Phenotypic correlations among alternative definitions of feed efficiency in grazing lactating dairy cows across parities and lactation stages

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Abstract

The objective of this study was to estimate correlations among alternative measures of energy conversion efficiency and energy balance (EB) across parities and lactation stages in grazing lactating dairy cows. Individual measurements of net energy intake (NEI) (n=8,183) from pasture and concentrate from 2,693 lactations on 1,412 cows were available. Residual energy production (REP) was defined as net energy of lactation (NEL) minus predicted energy requirements; energy conversion efficiency (ECE) was defined as NEL divided by NEI; and EB was defined as the difference between NEI and energy required for both maintenance and lactation. Residual energy intake (REI) was defined as NEI minus predicted energy requirements. A strong correlation existed between REI and EB (0.88; P<0.05) for parity three or greater early lactation, weakening in parity one (0.70; P<0.05). These differences in correlations between REI and EB for animals across parities in early lactation, indicated primiparous animals were using body energy for milk production and growth; nevertheless, these strong correlations suggested negative REI animals (i.e., more efficient) are also in more-negative EB. Our findings suggest REI could be a valuable tool for future genetic improvement, however, selection on REI could have detrimental effects on reproduction and health traits, thus, further research is warranted.

Keywords: feed efficiency; dairy; residual energy intake; energy balance; lactation

Introduction

The expanding world human population is contributing to increased global demand for animal-derived protein and energy sources. International interest in sustainable resource use efficiency is therefore intensifying. Improved system efficiency is required to fulfill the protein and energy demand of an expanding world human population. Residual feed intake, used predominately in growing animals as a measure of feed efficiency (Berry & Crowley 2013), is now increasing in interest in lactating dairy-cow populations (McParland et al. 2014). The definition of residual energy intake in lactating cows does however differ among studies (Coleman et al. 2010; McParland et al. 2014). Consequently, the applications and benefits of these definitions are different. Irrespective of the definition, estimates of feed efficiency in dairy cows must account for different functions involved in energy usage over the entire lactation; for example lipid and protein body mass changes (Berry et al. 2006). Several definitions of feed efficiency in lactating animals exist, but the inter-relationships among the alternative definitions of feed efficiency traits across parity and lactation stages have not been fully elucidated.

The objective of the present study was to quantify the inter-relationships among some efficiency traits and energy balance (EB) across parities and lactation stages in grazing lactating dairy cows.

Materials and methods

Data

Data were available from the Animal and Grassland Research and Innovation Centre, Teagasc Moorepark, Fermoy, Co. Cork, Ireland (50°7N; 8°16W), between the years 1988 and 2009, inclusive. All studies were undertaken on two adjacent research farms, namely, Curtin's Research Farm and the 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 description of database. Animals were fed predominately grazed grass. Swards constituted 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 DM per cow daily, offered in equal feeds during each milking. All cows were milked twice daily.

Individual cow milk yield was recorded daily, and 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, Hillerod, Denmark). Net energy requirements for lactation (NEL) was calculated as (Jarrige et al. 1986):

NEL = (0.054×((Fat yield / Milk yield) ×100) + 0.031× ((protein yield / Milk yield) ×100) + 0.028*-0.015) ×Milk yield where a standard lactose (i.e.. 5%) was assumed (Lactose yeild/milk yeild) ×100

Individual animal live weight was recorded weekly upon exit of the milking parlour using an electronic scale (Tru-Test Limited, Auckland, New Zealand); scales were calibrated weekly against known weights. Animal body condition score (BCS; scale 1 = emaciated, 5 = obese) was recorded every two to three weeks in increments of 0.25 (Edmonson et al. 1989). Cubic splines with six knot points at 20, 70, 120, 170, 220, and 270 days in milk (DIM), with a covariance structure fitted among knot points, were fitted through individual live weight and BCS 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 cow daily total DMI (i.e., grazed grass DMI plus concentrate DMI) was available on average 4.5 times per lactation. Energy values of the pasture and concentrate, as well as the energy sinks (where used) were based on the French net energy system where 1 unité fourragère du lait (UFL) is the net energy requirement for milk production equivalent of 1 kg standard air-dry barley (Jarrige et al. 1986) equivalent to 7.11 MJ net energy or 11.85 MJ metabolisable energy.

The net energy content of the concentrate fed was calculated each day from the chemical composition of the feed; where UFL content of the concentrate was not available (28% of records) the year-month average was assumed. Where an offered herbage UFL value was not available (10.3% of records), the year-month average was assumed. The within-month variation in the UFL content of both concentrate and offered herbage was low, with coefficients of variation of 2% and 8%, respectively. The UFL concentration of the offered herbage was calculated using the acid detergent fibre and crude protein estimation method in the laboratory (Jarrige 1989). Net energy intake (NEI) was defined as the sum of pasture and concentrate net energy intake.

Individual animal grass dry matter intake (DMI) at pasture was estimated using the n-alkane technique (Mayes et al. 1986). Net energy intake (NEI) from pasture and concentrate intake was estimated up to eight times per lactation on 2,693 lactations from 1,412 Holstein-Friesian cows. A total of 8,183 individual feed intake measurements were available. Lactation was divided into three lactation stages (8–90, 90–180, and > 180 days in milk). Three parity classes (1, 2, and 3+) were considered. The UFL value (French net energy system) of both herbage and concentrates were calculated for each intake record.

Efficiency traits

Energy balance (EB) was calculated as the difference between energy intake and energy required for both maintenance and lactation according to Jarrige (1989) and modified for Irish dairy systems by O'Mara (1996):

$$EB = NEI - \Delta NE - NEL - NEM - NEP$$

where NEI is daily net energy intake, ΔNE is an adjustment of daily net energy intake for the proportion of concentrates in the diet, NEL is daily net energy requirements for lactation, NEM is daily net energy for maintenance calculated as (1.4 + 0.6×live weight/100)×1.2, and NEP is daily net energy requirements for pregnancy (O'Mara 1996).

Residual energy intake (REI) and residual energy production (REP) for each day of lactation were defined as:

$$REI = NEL - [NEL\ \Sigma^{2}_{i=1}\ DIM^{i} + BW^{0.75} + BCS + BW^{0.75} \times BCS + \Delta BW^{+} + \Delta BW^{-} + \Delta BCS^{+} + \Delta BCS^{-} + \Delta BW^{+} \times BCS + \Delta BW^{-} + BCS$$

where REI is daily residual energy intake, REP is daily residual energy production, NEI is daily net energy intake, NEL is daily net energy requirements for lactation, $\Sigma^{2}_{C=1}$ DIM^{i} is days in milk included as a continuous variable with a linear and quadratic effect, $BW^{0.75}$ is metabolic live weight, BCS is body condition score, ΔBW^{+} describes animals gaining live weight, ΔBW^{-} describes animals loosing live weight, ΔBCS^{+} describes animals gaining BCS, and ΔBCS^{-} describes animals losing BCS.

Energy conversion efficiency (ECE) for each day of lactation was defined as the daily net energy requirements for lactation (NEL) divided by the daily net energy intake (NEI).

Results

Mean ECE, EB, REI, and NEI over the whole data set was 0.41 (SD=0.11), 3.68 UFL/d (SD=2.51 UFL/d), 0.00 UFL/d (SD=2.17 UFL/d), 16.23 UFL/d (SD=3.24 UFL/d), respectively. The mean NEI for first lactation heifers (14.19 UFL/d, SD=2.47 UFL) was less than second lactation cows (17.10 UFL/d, SD=2.87 UFL) and cows in their third or greater lactation (17.47 UFL/d, SD=3.13 UFL). Estimates of REI for first lactation heifers, ranged from -7.67 to 8.80 UFL/d (SD=1.86 UFL/d). Estimates of REI for second lactation cows ranged from a minimum of -7.45 UFL/d to a maximum of 8.19 UFL/d (SD=2.16 UFL/d), and ranged from -11.16 to 9.22 UFL/d (SD=2.43 UFL/d) among cows in their third or greater lactation.

The similarity between EB and REI across an entire lactation is illustrated in Figure 1. The trend in NEI, ECE, and REP across lactation is illustrated in Figure 2. Net energy intake increased in early lactation, remained constant in mid-lactation and started to decline in late lactation. Energy conversion efficiency declined rapidly in early lactation, with only a gradual decrease thereafter until the end of lactation. Residual energy production declined rapidly in both early and late stages of lactation, but remained constant throughout mid-lactation.

The correlations among the efficiency traits by stage of lactation (i.e., 8 to 90 DIM, 91 to 180 DIM, and >180 DIM) and parity (1, 2, 3+) are summarised in Table 1. The correlation between REI and EB strengthened from early to mid-lactation and was near unity from mid to late lactation across all parities. There was an effect of parity on REI, with heifers in their first lactation having lower average REI (-0.27 UFL/d) than cows in their third or greater lactation (-0.04 UFL/d). A strong correlation existed between REI and EB (0.88; P<0.05) for parity or greater early lactation animals; however, at the same stage in parity one, a weaker correlation existed (0.70; P<0.05). The correlations among the efficiency traits, EB, NEI and NEL across all parities and lactation stages are in Table 2. Estimates of REI were positively correlated with NEI (0.67; P<0.05) and negatively associated with ECE (-0.53; P<0.05) across all lactations (Table 2). The correlation between REP and ECE in parity one (0.59; P<0.05) early lactation strengthened in parity two (0.76; P<0.05), and parity 3+ (0.70; P<0.05),

Figure 1 Mean residual energy intake (REI) and mean energy balance (EB) of the population across lactation.

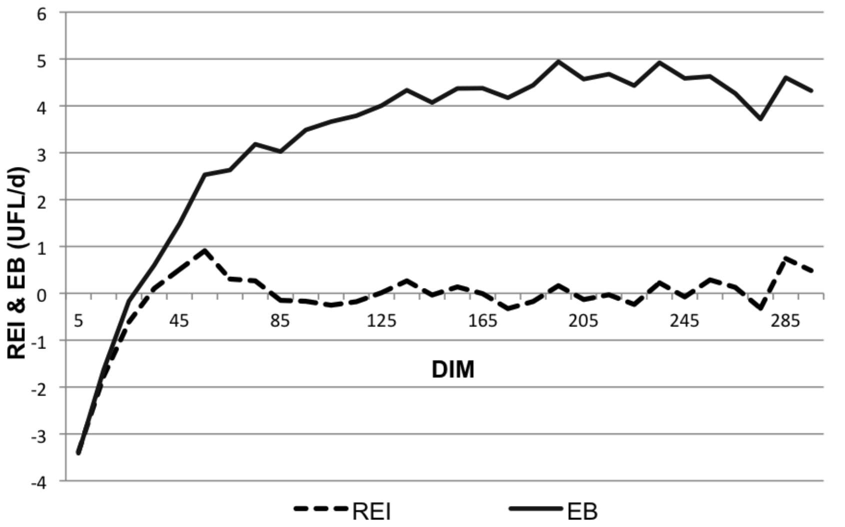
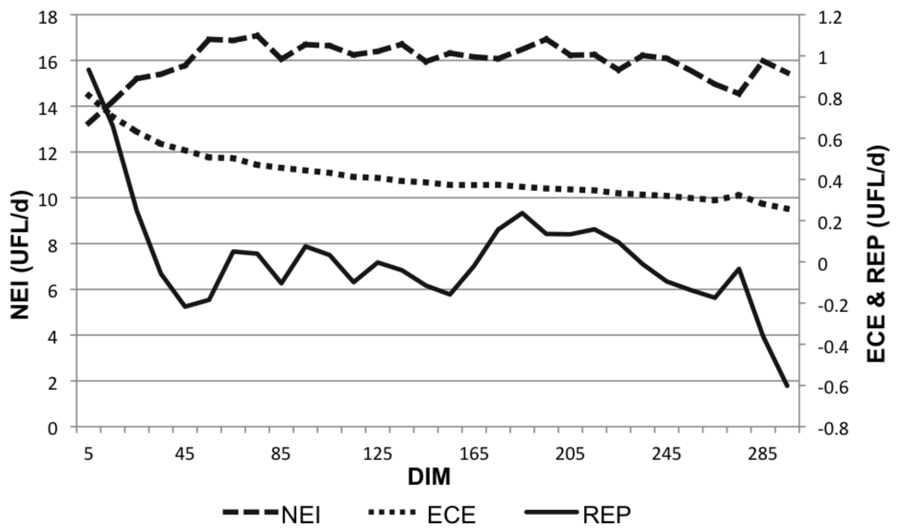


Figure 2 Mean net energy intake (NEI), mean energy conversion efficiency (ECE) and mean residual energy production (REP) of the population across lactation.



at the same stage of lactation. Furthermore, the correlation between REP and ECE strengthened across all lactation stages.

A strong correlation existed between ECE and EB across all parities in early lactation (-0.91, -0.90 and -0.92; P<0.05), however, as the lactation progressed these correlations weakened across all parities. A moderate correlation (-0.60; P<0.05) existed between ECE and NEI in parity one early lactation and remained similar for all parities at this stage of lactation; however, this correlation weakened considerably from the start to the end of lactation.

Animals with high REP values (i.e., efficient cows) produced greater milk yields. Moreover, increased REP was associated with lower REI and increased ECE. Increased ECE was associated with increased milk yield, lower total NEI and decreased body condition score. Furthermore, an increased ECE was associated with lower REI and a higher REP.

Discussion

International interest in feed efficiency and, in particular, energy intake and REI is increasing due to an increased global demand for animal-derived protein and energy sources. Future pasture-based systems of milk production will be characterised by the ability of a cow to produce the majority of milk solids from grazed pasture. Consequently, a trait to identify animals capable of producing more milk-solids from a restricted level of intake with no unfavourable repercussions on reproduction and performance would be highly beneficial to a breeding program.

In the present study, a refinement of REI was undertaken where the role of body reserves in energetic efficiency was accounted. The main difference between this alternative REI definition and those previously defined (Coleman et al. 2010), was including the interaction between metabolic live weight ($BW^{0.75}$) and body condition score (BCS). Body condition score measures depth of muscle (and fat), and is independent of skeletal size but energy kinetics are associated with body lipid mass not depth, e.g., larger animals have greater lipid mass, compared to a smaller animal both with the same BCS. The energy sinks (NEL, $BW^{0.75}$) and additional contributors to energy kinetics combined explained 57% of the variability in NEI, implying that REI represented only 43% of the total variance in NEI. This variation in NEI explained by the REI model was different to previous studies in lactating Holstein-Friesian dairy cows where the REI model of Coleman et al. (2010) explained 86% of the variation in feed intake. Nevertheless, additional variation in REI could be explained if the REI model included other systematic environmental effects such as parity, herd, year, and season.

The strong correlation between REI and EB suggests that negative REI animals (deemed more efficient animals) are also animals in more negative EB which is known to be unfavourably associated with reproductive performance (Beam & Butler 1998). The strong correlation between REI and EB for animals in parity three and early lactation was weaker for parity one animals at the same lactation stage, suggesting primiparous animals were using body energy for both milk production and growth. Furthermore, a positive correlation was observed between REI and NEI, and a negative correlation resulted between REI and ECE.

Table 1 Correlations among the efficiency traits, NEI and EB across parities and lactation stages.

Parity	DIM	Trait	ECE	EB (UFL/d)	REI (UFL/d)	REP (UFL/d)
1	8 – 90	EB	-0.91[1]			
		REI	-0.69	0.70		
		REP	0.59	-0.39	-0.64	
		NEI (UFL/d)	-0.60	0.81	0.56	-0.03
	90 - 180	EB	-0.78			
		REI	-0.74	0.94		
		REP	0.82	-0.55	-0.59	
		NEI	-0.34	0.81	0.69	-0.09
	> 180	EB	-0.65			
		REI	-0.67	0.96		
		REP	0.90	-0.54	-0.56	
		NEI	-0.27	0.86	0.78	-0.15
2	8 - 90	EB	-0.90			
		REI	-0.72	0.84		
		REP	0.76	-0.57	-0.63	
		NEI	-0.46	0.76	0.69	-0.07
	90 - 180	EB	-0.76			
		REI	-0.74	0.97		
		REP	0.87	-0.55	-0.56	
		NEI	-0.28	0.81	0.74	-0.07
	> 180	EB	-0.63			
		REI	-0.63	0.97		
		REP	0.94	-0.53	-0.53	
		NEI	-0.22	0.86	0.80	-0.09
3+	8 - 90	EB	-0.92			
		REI	-0.76	0.88		
		REP	0.70	-0.54	-0.57	
		NEI	-0.56	0.80	0.72	-0.04
	90 - 180	EB	-0.76			
		REI	-0.72	0.97		
		REP	0.86	-0.50	-0.49	
		NEI	-0.29	0.82	0.79	-0.03
	> 180	EB	-0.67			
		REI	-0.66	0.96		
		REP	0.92	-0.55	-0.54	
		NEI	-0.16	0.83	0.77	-0.09

[1]r < |0.05| were not different from zero. [2]One UFL is defined as the net energy content of 1 kg standard air-dry barley (Jarrige et al., 1986)

Table 2 Correlations among the efficiency traits, EB, NEI and NEL across all parities and lactation stages.

Trait	ECE	EB (UFL/d)	REI (UFL/d)	REP (UFL/d)	NEI (UFL/d)
EB	-0.79[1]				
REI	-0.53	0.82			
REP	0.60	-0.44	-0.54		
NEI	-0.22	0.74	0.67	0.00	
NEL	0.69	-0.16	0.00	0.56	0.52

[1]r < |0.05| were not different from zero. [2]One UFL is defined as the net energy content of 1 kg standard air-dry barley (Jarrige et al., 1986).

These results suggest that lower REI (i.e., increased efficiency) is associated with decreased energy intake and improved ECE. Our findings are consistent with those of Connor et al. (2013) and Van Arendonk et al. (1991), both of which used similar definitions of REI. Residual energy production was positively correlated with NEL; thus, low-yielding animals are less likely, on average, to rank highly on REP. Moreover, the correlation between ECE and EB declined rapidly in all stages of lactation while similar correlations existed across all parities, suggesting animals were most efficient in early lactation. The current study estimates that measurements of REI during mid- or late lactation (after 90 DIM) are more representative of REI throughout lactation than measurements obtained during early lactation (<90 DIM).

Analogous to residual gain as defined in growing cattle (Koch et al. 1963), REP may be defined as actual milk energy relative to expected milk energy based on milk energy of an animal and other energy sources. In contrast to REI, positive REP values are indicative of more feed efficient animals. Residual energy production was positively correlated with NEL, thus low-yielding animals are less likely, on average, to rank highly on REP.

Stage of lactation influenced ECE as cows in early lactation were losing live weight and using that energy for milk production, inevitably leading to an increase in feed efficiency. A high ECE value in early lactation, where cows are losing excess live weight could indicate potential metabolic disorders. In contrast to early lactation cows, late-lactation cows have a lower ECE value as these animals are gaining weight. Consequently, a lower ECE value should not be viewed negatively as cows need to gain live weight in late lactation so body reserves can be utilized when the cow begins the next lactation.

Conclusion

This is the first study to comprehensively describe the inter-relationships among alternative definitions of feed efficiency in intensive pasture-based lactating Holstein-Friesian dairy cows across parity and lactation stages. The measures of energy efficiency which represent net efficiency, for example REI, which is independent from maintenance and production, should be considered in order to improve efficiency in dairy cattle. Further research is warranted to determine what indirect effects might be evident in other traits especially those related to reproduction and health. Many of the correlations among the various measures of feed efficiency varied across lactation stages, however, with the particular estimates of efficiency investigated in this study, animals seemed to be more efficient in early lactation. Future research should incorporate a greater range of dairy cow breeds.

Acknowledgments

The authors gratefully acknowledge funding from the Irish Department of Agriculture, Food and Marine (Dublin, Ireland) Research Stimulus Fund project GENCOST, and funding from the Marie Curie project International Research Staff Exchange Scheme SEQSEL.

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