Alternatives to Linear Analysis of Energy Balance Data from Lactating Dairy Cows

E. Kebreab,* J. France,* R. E. Agnew,† T. Yan,† M. S. Dhanoa,‡ J. Dijkstra,§
D. E. Beever,* and C. K. Reynolds*,¹

*School of Agriculture, Policy and Development, The University of Reading,
Earley Gate, Reading RG6 6AR, United Kingdom

†The Agricultural Research Institute of Northern Ireland,
Hillsborough, Co. Down, Northern Ireland BT26 6DR, United Kingdom

‡Institute of Grassland and Environmental Research, Plas Gogerddan,
Aberystwyth, Dyfed SY23 3EB, United Kingdom

§Animal Nutrition Group, Wageningen Institute of Animal Sciences,
Wageningen University, Marijkeweg 40,
6709 PG Wageningen, The Netherlands

ABSTRACT

The current energy requirements system used in the United Kingdom for lactating dairy cows utilizes key parameters such as metabolizable energy intake (MEI) at maintenance (ME_m), the efficiency of utilization of MEI for 1) maintenance, 2) milk production (k_l), 3) growth (k_g), and the efficiency of utilization of body stores for milk production (k_t). Traditionally, these have been determined using linear regression methods to analyze energy balance data from calorimetry experiments. Many studies have highlighted a number of concerns over current energy feeding systems particularly in relation to these key parameters, and the linear models used for analyzing. Therefore, a database containing 652 dairy cow observations was assembled from calorimetry studies in the United Kingdom. Five functions for analyzing energy balance data were considered: straight line, two diminishing returns functions, (the Mitscherlich and the rectangular hyperbola), and two sigmoidal functions (the logistic and the Gompertz). Meta-analysis of the data was conducted to estimate k_g and k_t . Values of 0.83 to 0.86 and 0.66 to 0.69 were obtained for k_g and k_t using all the functions (with standard errors of 0.028 and 0.027), respectively, which were considerably different from previous reports of 0.60 to 0.75 for k_g and 0.82 to 0.84 for k_t . Using the estimated values of k_g and k_t , the data were corrected to allow for body tissue changes. Based on the definition of k_l as the derivative of the ratio of milk energy derived from MEI to MEI directed towards milk production,

ME_m and k_l were determined. Meta-analysis of the pooled data showed that the average k_l ranged from 0.50 to 0.58 and ME_m ranged between 0.34 and 0.64 MJ/kg of $BW^{0.75}$ per day. Although the constrained Mitscherlich fitted the data as good as the straight line, more observations at high energy intakes (above 2.4 MJ/kg of $BW^{0.75}$ per day) are required to determine conclusively whether milk energy is related to MEI linearly or not.

(**Key words:** energy metabolism, dairy cow, lactation)

Abbreviation key: BIC = Bayesian information criteria, E_l = energy in milk (MJ/d), k_g = the marginal efficiency of utilization of MEI for growth, k_l = the marginal efficiency of utilization of MEI for milk production, k_m = the marginal efficiency of utilization of MEI for maintenance, k_t = the marginal efficiency of utilization of body stores for milk production, MBW = metabolic body weight ($kg^{0.75}$), ME = metabolizable energy, MEI = ME intake (MJ/kg $^{0.75}$ /d), ME_m = ME requirement for maintenance (MJ/kg $^{0.75}$ /d), T_g = tissue gain (MJ/kg $^{0.75}$ /d), T_l = tissue loss (MJ/kg $^{0.75}$ /d).

INTRODUCTION

The metabolizable energy (ME) feeding system for ruminants, developed by Blaxter (1962), was first proposed for use in the United Kingdom by the Agricultural Research Council (ARC, 1965). A simplified system, based on these proposals, was subsequently recommended for adoption by the Ministry of Agriculture, Fisheries and Food (England and Wales). The original system (ARC, 1965) was revised substantially by ARC (1980), modified further by the Agricultural and Food Research Council (AFRC, 1990), and a new working version published in 1993 (AFRC, 1993). Key parameters in the current ME system for lactating dairy cows are: net energy requirement for maintenance (ME_m);

Received June 20, 2002.

Accepted December 27, 2002.

Corresponding author: E. Kebreab; e-mail: e.kebreab@reading.ac.uk.

¹Present address: Department of Animal Sciences, The Ohio State University, OARDC, 1680 Madison Ave. Wooster 44691-4096.

the efficiency of utilization of ME for 1) maintenance (k_m), 2) milk production (k_l), and 3) growth (k_g), and the efficiency of utilization of body stores for milk production (k_t). These values were determined largely using linear regression methods to analyze energy balance data from calorimetry experiments.

Over the last two decades, a considerable volume of research on the energy metabolism of dairy cows has been undertaken in the United Kingdom. These studies have highlighted a number of concerns over the current energy feeding system, particularly in relation to values for the aforementioned key parameters (Agnew and Yan, 2000). Underlying these concerns could be the rigid acceptance of linear methods in analyzing energy balance data.

The rate of energy retention by the growing ruminant is nonlinearly related to its level of ME intake (MEI) over the range of ingestion, as successive increments in daily intake at high intake levels produce progressively smaller increments in daily energy retention as body tissue. Blaxter and Wainman (1961) approximated this nonlinear relationship with two straight lines intersecting at zero energy retention (i.e., maintenance) for growing ruminants. The slope of the linear equation below maintenance gives the efficiency of utilization of ME for maintenance, and the slope of the linear equation above maintenance gives the efficiency of utilization of ME for tissue energy. However, Blaxter and Boyne (1978) subsequently proposed the Mitscherlich equation for describing the relationship between tissue energy retention and MEI in growing ruminants, based on a detailed analysis of more than 80 calorimetry experiments with sheep and cattle. The Mitscherlich equation, however, presupposes that the response of tissue energy retention to increments in MEI obeys the law of diminishing returns over all intake levels, which precludes an increasing slope over any segment of the response curve. To address this potential problem, France et al. (1989) proposed some sigmoidal or S-shaped functions for situations in which the law of diminishing returns does not apply to the rate of energy retention across the range described.

The objectives of the present study are to collate data from energy balance studies with lactating dairy cows, and to evaluate alternative mathematical functions to estimate parameters of energy metabolism in relation to milk production such as k_b , k_g , k_t , k_m , and ME_m . The approach utilizes linear and nonlinear models to estimate ME requirement for maintenance and the efficiency of utilization of ME for milk production and includes a novel method to determine the efficiency of utilization of ME for tissue energy during lactation and the efficiency of utilization of body stores for milk production. The results from the alternative approach are

then compared with traditional methods of analysis. The null hypothesis was that the relationship between MEI and milk energy is linear after correcting for tissue energy utilization and energy gain.

MATERIALS AND METHODS

The Database

A database containing energy balance data for 652 dairy cow observations was assembled from calorimetry studies conducted at the Centre for Dairy Research (CEDAR) at the University of Reading, the Agricultural Research Institute for Northern Ireland (ARINI), Queens University of Belfast and Grassland Research Institute, Hurley. Table 1 shows details of diet composition of the trials used to construct the database. The range of calorimetric data included in database is summarized in Table 2.

Mathematical Considerations

New approach. We define the efficiency of utilization of ME for milk energy, k_l , as the derivative:

$$k_l = \frac{d(\text{Milk energy derived from MEI})}{d(\text{MEI directed towards maintenance and milk production})} \quad [1]$$

Based on this definition, k_l can be found by plotting milk energy derived from MEI (y-axis, MJ/kg of BW^{0.75} per day) against MEI directed towards maintenance and milk production (x-axis, MJ/kg of BW^{0.75} per day) and finding the slope of the graph over the region where each increment in MEI is directed towards milk production (see Figure 1). When the cow is in positive tissue energy balance, some of the MEI is being directed towards tissue energy retention and therefore MEI is corrected as follows:

$$\text{Corrected MEI, } x = \text{MEI} - |\text{TE}|/k_g \quad [2]$$

where $|\text{TE}|$ denotes the magnitude of the tissue energy retention and k_g is the efficiency of utilization of MEI for tissue energy growth. A book value for k_g is 0.60 assuming a metabolizability ($[\text{ME}]/[\text{Gross energy}]$) of diet of 0.6 (AFRC, 1993). When the cow is in zero energy balance, all the MEI is being directed to maintenance and milk production and no correction is needed. When the cow is in negative energy balance, some of the milk energy (E_l , MJ/kg of BW^{0.75} per day) is derived from body stores and therefore E_l is corrected as follows:

$$\text{Corrected } E_l, y = E_l - |\text{TE}| \times k_t \quad [3]$$

Table 1. Diet composition and references (where applicable) of the trials used to construct the database. The trials were conducted at the Centre for Dairy Research (CEDAR), Agricultural Research Institute of Northern Ireland (ARINI), Queens University of Belfast (Queens) and Grassland Research Institute, Hurley (Hurley).

Centre	Trial	Diet composition		F:C ratio (DM basis)	Reference
		Forage (F)	Concentrate (C)		
ARINI	1	Fresh grass and either 0 or 2 kg/d of straw		2:1	Unpublished
ARINI	2	Grass silage	5.5 or 14 kg/d of concentrate (280 g CP/kg DM)	variable	Ferris et al. (2002)
ARINI	3,4	Fresh grass or grass silage that had undergone either an extensive or restricted fermentation, produced from the same sward			Cushnahan et al. (1995)
ARINI	5	Grass silage	5 kg/d of concentrate with 120 or 260 gCP/kg DM	3:1	Unpublished
ARINI	6	High digestibility grass silage offered ad libitum or restricted to 6.5 kg DM/d and low digestibility grass silage offered ad libitum	Starch or fibre based at 10 kg/d		Gordon et al. (1995b)
ARINI	7	Straw		1:4	Unpublished
ARINI	8	Three forage treatments were prepared from perennial ryegrass either ensiled directly or wilted and ensiled following 30 or 52 h to achieve DM concentration in the silages of 193, 286 and 437 g/kg, respectively. All silages were offered ad libitum	A concentrate containing 206 g CP/kg DM fed at 10 kg/d		Gordon et al. (2000)
ARINI	9	A grass silage based diet	4 concentrate proportions (0.37, 0.48, 0.59 and 0.70 of total DM)		Ferris et al. (1999)
ARINI	10	Either a complete diet (64:36 grass silage:concentrate offered ad libitum) or restricted concentrate.	Based on barley, maize gluten, molassed sugar-beet pulp, citrus pulp, soya bean meal, fish meal and protected fat		Gordon et al. (1995a)
ARINI	11	Dried grass (grass nuts)		2:1	Agnew et al. (1998)
ARINI	12	Grass silage ad libitum	Six protein concentrations (174 – 306 g/kg DM), two protein sources, and 2 concentrate levels		Carrick et al. (1996)
ARINI	13, 14, 15	Dried grass nuts only, dried grass nuts and concentrate, and grass silage and concentrate			Yan et al. (1997)
ARINI	16	12 silages prepared from perennial ryegrass, four at each of the first, second and third harvest of one season			Yan et al. (1996)
Queens	17–24	A total of 11 grass and grass silage-based diets. Forages were offered ad libitum with and without concentrate	Concentrate offered at a rate of either 0, 8 or 10 kg/d		Unsworth et al. (1994)
CEDAR	25	Urea-treated whole crop wheat (WCW) and grass silage		2:1	Sutton et al. (1998)
CEDAR	26, 27	Maize silage harvested at two stages of maturity, defined by DM content (low DM, 21% LDM and high DM, 38%, HDM)		2:1	Beever et al. (1998a)
CEDAR	28	WCW was fed with first-cut grass silage in the ratio 1:2, respectively. Treatments involved the replacement of WCW with NaOH treated WCW or altering the amount of concentrates		variable	Sutton et al. (2001)
CEDAR	29,30	TMR offered ad libitum, which comprised maize silage, grass silage, dried lucerne and a range of concentrate straights (19:13:6:62, respectively)	TMR		Beever et al. (1998b)
CEDAR	31	Maize silage (LDM and HDM) and grass silage mixture (3:1 ratio respectively) fed ad libitum	Four different concentrates varied in starch source and degradability and fed at 8.7 kg DM/d		Cammell et al. (2000)
CEDAR	32, 33	Primary growth fresh ryegrass cut and 6-week re-growth ryegrass cut three times ad libitum		2:1	Unpublished
CEDAR	34	Maize silage and grass silage (3:1) offered ad libitum	High or low starch concentrate (8.5 kg DM/d)		Unpublished
CEDAR	35	A mixture of grass silage:maize silage (3:1)	A high or low starch concentrate as part of a TMR, ad libitum or a restricted level of intake	1:1	Unpublished
CEDAR	36	Maize silage, grass silage, dried lucerne and a range of concentrate straights fed 30:10:14:35, respectively			Hattan et al. (2001)
Hurley	37	Mid and late season cuts of fresh perennial ryegrass and white clover			Cammell et al. (1986)

Table 2. Summary statistics of the calorimetric data used in the study.

	Mean	Standard deviation	Minimum	Maximum
Animal data				
DMI (kg/d)	17.4	3.97	6.61	27.7
Forage proportion	0.60	0.21	0.10	1.00
Milk yield (kg/d)	24.7	9.13	0.93	59.7
Live weight (kg)	579	70.9	385	826
Energy measurements (MJ/d)				
Gross energy	330	79.5	123	543
Fecal energy	88.6	29.2	28.4	169
Urinary energy	12.1	3.60	2.88	26.7
Methane	21.7	4.79	7.90	34.3
Heat production	125	25.5	67.9	255
Milk energy	79.5	28.6	2.79	160
Retained energy	2.82	22.0	-80.1	83.9
ME intake	207	49.3	75.7	347

where k_t is efficiency of utilization of tissue energy for milk production. A book value for k_t is 0.84 (AFRC, 1993). If, for example, 0.7 MJ/d of body stores are depleted and efficiency of tissue energy conversion to E_l is assumed as 0.84, and 3.3 MJ/d of milk produced, 2.7 MJ/d ($3.3 - 0.7 \times 0.84$) are directed towards milk production and a y -value of 2.7 MJ/d is entered on the graph for this observation.

Let y be regressed on x using the general equation:

$$y = f(x) + \varepsilon \quad [4]$$

where ε is an error term. The efficiency k_l , defined by equation [1] is then given by:

$$k_l = dy/dx, y > 0 \quad [5]$$

and the average efficiency ($\bar{k}_l$) between maintenance and N times maintenance ($N > 1$) given by:

$$\bar{k}_l = \frac{\int_{ME_m}^{N \times ME_m} k_l dx}{(N-1) \times ME_m} = \frac{\int_{ME_m}^{N \times ME_m} \frac{dy}{dx} dx}{(N-1) \times ME_m} \quad [6]$$

$$= \frac{\int_0^{y(N \times ME_m)} dy}{(N-1) \times ME_m} = \frac{y(N \times ME_m)}{(N-1) \times ME_m}$$

where ME_m denotes the value of x at $y = 0$, i.e., at maintenance. For example, if $f(x)$ is a straight line, then:

$$y = ax - b$$

$$dy/dx = a \quad [7,8,9]$$

$$\bar{k}_l = \frac{\int_{ME_m}^{N \times ME_m} a dx}{(N-1) \times ME_m} = a$$

i.e., the average efficiency is the slope of the line.

In addition to the conventional straight line, we investigate the Mitscherlich, rectangular hyperbola (both of which exhibit diminishing returns behavior), Gompertz and logistic (both sigmoidal) as candidates for $f(x)$. The functional forms adopted, together with formulae for ME_m , are given in Table 3. In the nonlinear models, the entities a , b , and c are positive parameters, and:

$$y_{\max} = a \quad [10,11]$$

$$y_{\min} = -b$$

The procedure for estimating k_g and k_t is as follows: rather than assume book values, we determine k_g and k_t from the database based on the principles expressed in equations [2] and [3]. For example, for the straight line candidate function, the following equation was fitted to the dataset:

$$E_l = a + b [MEI - (T_g/k_g)] + (T_l \times k_t) + \varepsilon \quad [12]$$

where T_g and T_l are tissue gain and loss, respectively (both MJ/kg of $BW^{0.75}$ per day).

The dataset contained information collected from several experiments conducted at four sites, and in some instances multiple observations were made on the same cow at different periods. Therefore, fixed effects of research center and random effects of experiments (because the trials represent a random sample of a larger population), cows and period within experiments were added to the model. PROC MIXED procedure in SAS (Littell et al., 1996; SAS, 2000) was used for analysis.

Table 3. Function forms used to describe the utilization of ME intake for milk production.

Candidate function	$f(x)$	ME _m
Straight line	$ax - b$	b/a
Mitscherlich	$a - (a + b)e^{-cx}$	$c^{-1}\ln[(a + b)/a]$
Rectangular hyperbola	$(a + b)x/(c + x) - b$	bc/a
Gompertz	$b\exp\left[(1 - e^{-cx})\ln\frac{a + 2b}{b}\right] - 2b$	$c^{-1}\ln\left\{\frac{\ln[(a + 2b)/b]}{\ln[(a + 2b)/(2b)]}\right\}$
Logistic	$\frac{b(a + 2b)}{b + (a + b)e^{-cx}} - 2b$	$c^{-1}\ln[2(a + b)/a]$

The results showed that there were no significant effects of cow and period ($P > 0.20$) and, therefore, random effects of cow and period were removed from subsequent analysis. The four other functional forms were also transformed to an expression similar to equation [12] and fitted to the dataset using the nonlinear mixed procedure (PROC NLMIXED in SAS, SAS, 2000) to optimize the parameter estimates.

Yan et al. (1997) using 12 nonpregnant lactating Holstein-Friesian cows offered forage-based diets experimentally determined the fasting heat production, F , of the cows to be 0.453 (SD 0.0354) MJ/kg of $BW^{0.75}$ per day. This value is higher than the value adopted by NRC (2001), which is 0.335 MJ/kg of $BW^{0.75}$ per day. Bayesian methods were used to merge the information from a prior estimate of the intercept (0.453, SD 0.0354) with that suggested by the data. A weighted average of the prior and observed estimates of the intercept was calculated by using the reciprocals of their respective variances as the weights. All the functions were fitted to the dataset by assigning the Bayesian estimate, parameter b , and the results compared with those obtained from unconstrained fitting.

Classical approach. Historically, energy balance data from lactating dairy cows were analyzed using the classical multiple linear regression approach of Moe et al. (1971):

$$MEI = a + \beta_1 MBW + \beta_2 E_l + \beta_3 T_g + \beta_4 T_l + \varepsilon \quad [13]$$

where MEI is ME intake (MJ/d), **MBW** is metabolic BW (kg of $BW^{0.75}$), E_l is energy in milk (MJ/d), T_g is tissue gain (MJ/d), and T_l is tissue loss (MJ/d). a is the regression constant which was assumed to represent the amount of ME intake that was not attributable to any specific variable in the model, β_1 , β_2 , and β_3 represent the unit amount of ME required for maintenance, milk production, and body gain, respectively, β_4 is the amount of dietary ME, which is spared per unit of body tissue energy loss and ε is error.

Based on efficiencies from equation [13], Moe et al. (1972) regressed net energy for lactation (MJ/kg of

$BW^{0.75}$ per day) against MEI (MJ/kg of $BW^{0.75}$ per day) to calculate k_l and ME_m. Net energy for lactation was calculated as follows:

$$NE_l = \text{milk gross energy} + (T_g/1.14) \quad [14] \\ - (0.84T_l) + 0.18 \text{ fetal mass} + 0.03 \text{ excess N}$$

where excess N is the digestible N intake minus N in milk (with its efficiency of conversion, which was assumed to be 0.625 (milk N/0.625)), fetus and that used for maintenance.

In the United Kingdom, book values (from AFRC, 1993) of 0.60 and 0.84 are used for k_g and k_b , respectively, to correct energy balance data from calorimetry experiments.

Three analyses were conducted using the classical approach. First, k_g and k_l values were estimated using multiple linear regression analysis (equation [13]). Second, NE_l was calculated and regressed against MEI using the k_g and k_l values of Moe et al. (1972). General linear regression procedure of Genstat (1992) was used to conduct both analyses. Finally, the data were corrected using k_g and k_l values of AFRC (1993) and a linear mixed model analysis carried out from which k_l and ME_m values were determined. The results of the above analyses were then compared with results for the alternative straight line (unconstrained, equation [12]) and Mitscherlich (constrained) models due to the superior fit of both of these models to our data based on Bayesian information criteria (**BIC**).

RESULTS

Estimating Efficiency Coefficients k_g and k_l

The efficiency coefficients k_g and k_l were estimated by fitting linear and nonlinear mixed models, corrected as equation [12], to the data (Table 4). In all cases, there was a good relationship between MEI and E_l ($P < 0.001$). Based on BIC and standard error of the models, the straight line had the best fit to the data followed by the Gompertz and the diminishing returns functions.

Figure 1. A relationship between metabolizable energy intake (MEI, MJ/kg of $BW^{0.75}$ per day) and milk energy output (MJ/kg of $BW^{0.75}$ per day) ($n = 652$). Symbols represent observed values and the lines are regression lines fitted using (a) straight line (b) Mitscherlich (c) rectangular hyperbola (d) logistic and (e) Gompertz. Solid lines represent unconstrained fit and broken lines constrained fit of the models.

The range of estimates for k_g across all functions was 0.83 to 0.86 (SE 0.028 and 0.029, respectively) and k_t was estimated to be 0.66 to 0.69 (SE 0.027 and 0.028, respectively).

Estimating $\bar{k}_l$

The unconstrained fitting of the functions to the data showed that in all cases, there was a similar goodness

Table 4. Parameter estimates and other measures when (a) unconstrained models were fitted to the data and (b) the intercept was constrained to a Bayesian estimate which was calculated by merging prior information of a measured fasting heat production value with that suggested by the data. Standard errors are given in brackets.

Item	Functions				
	Straight line	Mitscherlich	Rectangular hyperbola	Logistic	Gompertz
(a) Unconstrained fit					
a	0.55 (0.011)	7.81 (6.3)	15.6 (16.2)	1.29 (0.04)	2.08 (0.17)
b	0.28 (0.019)	0.34 (0.02)	0.34 (0.02)	0.13 (0.03)	0.08 (0.04)
c		0.076 (0.001)	24.7 (0.58)	1.57 (0.08)	0.69 (0.06)
k_g	0.84 (0.029)	0.83 (0.028)	0.83 (0.028)	0.86 (0.029)	0.85 (0.029)
k_t	0.66 (0.026)	0.66 (0.027)	0.66 (0.027)	0.69 (0.028)	0.67 (0.027)
σ (model) ¹	0.0562	0.0564	0.0564	0.0576	0.0562
BIC ²	-1783	-1778	-1778	-1744	-1779
R^2	0.87	0.86	0.86	0.85	0.87
ME _m ³	0.62	0.55	0.52	0.50	0.34
$\bar{k}_l$ ⁴	0.55	0.55	0.58	0.52	0.50
(b) Fixed intercept					
a	0.56 (0.005)	7.24 (2.05)	13.2 (3.65)	1.30 (0.04)	1.89 (0.09)
c		0.083 (0.025)	21.1 (6.20)	1.38 (0.03)	0.66 (0.02)
σ (model)	0.0565	0.0563	0.0570	0.0584	0.0571
BIC	-1783	-1783	-1782	-1738	-1771
R^2	0.85	0.86	0.86	0.83	0.84
ME _m	0.57	0.59	0.59	0.64	0.59
$\bar{k}_l$	0.56	0.55	0.55	0.55	0.56

¹Standard error of model = $\sqrt{\text{variance } (\sigma^2) \text{ of error}}$.

²BIC = Bayesian information criteria (smaller value means a better model).

³The net energy requirement for maintenance (ME_m, MJ/kg BW^{0.75} per day) for the straight line was calculated according to Moe et al. (1972) and Reynolds and Tyrrell (2000) by first regressing milk energy (E_l) on MEI (values reported in the table) and then regressing MEI on E_l [MEI = 1.48 (0.033) E_l + 0.73 (0.023)]. The two estimates of ME_m were then averaged.

⁴The average efficiency of utilization of MEI for milk production ($\bar{k}_l$) for the non-linear functions was calculated by setting the upper limit to 2.4 MJ/kg W^{0.75}/d.

of fit ($R^2 > 0.85$) (Table 4). However, the straight line, due to its lowest BIC and SE of model, was the best fitting function. The diminishing returns functions indicated an over-parameterization as the estimates of the parameter a were not significant. Although all the parameter estimates of the sigmoidal functions were significant ($P < 0.01$), they did not improve on the straight line fitting (Table 4). Based on the parameter estimates, ME_m and $\bar{k}_l$ were calculated. ME_m values ranged between 0.34 (Gompertz) to 0.62 MJ/kg of BW^{0.75} per day (straight line) and $\bar{k}_l$ from 0.50 (Gompertz) to 0.58 (rectangular hyperbola). Caution must be taken when comparing $\bar{k}_l$ because although the upper limit on all nonlinear functions when calculating $\bar{k}_l$ was fixed at 2.4 MJ/kg of BW^{0.75} per day, this limit expressed as a multiple of estimated ME_m varied across models because of the difference in estimated ME_m.

A Bayesian estimate (calculated by merging the experimentally determined value of F with that derived from the observations) was used to fix the parameter b in all the functions when fitting to the data (Table 4, Figure 1). The over-parameterization problem of the diminishing returns functions was resolved with the introduction of the fixed parameter and the Mitscherlich and straight line showed the best fit to the data

based on BIC and SE values. Some differences in ME_m values were observed in the constrained fittings, which ranged from 0.57 (straight line) to 0.64 MJ/kg of BW^{0.75} per day (logistic). The $\bar{k}_l$ was very similar in all the constrained fittings (0.55) and also showed some differences compared to values from the unconstrained fittings.

Classical Method of Analysis

The same procedures and calculations as reported by Moe et al. (1972) were carried out on the CEDAR and ARINI data. The linear regression of NE_l on ME (both scaled to metabolic BW) had an intercept of -0.408 ± 0.027 and a slope of 0.628 ± 0.015 (Figure 2). The maintenance requirement of the cows was 0.65 MJ ME/kg of BW^{0.75} per day. Based on dataset of similar size and Holstein-Friesian cows, Moe et al. (1972) reported a maintenance requirement of 0.49 MJ ME/kg of BW^{0.75} per day. It is interesting to note that efficiency of utilization of MEI for milk was similar but there was a larger estimate of maintenance energy requirement with our data.

The analysis shown in Figure 2 was based on the k_g and k_t values of Moe et al. (1972) (0.75 and 0.82,

Figure 2. Net energy for lactation and ME intake according to Moe et al. (1972). The linear regressions shown are for the current dataset (solid) and the equation of Moe et al. (1972) (dotted).

respectively). These efficiencies were recalculated using the classical method of analysis (equation [13]) and the results are shown in Table 5.

Our data were analyzed using the AFRC (1993) book values for correcting energy balance data ($k_g = 0.6$, $k_t = 0.84$). The linear mixed regression of the data gives an intercept of -0.21 (SE 0.021) and a slope of 0.50 (SE 0.02).

DISCUSSION

There have been various estimates of k_g in lactating dairy cows in the literature (e.g., Moe et al., 1970; ARC,

1980). The value of k_g recommended by ARC (1980) and adopted by AFRC (1993) is linked to feed quality and k_l ($k_g = 0.61$ assuming a feed quality of 12 MJ/kg DM of ME and 18.8 MJ/kg DM of gross energy). According to ARC (1980) and AFRC (1993), energy is used for body gain with almost the same efficiency as for milk production. On the other hand, NRC (2001) adopts the value of Moe et al. (1971) who reported that a metabolic change of lactation increases k_g from 0.60 in nonlactating cows to 0.75 ± 0.024 in lactating cows. Reynolds and Tyrrell (2000) quoted Armstrong and Blaxter (1965) that part of the reason for the 25% increase in efficiency could be the result of the use of acetate for milk synthesis rather than for oxidation in lactating cows. All the functions used in this study have consistently estimated k_g to be about 0.84 (SE = 0.028), which is closer to the value reported by Moe et al. (1971). It has been reported that efficiency of utilization of MEI for body energy gain is affected by level of MEI, stage of lactation, and genetic potential (Moe and Tyrrell, 1975). Therefore, some of the reasons for the small differences in k_g between this study and Moe et al. (1971) could be due to differences in methods of analysis, genetic potential of the cows or just randomness.

The values of k_t in this study (Table 5) are widely different from recommendations of ARC (1990), AFRC (1993) of 0.84 and NRC (2001) of 0.82, which was based on the Moe et al. (1971) estimate of 0.82 ± 0.022 . AFRC (1990) seems to misquote ARC (1980) giving the value of k_t as $k_l/0.80$ ($= 0.79$ assuming q_m is 0.6). The k_t from this study were much lower than previous recommendations and even when estimated using multiple linear regression (equation [13]), the value of k_t was very close to estimates using the new method of analysis (Table 5). One of the fundamental differences between the British national recommendation and this study is the nature

Table 5. Comparison of key parameters currently recommended for use in calculating energy requirement of dairy cows and the new method of analysis. The parameters are the average efficiency of utilization of metabolizable energy intake for milk production (k_l) and body gain (k_g), efficiency of utilization of tissue energy for milk production (k_t) and maintenance energy requirement (ME_m , MJ/kg^{0.75} of BW per day). From the alternative functions, the unconstrained straight line and constrained (fixed intercept) Mitscherlich were chosen for comparison with currently used values.

	Recommended		Our data			
	AFRC (1993)	NRC (2001) ¹	AFRC (1993) ²	Moe et al. (1971) ³	Straight line	Mitscherlich
k_g	0.60	0.75		0.86 (0.066)	0.84 (0.029)	0.83 (0.028)
k_t	0.84	0.82		0.68 (0.076)	0.66 (0.026)	0.66 (0.027)
ME_m	0.49	0.51	0.42	0.69 (0.075)	0.62	0.59
k_l	0.62	0.64	0.50 (0.02)	0.68 (0.022)	0.55	0.55
σ^4			0.0659	0.1216	0.0562	0.0563

¹NRC(2001) recommendations are based on Moe et al. (1971).

²Our data was corrected using the AFRC (1993) efficiency values and a linear mixed model fitted.

³Equation [13] was fitted to our data.

⁴Standard error of model = $\sqrt{\text{variance } (\sigma^2) \text{ of residual error}}$.

of the data used for the analysis. In the former, BW change was used as a measure of energy balance and it was assumed that BW change is directly proportional to energy balance while the later used calorimetric measurements of energy balance. There is some evidence (Flatt et al., 1969) that cows can be in negative energy balance without BW change. Therefore, the estimated k_t is biased upward if BW loss is used as a proxy for energy balance. Moe et al. (1971) also warned that differences in rumen fill and water replacing body fat utilized may mask live weight changes when the cow is in negative energy retention.

Using the classical method of analysis to estimate efficiencies from our dataset gave a considerably different result to that recommended by the British and American national research councils (Table 5). This indicates that there is a need to re-evaluate efficiencies and maintenance requirements for lactating dairy cows.

When the data were corrected using the new approach and the five functions that were specially parameterized for energy balance analysis were fitted, similar goodness of fit (R^2) values were obtained (Table 4). The same was true when the data were fitted either using a fixed value for the parameter b or without any constraint. The diminishing returns functions produced a large standard error for one of the parameter estimates during unconstrained fitting. The logistic and Gompertz showed much lower and significant standard errors for all three parameters estimated. The Gompertz was slightly better when the BIC and SE of model were considered, perhaps because of the nonsymmetrical nature of the curve when compared to the logistic function. Using previous knowledge of fasting heat metabolism to fix one of the parameters (b) reduced over-parameterization problems and the Mitscherlich showed a significant estimate of the theoretical maximum value of milk energy production (a). Biologically, it is more likely that the efficiency of conversion of MEI is higher when cows consume energy below their maintenance requirements (e.g., Blaxter and Boyne, 1978; AFRC, 1993) and decreases as the intake level increases, which is described by the Mitscherlich but not always the case with Gompertz and logistic (Table 4, Figure 1). The Mitscherlich has been used in energy balance studies before, e.g., Blaxter and Boyne (1978) used the function to describe the relationship between the rate of feed intake and the efficiency of utilization of gross energy for body gain in growing ruminants. Scarcity of observations approaching the asymptote makes the estimation of the parameter a (maximum milk energy) difficult. However, in estimating the maintenance requirement and energy efficiencies, precision of the parameter estimate for a is less relevant.

Estimates of maintenance requirement using the alternative approach (Table 4), traditional multiple regression analysis (Table 5) and analyzing data by correcting for k_g and k_t according to Moe et al. (1971) indicate that the value was constantly higher than in previous reports. Part of the reason could be genetic differences of cows used in this study compared with those in late 1960's and early 1970's. Another factor may be differences in type of diet fed to the cows. Preliminary analysis shows that cows fed dried grass had lower maintenance requirements than those fed maize silage-based diets, which was the major feed component in the experiments conducted at the University of Reading.

The $\bar{k}_l$ was lower in calculations from the best fit functions compared with recommended values (Table 5). The straight line model assumes that there is no change in k_l as the feeding level increases. The other functions allow the possibility of k_l changing with level of feeding and the diminishing returns functions predict a higher k_l at a lower MEI. However, although it might be biologically sensible, there is no statistical reason to suggest that feeding level affects k_l .

CONCLUSION

Our analysis of energy balance data shows considerable differences in estimates of efficiencies of energy conversion compared with previous analyses. The fact that using the same methodology led to large differences suggests that those recommendations made 30 yr ago may need to be revised. In an unconstrained fit, the nonlinear models did not improve the variation accounted for by the straight line. However, when the Bayesian estimate of the intercept was used, fitting the Mitscherlich to the data accounted for variation better than any of the other constrained functions, but marginally less than the unconstrained straight line that represented the null hypothesis in this set of analyses. The parameter estimates were significant and made biological sense. The Mitscherlich gave higher estimates of k_m compared with k_l and both efficiencies (and ME_m) can be estimated from a single equation that provides the possibility of investigating the relationship between k_l and level of feeding. Based on the best fit models, ME_m values were 0.62 and 0.59 MJ/kg^{0.75}/d (for the unconstrained straight line and constrained Mitscherlich, respectively) and $\bar{k}_l$ was 0.55 for both functions. To test conclusively whether milk energy is related to MEI linearly or not, data from high yielding dairy cows (with energy intakes of more than 2.4 MJ/kg W^{0.75} per day) are required.

ACKNOWLEDGMENTS

This study was partially funded by the Department for Environment, Food and Rural Affairs, the Milk Development Council and a consortium of industrial partners within a LINK Sustainable Livestock Production project: Feed into Milk. The authors thank the late G. Alderman for his contribution to the work, J. L. Corbett for discussions on energy metabolism and M. Denham for statistical advice.

REFERENCES

- Agnew, R. E., and T. Yan. 2000. Impact of recent research on energy feeding systems for dairy cattle. *Livest. Prod. Sci.* 66:197–215.
- Agnew, R. E., T. Yan, and F. J. Gordon. 1998. Nutrition of the high genetic merit dairy cow-energy metabolism studies. Pages 181–208 in *Recent Advances in Animal Nutrition*, Nottingham University Press, Nottingham, U.K.
- Agricultural and Food Research Council. 1990. Technical Committee on Responses to Nutrients, Report 5. Nutrient Requirements of Ruminant Animals: Energy. *Nutr. Abst. Rev. Ser. B* 60:729–804.
- Agricultural and Food Research Council. 1993. Energy and Protein Requirements of Ruminants. CAB International, Wallingford, U.K.
- Agricultural Research Council. 1965. The Nutrient Requirements of Farm Livestock, Volume #2, Ruminants. HMSO, London, U.K.
- Agricultural Research Council. 1980. The Nutrient Requirements of Ruminant Livestock, Technical Review. CAB, Farnham Royal, U.K.
- Beever, D. E., S. B. Cammell, J. D. Sutton, and D. J. Humphries. 1998a. The effect of stage of harvest of maize silage on the concentration and efficiency of utilisation of metabolisable energy by lactating cows. Pages 359–362 in *Energy Metabolism of Farm Animals*, CAB International, Wallingford, U.K.
- Beever, D. E., S. B. Cammell, J. D. Sutton, N. Rowe, and G. E. Perrott. 1998b. Energy metabolism in high yielding cows. Page 13 in *Proc. Brit. Soc. Anim. Sci.*, Scarborough, U.K.
- Blaxter, K. L. 1962. The Energy Metabolism of Ruminants. Charles C. Thomas, Springfield, IL.
- Blaxter, K. L., and F. W. Wainman. 1961. The utilisation of food by sheep and cattle. *J. Agric. Sci. (Camb.)* 57:419–425.
- Blaxter, K. L., and W. A. Boyne. 1978. The estimation of the nutritive value of feeds as energy sources for ruminants and the derivation of feeding systems. *J. Agric. Sci. (Camb.)* 90:47–68.
- Cammell, S. B., J. D. Sutton, D. E. Beever, D. J. Humphries, and R. H. Phipps. 2000. The effect of crop maturity on the nutritional value of maize silage for lactating dairy cows. Part I. Energy and nitrogen utilisation. *Anim. Sci.* 71:381–390.
- Cammell, S. B., D. J. Thompson, D. E. Beever, M. J. Haines, M. S. Dhanoa, and M. C. Spooner. 1986. The efficiency of energy utilisation in growing cattle consuming fresh perennial rye grass (*Lolium perenne* cv. Melle) or white clover (*Trifolium repens* cv. Blanca). *Br. J. Nutr.* 55:669–680.
- Carrick, I. M., D. C. Patterson, F. J. Gordon, and C. S. Mayne. 1996. The effect of quality and level of protein on the performance of dairy cattle of differing genetic merits. *Anim. Sci.* 62:642. (Abstr.)
- Cushnahan, A., C. S. Mayne, and E. F. Unsworth. 1995. Effects of ensilage of grass on performance and nutrient utilisation by dairy cattle. 2. Nutrient metabolism and rumen fermentation. *Anim. Sci.* 60:347–359.
- Ferris, C. P., M. A. McCoy, S. D. Lennox, D. C. Catney, and F. J. Gordon. 2002. Nutrient utilisation and energy balance associated with two contrasting winter milk production systems for high genetic merit autumn calving dairy cows. *Ir. J. Agric. Food Res.* 41:55–70.
- Ferris, C. P., F. J. Gordon, D. C. Patterson, M. G. Porter, and T. Yan. 1999. The effect of genetic merit and concentrate proportion in the diet on nutrient utilisation by lactating dairy cows. *J. Agric. Sci.* 132:483–490.
- Flatt, W. P., P. W. Moe, R. R. Oltjen, P. A. Putnam, and N. W. Hooven, Jr. 1969. Energy utilization by high producing dairy cows. II. Summary of energy balance experiments with lactating Holstein cows. Page 109 in *Proc. 4th Symp. Energy Metabolism*. EAAP Publication no. 12, Newcastle Upon Tyne, U.K.
- France, J., M. S. Dhanoa, S. B. Cammell, M. Gill, D. E. Beever, and J. H. M. Thornley. 1989. On the use of response functions in energy balance analysis. *J. Theor. Biol.* 140:83–99.
- Genstat 5 Committee. 1992. *Genstat 5 Reference Manual*. Oxford University Press, Oxford, U.K.
- Gordon, F. J., D. C. Patterson, M. G. Porter, and E. F. Unsworth. 2000. The effect of degree of grass wilting prior to ensiling on performance and energy utilisation by lactating dairy cattle. *Livest. Prod. Sci.* 64:291–294.
- Gordon, F. J., D. C. Patterson, T. Yan, M. G. Porter, C. S. Mayne, and E. F. Unsworth. 1995a. The influence of genetic index for milk production on the response to complete diet feeding and the utilisation of energy and nitrogen. *Anim. Sci.* 61:199–210.
- Gordon, F. J., M. G. Porter, C. S. Mayne, E. F. Unsworth, and D. J. Kilpatrick. 1995b. The effect of forage digestibility and type of concentrate on nutrient utilisation for lactating dairy cattle. *J. Dairy Res.* 62:15–27.
- Hattan, A. J., D. E. Beever, S. B. Cammell, and J. D. Sutton. 2001. Energy utilisation in high-yielding cows during early lactation. Pages 325–328 in *Energy Metabolism of Farm Animals*, EAAP Publication no. 103, Wageningen Pers, Wageningen, The Netherlands.
- Littell, R. C., G. A. Milliken, W. W. Straub, and R. D. Wolfinger. 1996. *SAS System for Mixed Models*. SAS Inst., Cary, NC.
- Moe, P. W., and H. F. Tyrrell. 1975. Efficiency of conversion of digested energy to milk. *J. Dairy Sci.* 58:602–610.
- Moe, P. W., H. F. Tyrrell, and W. P. Flatt. 1970. Partial efficiency of energy use for maintenance, lactation, body gain and gestation in the dairy cow. Pages 65–68 in *Energy Metabolism of Farm Animals*, EAAP Publication no. 13, Juris Verlag, Zurich, Switzerland.
- Moe, P. W., H. F. Tyrrell, and W. P. Flatt. 1971. Energetics of body tissue mobilization. *J. Dairy Sci.* 54:548–553.
- Moe, P. W., W. P. Flatt, and H. F. Tyrrell. 1972. Net energy value of feeds for lactation. *J. Dairy Sci.* 55:945–958.
- National Research Council. 2001. *Nutrient Requirements of Dairy Cattle*. 7th rev. ed. Natl. Acad. Press, Washington, DC.
- Reynolds, C. K., and H. F. Tyrrell. 2000. Energy metabolism in lactating beef heifers. *J. Anim. Sci.* 78:2696–2705.
- SAS/STAT User's Guide, Version 8 Edition. 2000. SAS Inst., Inc., Cary, NC.
- Sutton, J. D., R. H. Phipps, S. B. Cammell, and D. J. Humphries. 2001. Attempts to improve the utilisation of urea-treated whole-crop wheat by lactating dairy cows. *Anim. Sci.* 73:137–147.
- Sutton, J. D., S. B. Cammell, D. E. Beever, D. J. Humphries, and R. H. Phipps. 1998. Energy and nitrogen balance of lactating dairy cows given mixtures of urea-treated whole-crop wheat and grass silage. *Anim. Sci.* 67:203–212.
- Unsworth, E. F., C. S. Mayne, A. Cushnahan, and F. J. Gordon. 1994. The energy utilisation of grass silage diets by lactating dairy cows. Pages 179–181 in *Energy Metabolism of Farm Animals*, EAAP Publication No. 76, Mojacar, Spain.
- Yan, T., D. C. Patterson, F. J. Gordon, and M. G. Porter. 1996. The effects of wilting of grass prior to ensiling on the response to bacterial inoculation. 1. Silage fermentation and nutrient utilisation over three harvests. *Anim. Sci.* 62:405–417.
- Yan, T., F. J. Gordon, C. P. Ferris, R. E. Agnew, M. G. Porter, and D. C. Patterson. 1997. The fasting heat production and effect of lactation on energy utilisation by dairy cows offered forage-based diets. *Livest. Prod. Sci.* 52:177–186.