DIM.

Individual animal grass DMI at pasture was estimated using the n-alkane technique (Mayes et al., 1986) as modified by Dillon and Stakelum (1989). During the intake measurement period, cows were dosed twice daily before milking with paper bungs containing 500 mg of C32-alkane (n-dotriacontane) for 12 d. Fecal samples were collected from each cow twice daily during d 7 to 12. Subsequently, samples were bulked per cow, giving one sample per cow per intake measurement period; this sample was sub-sampled for gas chromatography analysis. Selected herbage samples were taken following close observation of cows grazing both after morning and evening milking on d 6 to 11 of the intake measurement period. The ratio of herbage C33-alkane (tritriacontane) to dosed C32-alkane was used to estimate DMI as outlined in detail by Dillon (1993).

Individual cow daily total DMI (i.e., grazed pasture DMI plus concentrate DMI) was available, on average, 4.5 times per lactation. Energy values of the pasture and concentrate were based on the French Net Energy system where 1 unité fourragère du lait (**UFL**) is the net energy requirements for lactation equivalent of 1 kg of standard air-dry barley (Jarrige et al., 1986) equivalent to 7.11 MJ of net energy or 11.85 MJ of ME. The energy values and energy sinks were also based on the French Net Energy system.

The UFL concentration of the offered herbage was calculated using the ADF and CP concentrations, which were measured in the laboratory (Jarrige, 1989). Concentrate UFL value was also calculated from the chemical composition of the feed. The net energy con-

tent of the concentrate fed was calculated for each day; where UFL content of concentrate was not available (28% of test-day records), the year-month average was assumed. Net energy content of the herbage offered (UFL/kg of DM) was also available; where an offered herbage UFL value was not available (10.3% of test-day records), the year-month average was assumed. The within-year-month variation in the UFL content of both concentrate and offered herbage was low, with a coefficient of variation of 2 and 7%, respectively. Net energy intake (**NEI**) was defined as the sum of pasture and concentrate net energy intake.

In total, 8,183 individual feed intake measurements were available from 2,693 lactations on 1,412 pasture-based Holstein-Friesian dairy cows.

Definitions of Energy Efficiency

Fourteen alternative definitions of energy efficiency, broadly classified into ratio and residual-based traits, were generated. Energy balance was also defined.

Energy balance (**EB**) was calculated as the difference between NEI and energy expended through lactation and maintenance according to Jarrige (1989) where the energy values of the feed were modified for Irish dairy systems by O'Mara (1996):

$$\text{EB} = \text{NEI} - \Delta\text{NE} - \text{NE}_{\text{L}} - \text{NE}_{\text{M}} - \text{NEP},$$

where NEI is daily net energy intake, ΔNE is an adjustment of daily net energy intake for the proportion of concentrates in the diet, NE_{L} is daily net energy requirements for lactation, NE_{M} is daily net energy for maintenance calculated as $(1.4 + 0.6 \times \text{live weight}/100) \times 1.2$, and NEP is daily net energy requirements for pregnancy (O'Mara, 1996).

Residual Traits. Residual energy intake for each day of lactation was defined as the residuals from the regression of NEI on energy sinks and other energy sources as

$$\text{REI} = \text{NEI} - [\text{NE}_{\text{L}} + \text{parity} + \sum_{i=1}^{2}\text{DIM}^{i} + \text{BW}^{0.75} + \text{BCS}$$
$$+ \text{BW}^{0.75} \times \text{BCS} + \Delta\text{BW}^{+} + \Delta\text{BW}^{-} + \Delta\text{BCS}^{+} + \Delta\text{BCS}^{-}$$
$$+ \Delta\text{BW}^{+} \times \text{BCS} + \Delta\text{BW}^{-} \times \text{BCS}],$$

where REI is daily residual energy intake, NEI is daily net energy intake, NE_{L} is daily net energy requirements for lactation, parity (1, 2, 3+), $\sum_{i=1}^{2}\text{DIM}^{i}$ is DIM included as a continuous variable with a linear and quadratic effect, and $\text{BW}^{0.75}$ is metabolic live weight. The energy generated from a 1 kg loss in live weight is less than the energy required for a 1 kg gain in live weight

(O'Mara, 1996); therefore, piecewise regression was applied to live weight and BCS in the REI model where ΔBW^{+} describes animals gaining live weight, ΔBW^{-} describes animals losing live weight, whereas ΔBCS^{+} describes animals gaining BCS, and ΔBCS^{-} describes animals losing BCS. No multicollinearity existed in the multiple regression model.

An alternative definition for residual energy intake (i.e., **REI$_{\text{maint}}$**) was defined as the residuals from the previously described regression plus both the regression coefficient on $\text{BW}^{0.75}$ times the actual $\text{BW}^{0.75}$ of the individual, and the regression coefficient on the interaction between $\text{BW}^{0.75} \times \text{BCS}$ times the respective phenotypic value.

Analogous to residual gain in growing cattle (Koch et al., 1963), residual energy production (**REP**) for each day of lactation was defined from the residuals of a least squares regression model regressing NE_{L} on NEI plus energy sinks and other energy sources, similar to that described by Coleman et al. (2010):

$$\text{REP} = \text{NE}_{\text{L}} - [\text{NEI} + \text{parity} + \sum_{i=1}^{2}\text{DIM}^{i} + \text{BW}^{0.75} + \text{BCS}$$
$$+ \text{BW}^{0.75} \times \text{BCS} + \Delta\text{BW}^{+} + \Delta\text{BW}^{-} + \Delta\text{BCS}^{+} + \Delta\text{BCS}^{-}$$
$$+ \Delta\text{BW}^{+} \times \text{BCS} + \Delta\text{BW}^{-} \times \text{BCS}],$$

where REP is daily residual energy production, NE_{L} is daily net energy requirements for lactation, NEI is daily net energy intake, parity (1, 2, 3+), $\sum_{i=1}^{2}\text{DIM}^{i}$ is DIM included as a continuous variable with a linear and quadratic effect, $\text{BW}^{0.75}$ is metabolic live weight, ΔBW^{+} describes animals gaining live weight, ΔBW^{-} describes animals losing live weight, ΔBCS^{+} describes animals gaining BCS, and ΔBCS^{-} describes animals losing BCS. No multicollinearity existed in the multiple regression model.

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Analogous to residual intake and gain as defined by Berry and Crowley (2012), residual intake and energy production (**RIEP**) was defined using both REI and REP, both standardized to have a variance of 1:

$$\text{RIEP} = \widetilde{\text{REP}} - \widetilde{\text{REI}},$$

where $\widetilde{\text{REP}}$ is residual energy production standardized to a variance of 1, and $\widetilde{\text{REI}}$ is residual energy intake

standardized to a variance of 1. Standardizing both traits to a common variance (i.e., here 1) would result in equal emphasis on both REI and REP; otherwise a greater emphasis would be placed on the trait with the greater variance (Berry and Crowley, 2013).

Ratio Traits. Energy conversion efficiency (**ECE**), and its reciprocal, energy conversion ratio (**ECR**) for each day of lactation were defined as

$$ECE = \frac{NE_L}{NEI}, \ ECR = \frac{NEI}{NE_L},$$

where NE_L is the daily net energy requirements for lactation and NEI is the daily net energy intake.

Energy conversion efficiency was refined to (1) consider the energy kinetics from live weight and BCS change in both the numerator and denominator (**ECE$_{adj}$**), and (2) also consider the energy requirement for maintenance plus the interaction between $BW^{0.75}$ and BCS in the numerator of ECE$_{maint}$:

$$ECE_{adj} =$$
$$\frac{NE_L + b\Delta BW^+ + b\Delta BCS^+ + b\Delta BW^+ \times BCS}{NEI - b\Delta BW^- - b\Delta BCS^- - b\Delta BW^- \times BCS},$$

$$ECE_{maint} = \frac{\begin{array}{c} NE_L + bBW^{0.75} + bBW^{0.75} \times BCS + b\Delta BW^+ \\ + b\Delta BCS^+ + b\Delta BW^+ \times BCS \end{array}}{NEI - b\Delta BW^- - b\Delta BCS^- - b\Delta BW^- \times BCS},$$

where NE_L is daily net energy requirements for lactation, NEI is daily net energy intake, $b\Delta BW^+$ describes animals gaining live weight and the associated regression coefficient (b) from the REI model, $b\Delta BW^-$ describes animals losing live weight and the associated regression coefficient (b) from the REI model, $b\Delta BCS^+$ describes animals gaining BCS and the associated regression coefficient (b) from the REI model, $b\Delta BCS^-$ describes animals losing BCS and the associated regression coefficient (b) from the REI model, and $bBW^{0.75}$ is metabolic live weight and the associated regression coefficient (b) from the REI model.

Analogous to partial efficiency of growth (Kellner, 1909) used in growing cattle, partial efficiency of milk energy production (**PEMEP**) and partial efficiency of milk energy production based on nutritional tables (**PEMEP$_{Nut}$**) were defined as

$$PEMEP = \frac{NE_L}{NEI - bBW^{0.75} + \alpha},$$
$$PEMEP_{Nut} = \frac{NE_L}{NEI - NE_M + \alpha},$$

where NE_L is daily net energy requirements for lactation, NEI is daily net energy intake, NE_M is the net energy requirement for maintenance (Jarrige et al., 1986), α is a shift parameter, and $bBW^{0.75}$ is metabolic live weight and its associated regression coefficient (b) from the previously described REI model. A shift parameter of 20 was applied.

Metabolic efficiency (**MEff**) was defined as

$$MEff = \frac{NEI - NE_L}{BW^{0.75}},$$

where NEI is daily net energy intake, NE_L is net energy requirements for lactation, and $BW^{0.75}$ is metabolic live weight.

Feed to live weight (**FtW**) was defined as

$$FtW = \frac{NEI}{BW^{0.75}}$$

where NEI is daily net energy intake, and $BW^{0.75}$ is metabolic live weight.

Kleiber ratio (**KR**; Kleiber, 1961) in growing animals is defined as ADG divided by metabolic live weight. An analogous KR trait in dairy cattle was defined as

$$KR = \frac{NE_L}{BW^{0.75}},$$

where NE_L is the net energy requirements for lactation and $BW^{0.75}$ is metabolic live weight.

Statistical Analysis

Pearson correlations were estimated among the different traits. A *t*-test was used to determine the significance of the difference in mean efficiency between groups of animals.

RESULTS

Descriptive Statistics

The mean, standard deviation, and coefficient of variation for the production measures are in Table 1. The coefficient of variation was greatest for milk yield (32%) and least for $BW^{0.75}$ (9%). A moderate coefficient of variation existed for the 2 component traits of ECE, NEI (20%) and NE_L (28%). Descriptive statistics for the alternative efficiency traits are in Table 2. The coefficient of variation for the different ratio traits varied from 16% (ECE$_{maint}$) to 27% (ECR); the coefficient of variation for energy balance was 76%. The coefficient

Table 1. Number of observations (N), mean, standard deviation, and coefficient of variation for the production traits

Trait[1]	N	Mean	SD	CV
Milk yield (kg)	8,183	21.73	6.99	32.19
Milk fat yield (kg)	8,183	0.86	0.25	29.79
Milk protein yield (kg)	8,183	0.75	0.22	29.09
NE_L (UFL/d)	8,183	7.04	1.97	27.98
NEI (UFL/d)	8,183	16.23	3.24	19.98
BCS (scale 1 to 5)	7,086	2.80	0.33	11.82
$BW^{0.75}$ (kg)	7,086	111.04	9.96	8.97

[1]NEI = net energy intake; BCS score: scale 1 = emaciated, 5 = obese; $BW^{0.75}$ = metabolic live weight. UFL = unité fourragère du lait (net energy requirements for lactation equivalent of 1 kg of standard air-dry barley).

of variation for REI, REP, or RIEP, when estimated using least squares regression, was undefined because the mean of the residuals is, by definition, zero. Using the mean of NEI and NE_L as the denominator in the calculation of the coefficient of variation for REI and REP, respectively, the respective coefficient of variation for REI and REP was 13 and 15%.

The percentage variance in NEI explained by factors defined in the REI model are in Table 3. The partial regression coefficient of NEI on NE_L was 1.12 UFL/d per UFL/d of NE_L (Table 3); additionally, the partial regression coefficient of NEI on $BW^{0.75}$ (i.e., an approximation for animal size) was 0.17 UFL/d per kg of $BW^{0.75}$ when all interaction terms were included in the REI model. The partial regression coefficient in the REI model for live weight gain was negative (-1.76 UFL/d per $kg^{0.75}$/d), but positive (6.31 UFL/d per $kg^{0.75}$/d) for live weight loss; live weight loss values were represented as negative values in the data. Only ΔBCS^+ and ΔBW^+ in the REI model were not ($P > 0.05$) associated with NEI. The proportion of the variance in NEI explained by just the main effects in the REI model was 0.53; including all interaction terms increased the proportion of the variance explained to 0.59. The partial regression coefficient from the REP model of NE_L on NEI was 0.28 UFL/d per UFL/d of NEI. Additionally, the partial regression coefficient of NE_L on $BW^{0.75}$ was 0.05 UFL/d per kg $BW^{0.75}$. The proportion of the variance in NE_L explained by just the main effects in the REP model was 0.67; including all interaction terms increased the proportion of the variance explained to 0.72.

The most efficient 10% of test-day records, as determined by REI (n = 709), on average were associated with an NEI of 7.59 UFL/d less (average NEI of the entire population was 16.23 UFL/d) than the NEI associated with the least efficient 10% of test-day records based on REI ($P < 0.05$). Furthermore, the most efficient 10% of test-day records, based on REI, were as-

Table 2. Number of observations (N), mean, standard deviation, and coefficient of variation for the different efficiency traits and energy balance

Trait[1]	N	Mean	SD	CV
EB (UFL/d)	7,086	3.24	2.46	75.84
ECR	8,183	2.43	0.67	27.48
ECE	8,183	0.44	0.11	25.43
ECE_{adj}	7,086	0.45	0.10	21.88
ECE_{maint}	7,086	0.98	0.16	16.24
PEMEP	7,086	0.41	0.11	26.46
$PEMEP_{Nut}$	7,086	0.23	0.06	24.16
MEff ($UFL/kg^{0.75}$)	7,086	0.08	0.02	26.82
FtW ($UFL/kg^{0.75}$)	7,086	0.15	0.02	16.98
KR ($UFL/kg^{0.75}$)	7,086	0.06	0.02	26.27
REI (UFL/d)	7,086	0.00	2.17	13.37[2]
REI_{maint} (UFL/d)	7,086	8.56	2.53	29.56
REP (UFL/d)	7,086	0.00	1.06	15.06[2]
REP_{maint} (UFL/d)	7,086	8.56	1.68	19.63
RIEP (UFL/d)	7,086	0.00	1.75	0.00

[1]EB = energy balance; ECR = energy conversion ratio; ECE = energy conversion efficiency; ECE_{adj} = energy conversion efficiency adjusted; ECE_{maint} = energy conversion efficiency taking account of maintenance; PEMEP = partial efficiency of milk energy production; $PEMEP_{Nut}$ = partial efficiency of milk energy production based on nutritional tables; MEff = metabolic efficiency; FtW = feed to live weight; KR = Kleiber ratio; REI = residual energy intake; REI_{maint} = residual energy intake taking account of maintenance; REP = residual energy production; REP_{maint} = residual energy production taking account of maintenance; RIEP = residual intake and energy production. UFL = unité fourragère du lait (net energy requirements for lactation equivalent of 1 kg of standard air-dry barley).

[2]Mean of NEI (16.23) and NE_L (7.04).

sociated with superior ($P < 0.05$) ECE (0.55) compared with the least efficient 10% of test-day records (0.33 UFL/d). Moreover, the most efficient 10% of test-day records based on REI were, on average, in negative EB (-0.02 UFL/d) throughout lactation ($P < 0.05$), whereas the least efficient 10% of test-day records were not (i.e., 7.38 UFL/d). No difference ($P > 0.05$) existed between the most and least efficient REI groups for $BW^{0.75}$, BCS, or NE_L.

Mean performance of the top-ranked (i.e., 10%) test-day records based on REI (n = 709), REP (n = 709), and RIEP (n = 709) are in Table 4. The top 10% of test-day records ranked on REI were, on average, in negative EB (-0.02 UFL/d) ($P < 0.05$), unlike the mean EB of the bottom 10% of test-day records ranked on both REP (1.51 UFL/d) and RIEP (0.25 UFL/d). Test-day records ranked on REP were associated with the greatest ($P < 0.05$) milk yield (28.03 kg) compared with the top test-day records ranked on REI (21.96 kg) or RIEP (25.56 kg). The top 10% of test-day records ranked on RIEP had the greatest ($P < 0.05$) ECE (0.58, $P < 0.05$) compared with either REI or REP (0.55 UFL/d). No difference ($P > 0.05$) in ΔBW, ΔBCS, and $BW^{0.75}$ existed among the top 10% of test-day records ranked on either REI, REP, and RIEP.

Table 3. Percentage variance in net energy intake (NEI), regression coefficients (SE in parentheses), and the significance of each variable in the residual energy intake (REI) model

Variable[1]	% Variance	Regression coefficient	P-value
NE_L (UFL/d)	28.20	1.12 (0.02)	0.0001
Parity	21.27		
1		−0.55 (0.08)	0.0001
2		0.25 (0.07)	0.0002
3		0.00	0.0001
DIM	0.07	0.04 (0.002)	0.0001
DIM^2	0.24	0.00009 (0.00001)	0.0001
$BW^{0.75}$ (kg)	27.80	0.17 (0.02)	0.0001
BCS (scale 1 to 5)	0.06	3.28 (0.85)	0.0001
$BW^{0.75} \times$ BCS	9.42	−0.03 (0.01)	0.0002
$\Delta BW+$ (kg)	1.74	−1.76 (1.03)	0.0861
ΔBW^- (kg)[2]	2.78	6.31 (1.55)	0.0001
ΔBCS^+ (scale 1 to 5)	0.89	−15.15 (27.95)	0.5878
ΔBCS^- (scale 1 to 5)[2]	3.04	95.40 (19.24)	0.0001
$\Delta BW^+ \times$ BCS	1.91	0.98 (0.36)	0.0068
$\Delta BW^- \times$ BCS	2.62	−1.39 (0.51)	0.0071

[1]Parity = 1, 2, 3+; DIM = DIM fitted as linear effect; DIM^2 = DIM fitted as quadratic effect; $BW^{0.75}$ = metabolic live weight; BCS scale: 1 = emaciated, 5 = obese; ΔBW^+ = animals gaining live weight; ΔBW^- = animals losing live weight; ΔBCS^+ = animals gaining BCS; ΔBCS^- = animals losing BCS. UFL = unité fourragère du lait (net energy requirements for lactation equivalent of 1 kg of standard air-dry barley).

$$REI = NEI - [NE_L + parity + \sum_{i=1}^{2} DIM^i + BW^{0.75} + BCS + BW^{0.75} \times BCS + \Delta BW^+ + \Delta BW^- + \Delta BCS^+$$
$$+ \Delta BCS^- + \Delta BW^+ \times BCS + \Delta BW^- \times BCS],$$

[2]Phenotypic values included in the analysis for loss are negative.

Correlations Among the Efficiency Traits

Correlations between the different efficiency traits and EB are in Table 5. Absolute correlations between the residual efficiency traits with EB were strong and varied from 0.70 (RIEP) to 0.81 (REI). The absolute correlations between the ratio traits and EB were strong, varying from 0.82 (ECE_{maint}) to 0.99 (MEff). The correlation between both REI and REI_{maint} with EB was 0.81 and 0.80, respectively. Both REI and REP were identically correlated (|0.88|) with their sum, RIEP. Kleiber ratio was uncorrelated with both REI and REI_{maint}.

Correlations between ECE with both ECE_{adj} and ECE_{maint} were 0.96 and 0.65, even though the difference between ECE_{adj} and ECE_{maint} was just the inclusion of maintenance ($BW^{0.75}$) plus the interaction between $BW^{0.75}$ and BCS in the numerator of ECE_{maint}; the correlation between ECE_{adj} and ECE_{maint} was 0.66. The correlation between PEMEP with both ECE_{adj} and ECE_{maint} was 0.87 and 0.50, respectively. A strong correlation existed between ECE_{adj} and KR (0.73), whereas the correlation between ECE_{maint} and KR (0.15) was much weaker. The correlation between ECE_{adj} and FtW (−0.19) was weak, whereas the correlation between ECE_{maint} and FtW was moderate (−0.64). Both PEMEP and $PEMEP_{Nut}$ were strongly correlated (0.92). Correlations between ECE and both PEMEP and $PEMEP_{Nut}$ were 0.89 and 0.88, respectively.

Correlations Between Efficiency and Production Traits

Correlations among the various efficiency and production traits are in Table 6. Residual energy intake was uncorrelated with NE_L; however, weak correlations ($P < 0.05$) existed between REI with milk, fat, and protein yield (0.08, −0.04 and 0.09, respectively). The correlation between REI_{maint} with milk yield, $BW^{0.75}$ and BCS was 0.14, 0.18, and −0.43 respectively. Milk yield was positively correlated with almost all ratio traits that included NE_L in the numerator (i.e., ECE, ECE_{adj}, ECE_{maint}, PEMEP, $PEMEP_{Nut}$, KR, and FtW) and all residual traits, but negatively correlated with ECR, MEff, and EB. Moreover, RIEP was negatively correlated with NEI (−0.38). Strong correlations existed between milk fat yield and ECE (0.69), PEMEP (0.78), $PEMEP_{Nut}$ (0.91), and KR (0.91). Additionally, milk protein yield was strongly correlated with both $PEMEP_{Nut}$ (0.89) and KR (0.92). In addition, KR was strongly correlated with NE_L (0.95); a strong correlation also existed between FtW and NEI (0.90). Metabolic live weight and BCS were weakly correlated with the majority of the efficiency traits investigated (Table 6).

DISCUSSION

International interest in feed efficiency, and in particular NEI and REI, is intensifying due to a greater

Table 4. The top 10% of test-day records based on residual energy intake (REI), residual energy production (REP), and residual intake and energy production (RIEP)[1]

Item	ECE	EB (UFL/d)	NEI (UFL/d)	NE_L (UFL/d)	Milk yield (kg)	ΔBW (kg)	ΔBW <60 d (kg)	ΔBW >200 d (kg)	ΔBCS	BW[2] (kg)	REI (UFL/d)	REP (UFL/d)	RIEP (UFL/d)
REI	0.55[a]	−0.02[a]	12.94[a]	7.04[a]	21.96[a]	0.21	−0.17	0.38[a]	−0.0007[a]	549.71	−3.82[a]	1.01[a]	2.71[a]
REI_2	0.56[a]	−0.02[a]	13.21[b]	7.30[b]	23.06[b]	0.21	−0.12	0.47[b]	−0.001[b]	551.41	−2.98[b]	0.49[b]	1.84[b]
REP	0.55[a]	1.51[b]	16.65[c]	9.01[c]	28.03[c]	0.21	−0.12	0.37[a]	−0.0009[b]	546.17	−2.08[c]	1.93[c]	2.78[ac]
RIEP	0.58[b]	0.25[c]	14.49[d]	8.24[d]	25.56[d]	0.20	−0.14	0.38[a]	−0.0008[b]	546.54	−3.38[d]	1.69[d]	3.16[d]

[a-d] Within a column, means with different superscripts are significantly different from each other.

[1] REI = residual energy intake; REI_2 = Coleman et al., 2010, residual feed intake definition; REP = residual energy production; RIEP = residual intake and energy production; ECE = energy conversion efficiency; EB = energy balance; NEI = net energy intake; NE_L = net energy; ΔBW = animals gaining and losing live weight; ΔBCS = animals gaining and losing BCS. UFL = unité fourragère du lait (net energy requirements for lactation equivalent of 1 kg of standard air-dry barley).

[2] Metabolic live weight ($BW^{0.75}$) converted to actual live weight (BW).

global demand for animal-derived protein and energy sources. Moreover, monitoring individual animal or herd NEI and efficiency has other uses, such as simultaneously trying to minimize the environmental footprint of an expanding global livestock sector. Future pasture-based systems of milk production will be characterized by the ability of a cow to produce the majority of milk solids from grazed pasture. A trait which could identify animals capable of producing increased milk solids from restricted levels of feed intake, independent of performance, would therefore be beneficial to a breeding program for increased production efficiency. In the present study, ample variation existed in the different efficiency traits investigated.

Residual Traits

The partial regression coefficients in the REI model suggested that a 535-kg cow (i.e., the average live weight of cows in the study) yielding, on average, 7.04 UFL/d of NE_L with no ΔBCS had a predicted NEI of 16.75 UFL/d. The partial regression coefficient of NEI on NE_L (1.12 UFL/d) suggested that for every UFL increase in NE_L, NEI was expected to increase by 1.12 UFL/d.

The REI definition in the present study included an interaction between $BW^{0.75}$ and BCS, which is similar to Veerkamp et al. (1995), Vallimont et al. (2011), and McParland et al. (2014). This term was, however, not included in other REI definitions (e.g., Coleman et al., 2010; Pryce et al., 2014). Body condition score is independent of skeletal size and is a measure of depth of muscle and subcutaneous fat. Energy kinetics is associated with body lipid mass, not necessarily fat depth. For this reason a larger animal (i.e., greater $BW^{0.75}$) with the same BCS (i.e., subcutaneous fat depth) is expected to have greater lipid mass compared with a smaller animal. An interaction between BCS and $BW^{0.75}$ was required to capture this (Savietto et al., 2014).

The energy sinks (e.g., NE_L, $BW^{0.75}$) and additional contributors to energy kinetics (e.g., ΔBW^-) combined, explained 59% of the variability in NEI, implying that REI represented only 41% of the total variance in NEI; the likely contribution of errors in the estimation of, for example, grass DMI using the n-alkane technique, suggests that this 41% may actually be the upper limit. Systematic environmental effects such as parity, herd, year, and season are also likely to contribute to this variability. This variability in NEI explained by the REI model was nonetheless less than documented in previous studies in lactating Holstein-Friesian dairy cows. The REI model of Coleman et al. (2010) explained 86% of the variation in feed intake. For comparative purposes, the more traditional definition of residual

Table 5. Pearson correlations among the different efficiency traits and energy balance

Trait[1]	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. EB														
2. ECR	0.70													
3. ECE	−0.80	−0.87												
4. ECE$_{adj}$	−0.76	−0.89	0.96											
5. ECE$_{maint}$	−0.82	−0.57	0.65	0.66										
6. PEMEP	−0.64	−0.80	0.89	0.87	0.50									
7. PEMEP$_{Nut}$	−0.49	−0.84	0.88	0.87	0.36	0.92								
8. MEff	0.99	0.67	−0.77	−0.76	−0.83	−0.65	−0.49							
9. FtW	0.71	0.10	−0.19	−0.19	−0.64	−0.10	0.19	0.75						
10. KR	−0.25	−0.74	0.73	0.73	0.15	0.71	0.92	−0.21	0.49					
11. REI	0.81	0.47	−0.57	−0.57	−0.81	−0.47	−0.25	0.85	0.78	0.05				
12. REI$_{maint}$	0.80	0.44	−0.56	−0.56	−0.56	−0.38	−0.20	0.81	0.74	0.05	0.86			
13. REP	−0.42	−0.56	0.62	0.62	0.38	0.56	0.60	−0.40	0.0006	0.52	−0.53	−0.45		
14. REP$_{maint}$	−0.10	−0.26	0.29	0.29	0.43	0.38	0.40	−0.12	0.13	0.34	−0.33	0.12	0.63	
15. RIEP	−0.70	−0.61	0.68	0.68	0.69	0.59	0.48	−0.71	−0.44	0.28	−0.88	−0.75	0.88	0.55

[1]EB = energy balance; ECR = energy conversion ratio; ECE = energy conversion efficiency; ECE$_{adj}$ = energy conversion efficiency adjusted; ECE$_{maint}$ = energy conversion efficiency taking account of maintenance; PEMEP = partial efficiency of milk energy production; PEMEP$_{Nut}$ = partial efficiency of milk energy production based on nutritional tables; MEff = metabolic efficiency; FtW = feed to live weight; KR = Kleiber ratio; REI = residual energy intake; REI$_{maint}$ = residual energy intake taking account of maintenance; REP = residual energy production; REP$_{maint}$ = residual energy production taking account of maintenance; RIEP = residual intake and energy production. Correlations <|0.03| were not different from zero.

feed intake (i.e., **RFI** = dry matter intake minus year, fat, protein and lactose yield, BW$^{0.75}$, ΔBW, and BCS; Coleman et al., 2010) was calculated on the current data set. The correlation between the traditional RFI definition of Coleman et al. (2010) and our alternative REI definition was less than unity (0.72). Similarly, the correlation between our REI definition and that of Connor et al. (2013; REI = energy intake minus parity effect, BW$^{0.75}$, ADG, and ECM yield) was also less than unity (0.73). The REI model of Connor et al. (2013) explained 72% of the variation in energy intake.

Consequently, we believe that the alternative definition of REI in the present study should be considered for future studies on RFI, as our definition better accounts for lipid mass (change).

Residual energy intake was, as expected, uncorrelated with NE$_L$, BW$^{0.75}$, and BCS since REI was estimated using multiple regression which included these traits. Despite the milk production traits (i.e., milk, fat, and protein) comprising the definition of NE$_L$ in the REI model, relatively weak correlations ($P < 0.05$) still existed between REI and milk, fat, and protein yield.

Table 6. Correlations between the various efficiency and production traits and energy balance

Trait[1]	NEI	NE$_L$	Milk yield	Fat yield	Protein yield	ΔBW	ΔBCS	BCS	BW$^{0.75}$
EB	0.71	−0.16	−0.18	−0.22	−0.12	0.37	0.42	−0.07	0.26
ECR	0.15	−0.65	−0.65	−0.65	−0.62	0.33	0.40	−0.02	0.13
ECE	−0.22	0.67	0.66	0.69	0.63	−0.41	−0.50	0.06	−0.11
ECE$_{adj}$	−0.20	0.66	0.64	0.66	0.63	−0.19	−0.36	0.09	−0.09
ECE$_{maint}$	−0.63	0.07	0.10	0.10	−0.04	−0.11	−0.15	−0.40	−0.23
PEMEP	−0.04	0.78	0.73	0.78	0.73	−0.34	−0.39	0.15	0.31
PEMEP$_{Nut}$	0.23	0.93	0.89	0.91	0.89	−0.31	−0.40	0.08	0.16
MEff	0.70	−0.15	−0.16	−0.20	−0.11	0.36	0.41	−0.09	0.15
FtW	0.90	0.50	0.48	0.43	0.53	0.17	0.13	−0.09	0.12
KR	0.41	0.95	0.92	0.91	0.92	−0.23	−0.35	−0.02	−0.02
REI	0.67	0.00	0.08	−0.04	0.09	0.00	0.00	0.00	0.00
REI$_{maint}$	0.72	0.09	0.14	0.02	0.15	0.06	0.12	−0.43	0.18
REP	0.00	0.52	0.38	0.60	0.44	0.00	0.00	0.00	0.00
REP$_{maint}$	0.22	0.42	0.34	0.45	0.38	0.10	0.18	−0.64	0.27
RIEP	−0.38	0.27	0.17	0.36	0.19	0.00	0.00	0.00	0.00

[1]EB = energy balance; ECR = energy conversion ratio; ECE = energy conversion efficiency; ECE$_{adj}$ = energy conversion efficiency adjusted; ECE$_{maint}$ = energy conversion efficiency taking account of maintenance; PEMEP = partial efficiency of milk energy production; PEMEP$_{Nut}$ = partial efficiency of milk energy production based on nutritional tables; MEff = metabolic efficiency; FtW = feed to live weight; KR = Kleiber ratio; REI = residual energy intake; REI$_{maint}$ = residual energy intake taking account of maintenance; REP = residual energy production; REP$_{maint}$ = residual energy production taking account of maintenance; RIEP = residual intake and energy production. NEI = net energy intake; ΔBW = animals gaining and losing live weight; ΔBCS = animals gaining and losing BCS; BW$^{0.75}$ = metabolic live weight. Correlations <|0.03| were not different from zero.
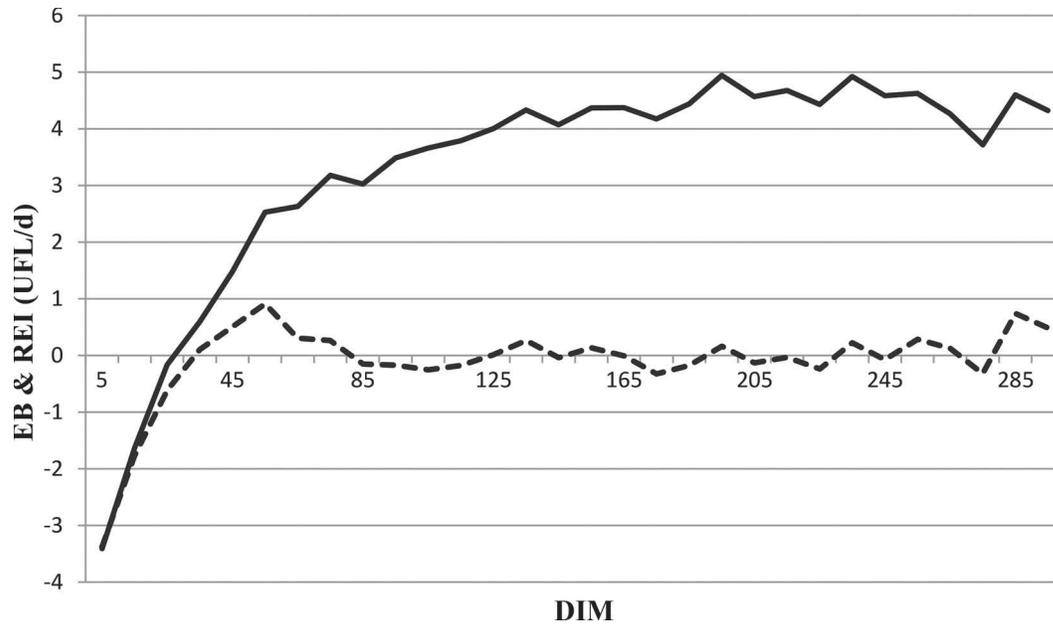
Figure 1. Mean energy balance (EB; ——) and residual energy intake (REI; - - -) of the population across lactation.

Consequently, milk, fat, and protein yield should be included individually in the REI model to guarantee total independence of fat, and protein yield from REI. When NE_L in the REI model was substituted with milk, fat, and protein yield, then REI was uncorrelated with these yield traits. The partial regression coefficient of NEI on milk, fat, and protein yield was 0.008, 1.14, and 8.85 kg, respectively. The correlation between the REI definition using NE_L as a measure of energy required for milk production, and REI using milk yield, fat yield, and protein yield as measures of energy required for milk production was 0.95.

The strong correlation between REI and EB (0.81) signifies that negative REI (i.e., deemed more efficient animals) animals were also, on average, in more negative energy balance. Negative energy balance is known to be unfavorably associated with reproductive performance (Beam and Butler, 1999; Collard et al., 2000). The similarity between EB and REI across lactation is further illustrated in Figure 1. This strong association between REI and EB is not unexpected given their mathematical similarity (Savietto et al., 2014). The correlation between REI and EB was strongest (0.96) in mid-lactation (90–180 DIM) when average live weight change was close to zero (mean Δ live weight of 0.22 kg/d). When live weight change is zero, then live weight change does not contribute to the REI model, and thus REI is mathematically equivalent to energy balance (Veerkamp, 2002). Although antagonistic genetic correlations (e.g., REI and fertility) can be overcome within a balanced breeding goal, the appropriate weightings

within a selection index require precise estimates of the necessary genetic correlations. This means that if REI is to be considered in a breeding goal, precise estimates of the genetic correlations with health and fertility traits (and others) are required. An alternative would simply be to include DMI itself in a breeding goal with the appropriate weighting; this would be mathematically similar to including REI in the breeding goal if all other traits in the REI model were also in the breeding goal. The relative weighting on all other traits in the breeding goal would then be independent of their associated energy cost which may vary by time of the year (Wall et al., 2008), thus affecting the complexity of the calculations.

The definition of REI in the present study, and elsewhere, on average, penalizes a smaller animal (i.e., reduced live weight) compared with a larger animal all else being equal. This is because the energy required to maintain the extra live weight is used to derive predicted NEI which, when subtracted from actual NEI, gives REI. Therefore, an alternative definition of REI, REI_{maint}, was defined in the present study where the energy demand of live weight (i.e., $BW^{0.75}$ times the regression coefficient on $BW^{0.75}$) and lipid mass (i.e., $BW^{0.75} \times BCS$) was added back to REI. The correlation between REI and REI_{maint} was less than unity (0.86, $P < 0.05$). Although REI_{maint} is not independent of $BW^{0.75}$, which is a reported advantage of REI, this is of little consequence if REI is used in a holistic breeding goal which also includes live weight (Berry and Crowley, 2013). The negative correlation between REI_{maint}

and BCS nonetheless indicates that this approach to select for greater efficiency through both reduced NEI and body size (i.e., REI_{maint}) will not be detrimental to BCS. This is important because BCS is related to animal performance (Roche et al., 2009). The comparison of REI and REI_{maint} can be further illustrated by evaluating 2 cows from the data set. Both cows had identical REI (-3.07 UFL/d) and NE_L (4.08 UFL/d) values but had different live weight (480 kg vs. 610 kg). The lighter cow consumed less (average of 9.01 UFL/d) and had a greater ECE value (0.45); in contrast, the heavier cow consumed more (average of 13.67 UFL/d) and had a lesser ECE value (0.29). The REI_{maint} was lower (i.e., superior; 15.85 UFL/d) for the lighter cow compared with the heavier cow (20.86 UFL/d). Thus, the REI_{maint} trait considers the greater energy costs associated with a heavier cow, although this is of little consequence for breeding programs if live weight is also included in the breeding goal.

Analogous to residual gain as defined in growing cattle (Koch et al., 1963), REP may be defined as actual milk energy produced relative to expected milk energy produced based on the NE_L of an animal and other energy sinks and sources (Coleman et al., 2010). In contrast to REI, positive REP values are indicative of more energy-efficient animals. The moderate correlation between REP and REI (-0.53) suggests they are indeed different traits. The more negative REI animals (i.e., deemed more efficient) are expected to, on average, have a greater NEI but have the same milk energy output. In contrast, the more positive REP animals (i.e., deemed more efficient) are expected to, on average, consume the same NEI, but produce, on average, more milk energy output. The benefits of both REI and REP were combined to generate RIEP, which is analogous to RIG as defined in growing cattle (Berry and Crowley, 2012). The results substantiate the benefits of RIEP, when accessing the performance of the top 10% of test-day records ranked on REI, REP, and RIEP (Table 4). The top-ranked 10% of RIEP test-day records were associated with more milk when compared with the top ranked REI test-day records. Additionally, the top RIEP test-day records had the greatest ECE in comparison to both the REP and REI test-day records; therefore, RIEP might be a trait more favored by the producer because it simultaneously increases NE_L and reduces NEI.

Ratio Traits

Many of the correlations among the ratio traits in the present study differed from unity, implying that each trait is depicting a somewhat different aspect of efficiency. Almost all traits which explicitly included NE_L in the numerator (ECE, ECE_{adj}, PEMEP, and KR) were strongly correlated with milk yield, indicating these traits were predominantly influenced by NE_L.

Energy conversion efficiency, and its reciprocal ECR, are most commonly used internationally across species (Tolkamp et al., 2010). Selection on the former has, however, been shown to be associated with greater live weight loss and reduced BCS throughout lactation (Vallimont et al., 2011). The correlations from the present study substantiate this. The correlation between ECE and ΔBCS (-0.50) suggests that 25% of the variation in ECE was due to BCS mobilization, which indicates that loss of BCS throughout lactation contributes to higher ECE values thereby questioning the suitability of ECE as a measure of efficiency. Energy conversion efficiency was therefore redefined in the present study where the contribution of body tissue mobilization to energetic efficiency was accounted for in both ECE_{adj} and ECE_{maint}. Nonetheless, the ECE_{adj} trait was not completely effective in achieving the desired outcome as greater ECE_{adj} was still associated with loss in live weight and body condition although the correlations had weakened. The correlations with BCS and live weight change were further weakened with the ECE_{maint} trait, but the correlations remained negative, implying that both BCS and live weight loss were still contributing to variability in ECE_{maint}.

Both definitions of PEMEP in the present study were novel and represented the proportion of NEI used for milk production having accounted for maintenance energy requirements. Both PEMEP and $PEMEP_{Nut}$ were defined similarly, except for the calculation of maintenance energy, which resulted in a strong correlation between them. The moderately negative correlation of PEMEP and $PEMEP_{Nut}$ with BCS and live weight change suggested that the loss of live weight and BCS throughout lactation contributed to high PEMEP and $PEMEP_{Nut}$ values as was the case for ECE.

Similar to PEMEP, although KR is not a feed efficiency measure per se, it can be used as a measure of feed efficiency if all animals are fed the same restricted diet, as could be argued to exist in grazing production systems (e.g., the present study). Nonetheless, KR was strongly correlated with $PEMEP_{Nut}$, suggesting these traits were almost identical. The main advantage of KR is that it does not require any measure of feed intake.

The FtW trait defined in the present study and elsewhere (Coleman et al., 2010) provides an indication of cow intake capacity, which is important as successful grazing systems require dairy cows that are adapted to achieving large intakes of high-quality forage. Like KR, FtW does not require feed intake observations and can thus be calculated using data that are routinely available on some farms. In the present study, FtW was

further modified where NE_L was subtracted from NEI in the numerator to generate the MEff trait. Energy balance is close to a linearization of MEff because EB is formulated when the dominator (i.e., live weight) is interchanged to the numerator; thus, a very strong correlation between both is expected. Also, because of this strong correlation, both MEff and EB had similar correlations with the production traits. Nonetheless, the statistical properties of ratio traits suggest that for breeding programs at least, linearized traits are more favorable (Berry and Crowley, 2013).

CONCLUSIONS

This is the first study to comprehensively describe the inter-relationships among alternative definitions of energy efficiency in intensive pasture-based lactating Holstein-Friesian dairy cows. Given the potential of REI to reduce feed intake and therefore variable costs associated with milk production, our findings suggest REI could be a valuable tool for future genetic improvement. However, the existence of genetic variation in such a trait as well as the estimation of precise correlations between REI and both reproduction and health traits (as well as other traits) need to be quantified. Several alternative efficiency definitions were developed in the present study, each with their own respective strengths and weaknesses. For example, the ratio traits are easy to calculate and understand particularly by producers; however, they are correlated with the component traits and do not fully account for the contribution of, for example, BCS change, to energy available. Residual energy intake is more difficult to explain and therefore understand by producers, but it is independent of the components of energy kinetics included in its derivation. The eventual decision on which feed intake or efficiency measure to use is of course dependent on the end use. For example, a ratio trait may be more suitable for management purposes at a herd level, an REI type trait may be more useful in research experiments attempting to elucidate the factors associated with inter-animal variability in efficiency, whereas an REI-type trait or DMI itself may be more applicable in a breeding program. Many of the correlations among the various measures of feed efficiency differed from unity, implying that each trait is measuring a different aspect of efficiency.

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