Genotype and Diet Effects on Energy Balance in the First Three Lactations of Dairy Cows

M. P. Coffey,[1] G. Simm,[1] J. D. Oldham,[1] W. G. Hill,[2] and S. Brotherstone[1,2]
[1]Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, UK
[2]Institute of Cell, Animal and Population Biology, School of Biological Sciences,
University of Edinburgh, West Mains Road, Edinburgh, EH9 3JT, UK

ABSTRACT

Dairy cows make strategic use of body energy to support early lactation and replenish this lost energy later in lactation, thereby creating body energy profiles that vary both within lactation and across lactations. The interaction between genotype and diet energy content is interesting from a management viewpoint and from a cow survival viewpoint. In this study, we modeled energy balance over 3 lactations using a multivariate random regression model, for cows from the Langhill Dairy Cattle Research Centre. This herd has been selected for maximum production or to remain at the UK national average for production (control group) and has been fed 2 diets of different energy density (high or low concentrate). Cows in the various groups differed in body condition score and the way they lost and regained body lipid. Cows selected for maximum production on a low-concentrate diet lost the greatest amount of body lipid (0.54 condition score units) after 3 lactations. Cows selected for maximum production lost more than control cows on either diet, indicating that selection mainly for yield has predisposed cows to utilize body energy to support lactation on diets spanning the range used here. Cows selected for maximum production were heavier at first calving than control cows but lost more weight and regained more weight so that at the end of each lactation, cows in the 2 groups did not differ significantly in weight. Cows use body lipid to support lactation over 3 lactations and the profile of that use varies according to genotype and diet.
(**Key words:** energy balance, genotype, survival)

Abbreviation key: CL = control line of cows, **EB1** = energy balance calculated from feed intake measures, **EB2** = energy balance calculated from BCS changes, **FI** = feed intake, **LWT** = live weight, **MY** = milk yield, **NEB** = negative energy balance, **SL** = select line (cows selected for maximum fat plus protein production).

INTRODUCTION

In high-yielding dairy cows, the peak of daily feed intake usually occurs after the peak of milk output. This disassociation in timing leads to a period in early lactation when cows cannot meet their energy requirements solely from ingested feed and they mobilize body energy to meet the deficit. This state is commonly known as negative energy balance (**NEB**) and is unfavorably associated with a range of health traits (Collard et al., 2000; Gillund et al., 2001; Sondergaard et al., 2002) and fertility (Veerkamp et al., 2000; Dechow et al., 2002; Wathes et al., 2002). It is considered undesirable not only for its direct economic cost in terms of health and fertility but also from a welfare viewpoint (Nielsen et al., 1999).

The economic consequences of higher involuntary culling rates due to poorer health generally leads farmers to select cows for a combination of production and survival. However, recent selection objectives that favor production to a greater extent may have led to cows that are unable to maintain high yields over many lactations. Failure to replenish body lipid lost in one lactation reduces the availability of body lipid to support subsequent lactations, potentially leading to early culling.

Research to identify nutritional methods of overcoming NEB has been reported (e.g., Doepel et al., 2002) and work to improve fertility through reducing NEB is currently underway (P. Garnsworthy, personal communication, 2003). Phenotypic NEB could be described as an outcome state that is a result of the genetic relationship between milk yield, feed intake, and body lipid content, and the interaction with the management environment. This trivariate relationship between the traits associated with energy balance changes as lactation progresses and describes nutrient partitioning. The difference in partitioning priorities between animals of differing genotype for yield and on different planes of nutrition is not well documented. Genetic correlations between yield and feed intake indicate that the expected increase in feed intake is less than that required to cover the extra energy requirements for yield when

selection is for yield alone (Veerkamp, 1998), leading to a net loss of body lipid. Continuing with this selection policy is likely to result in a greater loss of body condition in animals selected for yield. The appropriate loss and replenishment cycle for body lipid in dairy cows is unknown and may differ for different feeding regimens.

Body condition scoring is a technique of appraising the body lipid content of dairy cows (Lowman et al., 1976) that is used routinely in the dairy industry. Body condition score is a good predictor of total body lipid content (Fox et al., 1999) and has a heritability of around 0.30, similar to that of production (Jones et al., 1999; Coffey et al., 2001; Dechow et al., 2002). These features of BCS make it a candidate for inclusion in future selection indices that incorporate a wider range of direct measures of cost and that include improved health and welfare and reduced environmental impact as part of the goal. To incorporate body energy into selection indices, more information is required on the relationship between body energy changes in early and later productive life and how that relationship is affected by genotype and nutrition. This will enable selection for a genotype with an appropriate lifetime body energy profile that optimizes profitability consistent with consumers' expectations for animal production systems.

The objectives of this study were: 1) to calculate daily energy balance for 3 consecutive lactations for individual cows from the Langhill Dairy Cattle Research Centre and 2) to investigate the influence of genotype and concentrate feeding level on energy balance profiles.

MATERIALS AND METHODS

Data

Data were extracted for all cows in lactations 1 to 3 from the database of Langhill records collected from 1990 until July 2002. At this point, the trial to record feed intake used in this study was terminated and the data set consisted of animals that had a range of lactations completed under the trial up to lactation 3. The data included records of milk production and composition, live weight (**LWT**), BCS, and fresh feed intake (**FI**) for 2 lines of cows. These lines have been continuously selected for kilograms of fat plus protein [select line (**SL**)] or selected to remain close to the average genetic merit for fat plus protein production for all animals evaluated in the UK [control line (**CL**)]. Approximately equal numbers of SL and CL cows were housed together and offered either a high- or low-concentrate diet as a TMR for a minimum of 26 wk or a maximum of 38 wk of each lactation. Animals that calved early in the calving season (which started around August each year) were kept on trial for the full 38 wk providing that the

38 wk of recording was finished in June of the following year. If an animal calved too late to have the full 38 wk recorded before June, the animal was removed from the trial after 26 wk of recording. Outside this period of recording, cows received a standard TMR when housed, or grazed grass. The diets were formulated to contain approximately 1500 or 2500 kg (1.5 or 2.5 tonnes) of concentrate per lactation for the low- and high-concentrate diets, respectively, representing low and moderately high concentrate usage in the United Kingdom.

Milk yield (**MY**) data consisted of summed daily yield measured at the morning and evening milking up to 305 d after calving. Aberrant records were removed from the main data set; these records were apparently caused by illness or estrus, or were milk records known to be in error if the value at any milking was more than 3 standard deviations different from the mean of all other records for the same parity, feed group, genetic line, or day of lactation. This resulted in the removal of 1382 daily records out of 757,952 individual daily recordings from 995 animals, of which only 26 animals had more than 10 daily records removed. From this main edited data set, records for each of the 4 traits analyzed (MY, BCS, LWT, and FI) were extracted separately for all animals that had been recorded on the feed intake trial for at least 1 wk. This produced records for 501 animals. Of these, 90 had a maximum of one lactation of feed intake data, 88 had a maximum of 2 lactations of data, and 323 had 3 lactations of feed intake data.

Live weight was measured and BCS assessed at the same time once weekly after the morning milking. Body condition score was assessed by the same operator over the entire period of record collection, using a 0 to 5 scale with 0.25 intervals (Lowman et al., 1976), where 0 = thin and 5 = very fat. Food was available ad libitum and individual intakes were recorded through Calan Broadbent gates (before 2001) or HOKO automatic feed measurement gates (from 2001 to 2002). For data collected by Calan Broadbent gates, daily FI was calculated from measurements of feed offered and refused on each of 4 consecutive days (Monday to Thursday). Feed offered was weighed on one morning; refusals were weighed and removed the following morning. For data collected in the last year of the trial through HOKO feeders, daily FI was recorded automatically every day. Feed offered was adjusted periodically such that feed refused remained at around 10% of the total offered. Cows observed to habitually waste food by throwing it were removed from the trial because FI data for these animals would be biased upwards. Table 1 shows the number of observations for each trait, in each lactation. Effective energy intake for those days where FI was

Table 1. Number of records in each of the 7 residual error classes and the corresponding residual error variances (REV) for milk (kg^2), fresh feed intake (FI kg^2), body condition score (BCS units$^2 \times 100$), and live weight (LWT kg^2).

Days of lactation	Milk		Feed intake		BCS		Live weight	
	Records	REV	Records	REV	Records	REV	Records	REV
Lactation 1								
1 to 6	938	34.7	171	126.6	144	1.48	154	599.3
7 to 9	1238	17.7	477	96.8	176	1.08	179	365.8
10 to 12	1288	9.6	590	49.3	183	1.17	186	322.6
13 to 15	1308	5.5	655	31.3	201	0.59	205	135.0
16 to 29	6339	3.3	3406	15.9	894	1.15	905	152.1
30 to 99	33,026	3.5	18,789	16.9	4583	0.88	4694	111.1
100 to 305	94,901	2.9	37,655	17.0	12,031	1.04	12,343	116.6
Lactation 2								
1 to 6	688	65.8	141	138.2	116	3.02	119	334.8
7 to 9	1151	33.1	429	55.4	153	3.31	157	349.2
10 to 12	1168	15.0	494	37.6	161	1.65	162	239.3
13 to 15	1190	8.8	482	20.6	145	2.07	148	142.8
16 to 29	5537	5.6	2534	19.7	719	0.76	746	162.7
30 to 99	27,329	5.6	13,282	21.8	3628	1.04	3723	119.1
100 to 305	75,217	3.4	24,856	25.3	9413	1.05	9609	134.0
Lactation 3								
1 to 6	491	79.5	101	117.1	100	2.08	102	541.8
7 to 9	892	43.5	285	45.4	110	2.31	113	571.0
10 to 12	911	19.3	324	41.7	123	1.21	128	248.5
13 to 15	909	14.1	353	25.4	116	1.95	118	171.2
16 to 29	4329	10.5	1723	28.5	572	0.92	585	203.5
30 to 99	21,052	8.7	8652	24.3	2736	1.05	2777	141.1
100 to 305	55,909	4.5	16,170	27.4	7138	0.94	7188	154.7

measured was estimated using the effective energy system of Emmans (1994).

Model for Analysis

Variance component estimation was performed using the ASREML statistical package (Gilmour et al., 1998) with a multivariate random regression model. Because pedigree information was not included in the analysis, animal solutions are combined animal genetic and permanent environmental effects. The difference between the analysis presented here and that of Coffey et al. (2002) is that in this study, we analyzed all 3 lactations together for each trait so lactations are considered separate but correlated traits. The random regression model fitted in this study was:

$$y_{it} = \boldsymbol{F}_{it} + \sum_{m=0}^{f-1} \beta_m \boldsymbol{P}_m(t) + \sum_{m=0}^{k-1} \lambda_{im} \boldsymbol{P}_m(t) + \varepsilon_{it} \quad [1]$$

where y_{it} = trait (MY, BCS, FI, or LWT) for animal i on day t, $\boldsymbol{F}_{it}$ represents fixed effects of genetic line (2 groups), feed group (2 groups), time of measurement (year and week of measurement), diet type (TMR or grass), pregnancy group (not pregnant and pregnant for up to 70, 100, 130 and continuing up to 280 d in classes of 30 d) and the covariates percentage North

American Holstein genes (linear) and the difference between age at calving and mean age at calving for this lactation in months (linear and quadratic) for animal i. β_m are the fixed regression coefficients, λ_{im} are the random regression coefficients associated with the animal and lactation plus its permanent environment and ε_{it} is the residual error associated with days since calving t in that lactation. $P_m(t)$ is the mth Legendre polynomial evaluated at t and the parameters f and k are the order of the fixed and random polynomials respectively. Legendre polynomials were used because they are easy to manipulate, have good convergence properties and, as they are orthogonal polynomials, yield lower correlations between the coefficients than do ordinary polynomials.

Milk yield, BCS, FI, and LWT were analyzed separately. In each analysis, lactational values for lactations 1, 2, and 3 were considered separate but correlated traits. Residual, or measurement, errors were expected to have heterogeneous variances through the course of each lactation, with larger variances at the beginning of lactation and around peak yield. Different residual errors were therefore associated with observations over time. Based on previous analyses of similar data (Coffey et al., 2002), residual error classes were defined as d 1 to 6, 7 to 9, 10 to 12, 13 to 15, 16 to 29, 30 to 99, and 100 to 305. These classes were defined to provide

sufficient records in each class in early lactation but also to produce sufficient granularity of the data at the early part of lactation when changes are greatest. Within classes, residual errors were assumed to be homogeneous and between classes, residual covariances were assumed to be zero. Fixed regressions, which model the general shape of the curve and are common to all animals, were fitted for all traits as polynomials of order five based on previous analyses of similar data (Coffey et al., 2002). Fourth-order polynomials were used to model the animal's genetic plus permanent environment effect.

Daily solutions for days of lactation 4 to 305 obtained from the analysis were used to calculate daily values on the phenotypic scale for all cows in the data set, for all traits. Energy balance was derived using either daily milk yield and daily feed intake (**EB1**) or predicted body protein and lipid changes (**EB2**) after converting all measures to energy equivalents using the effective energy system of Emmans (1994). Both methods included energy used for maintenance and activity that was dependent on both feed composition and live weight. Details of the formulas used to convert to effective energy equivalents are given by Coffey et al., (2001).

The method of calculating daily body lipid content relies on an estimate of gut fill predicted from FI and feed composition. Feed composition was analyzed weekly and occasionally the change in composition was sufficient to cause a large change in predicted body lipid content from one day to the next at the boundary of the change in feed composition. Therefore, when body lipid or body protein changed by more than 1.5 kg, the daily change was set to be the same as the day before to smooth out large fluctuations in body energy change that were an artifact of the calculation method. Energy retained from feed was discounted at a rate of 1.8% of energy intake above maintenance per multiple of maintenance requirements (ARC, 1980).

The energy required to grow the fetus was calculated from daily predicted protein and lipid retention in the fetus using formulas from ARC (1980) and was assumed constant for all cows. The effective energy required for fetal growth was assumed the same as for maternal growth because the effective energy system (Emmans, 1994) does not consider fetal growth. This adjustment affects only EB1. The effects of the weight of the conceptus (fetus plus placenta plus fluid) on the prediction of empty body weight were accounted for, in part, by modeling total conceptus weight using an exponential growth curve from day of conception (ARC, 1980). The parameters of this curve were adjusted to result in a weight of gravid uterus at 281 d of gestation of 71, 78, and 85 kg, respectively, for lactations 1 to 3, to account for assumed increases in weight of 10% per lactation

for this component in larger and older cows. The daily predicted weight of conceptus was subtracted from empty body weight to reduce any upwards bias on body lipid estimation by the presence of conceptus that would otherwise have affected EB2. The daily predicted weight of conceptus was assumed to be constant for all cows of the same parity.

RESULTS

The data set comprised 501 cows that had at least one lactation with FI records. Of the animals that had at least 3 lactations with FI records there were 97 and 93 SL cows, and 69 and 64 CL cows in the low- and high-concentrate groups, respectively. Estimates of error variance (Table 1) found in this analysis are, as expected, very similar to those found by Coffey et al. (2002), except for FI in the first error variance class, where the values are generally lower in this study. (In the present study, we used all records for animals on the feed intake trial, whereas in the previous analysis only those animals having at least 3 lactations on the trial were included.) Error variances for LWT are similar to those reported by Koenen and Groen (1998); those for BCS are similar to those reported by Koenen et al. (2001).

Correlations for EB1, EB2, and cumulative EB2 between a selection of days in each lactation for all cows that had at least 3 lactations of feed intake data are given in Table 2. For daily EB1 and EB2, the correlations between the same days in successive lactations are higher than for those between lactations 1 and 3. For cumulative EB2, correlations between lactations 1 and 2 range from 0.37 in early lactation to 0.80 in late lactation, and between lactations 2 and 3, the correlations are higher, ranging from 0.67 in early lactation to 0.83 in late lactation. Between lactations 1 and 3, the correlations are similar to those for lactations 1 and 2 and are still high, ranging from 0.31 to 0.73. These correlations are higher than those reported by Coffey et al., (2002) because, in the current study, data for all lactations are included in the model as separate but correlated traits.

Average daily MY, fresh FI, LWT, and BCS for all 4 groups of cows are given in Figures 1 to 4, respectively. As expected, the SL cows on the high-concentrate diet had the highest daily yield (Figure 1). The SL cows on the low-concentrate diet produced more milk than the CL cows on the high-concentrate diet; the difference between these 2 groups was most pronounced in the third lactation. Although diet affected yield in both SL and CL cows during lactation, by the end of lactation daily MY was similar among SL cows irrespective of diet, and among CL cows irrespective of diet. However,

Table 2. Correlations between energy balance measures[1] on specific days of lactation across lactations for all animals with at least 3 lactations (L1, L2, L3) of recorded feed intake.

Day	EB1			EB2			Cumulative EB2		
	L1/L2	L2/L3	L1/L3	L1/L2	L2/L3	L1/L3	L1/L2	L2/L3	L1/L3
7	0.13	−0.03	−0.01	0.08	0.04	0.04	0.37	0.67	0.31
14	0.22	0.11	0.07	−0.01	0.05	−0.04	0.58	0.71	0.51
21	0.24	0.08	0.08	0.14	−0.03	0.09	0.65	0.74	0.55
28	0.24	0.13	0.08	0.26	0.25	0.23	0.68	0.76	0.57
35	0.21	0.13	0.07	0.34	0.32	0.23	0.70	0.78	0.59
42	0.21	0.12	0.05	0.31	0.32	0.26	0.71	0.79	0.60
49	0.15	0.12	0.08	0.12	0.27	0.12	0.72	0.79	0.61
56	0.18	0.17	0.11	0.43	0.42	0.30	0.73	0.80	0.62
63	0.18	0.20	0.11	0.34	0.31	0.28	0.74	0.80	0.63
70	0.23	0.21	0.15	0.14	0.24	−0.05	0.75	0.80	0.64
77	0.22	0.20	0.17	0.31	0.30	0.22	0.76	0.81	0.64
84	0.17	0.23	0.17	0.04	0.07	0.02	0.76	0.81	0.65
91	0.19	0.26	0.21	0.20	0.16	0.21	0.77	0.81	0.66
98	0.23	0.27	0.20	0.36	0.24	0.31	0.78	0.81	0.67
120	0.22	0.27	0.17	0.00	0.01	−0.02	0.79	0.81	0.68
150	0.30	0.28	0.16	0.12	0.41	0.21	0.80	0.81	0.71
180	0.31	0.32	0.26	0.18	0.31	0.21	0.79	0.81	0.72
210	0.28	0.40	0.18	0.21	0.28	0.12	0.79	0.82	0.72
240	0.26	0.40	0.27	0.15	0.22	0.03	0.78	0.83	0.73

[1]EB1 = Energy balance calculated from feed intake measures, EB2 = energy balance calculated from BCS changes.

the SL cows did have higher yields at the end of lactation than the CL cows.

Feed intake was greatest for SL cows on the low-concentrate diet (Figure 2) and SL cows had a higher FI on both diets than CL cows, with the difference between the groups being greatest in the third lactation. Cows selected for maximum production were also heavier by 44 kg ($P < 0.005$) at the start of each lactation (Figure 3), and lost more weight than CL cows such that all groups were of approximately equal weight at the end of each lactation. Cows selected for maximum production had significantly higher BCS at the start of the first lactation ($P < 0.005$) and significantly lower BCS by d 18 of lactation 2, and d 12 of lactation 3 ($P < 0.005$). The SL cows lost more body condition at the end of the third lactation (0.53 and 0.46 BCS units) than CL cows, for high- and low-concentrate diets respectively ($P < 0.005$), such that SL cows on a low-concentrate diet had lost the greatest amount of body condition and had the lowest BCS at the end of the third lactation (0.54 BCS units).

The average daily energy balance (EB1) is given in Figure 5. Cows have a NEB of about 50, 75, and 125 MJ/d in early lactation in lactations 1, 2, and 3 respectively. Figure 6 shows the cumulative body energy content
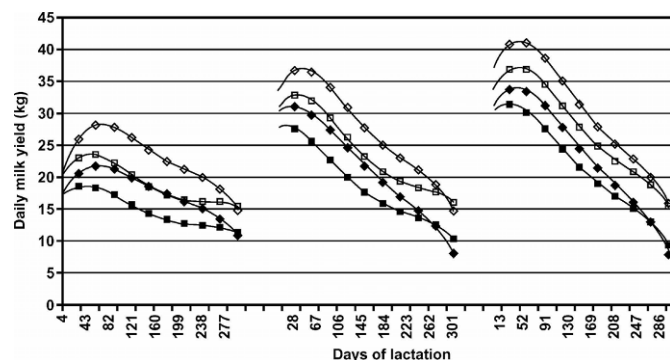

Figure 1. Average milk yield (kg) by day of lactation for lactations 1, 2, and 3 for cows in groups: low-concentrate control (■), low-concentrate selected for maximum production (□), high-concentrate control (◆), and high-concentrate select for maximum production (◇).
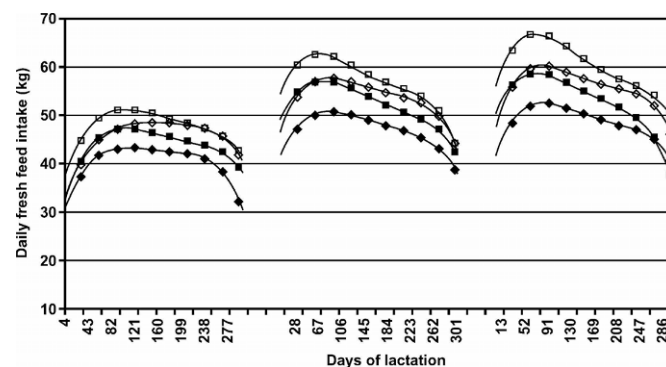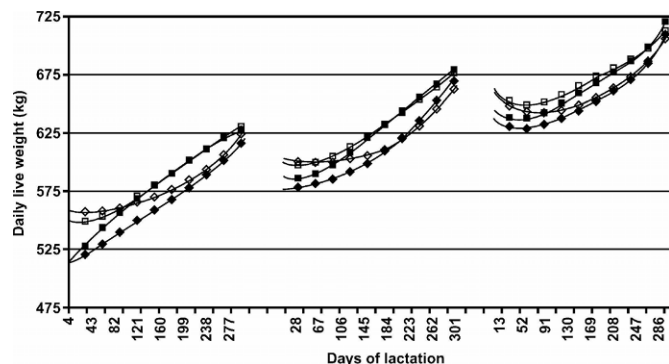

Figure 2. Average fresh feed intake (kg) by day of lactation for lactations 1, 2, and 3 for cows in groups: low-concentrate control (■), low-concentrate selected for maximum production (□), high-concentrate control (◆), and high-concentrate selected for maximum production (◇).

Figure 3. Average live weight (kg) by day of lactation for lactations 1, 2, and 3 for cows in groups: low-concentrate control (■), low-concentrate selected for maximum production (□), high-concentrate control (◆), and high-concentrate selected for maximum production (◇).

Figure 5. Average daily energy balance (MJ) calculated from feed intake and milk yield by day of lactation for lactations 1, 2, and 3 for cows in groups: low-concentrate control (■), low-concentrate selected for maximum production (□), high-concentrate control (◆), and high-concentrate selected for maximum production (◇).

(lipid and protein) from first calving derived from EB2. The effect of diet was significant for both genetic groups and all groups became significantly different for cumulative body energy content by d 15 of lactation 1. However, CL cows were not significantly different from each other after d 45 of lactation 1. The SL cows had significantly less ($P < 0.005$) body energy than CL cows throughout the 3 lactations and SL cows on a high-concentrate diet had significantly less ($P < 0.005$) body energy than SL cows on a low-concentrate diet after d 6 and throughout the 3 lactations. The biggest difference in body energy content at the end of the third lactation was 3206 MJ, and occurred between the SL and CL cows on the low-concentrate diet.

DISCUSSION

This study is a more detailed analysis of energy balance over 3 lactations for 2 genotypes on 2 diets than

that reported in Coffey et al. (2002). Coffey et al. (2002) used a multivariate random regression model that allowed incomplete lactations and records for animals without 3 lactations of feed intake data to be included in the analysis. The results presented here demonstrate that a selection objective emphasizing production alone results in cows that have significantly less body energy (Figure 6), although they are the same weight (Figure 3), predominantly because they have less body lipid at the end of 3 lactations (Figure 4). This gradual erosion of body energy stores may be of concern from health, welfare, and profitability viewpoints.

As expected, the SL cows gave more milk on both the high- and low-concentrate diets (Figure 1) and had a higher fresh FI on the low-concentrate diet, particularly
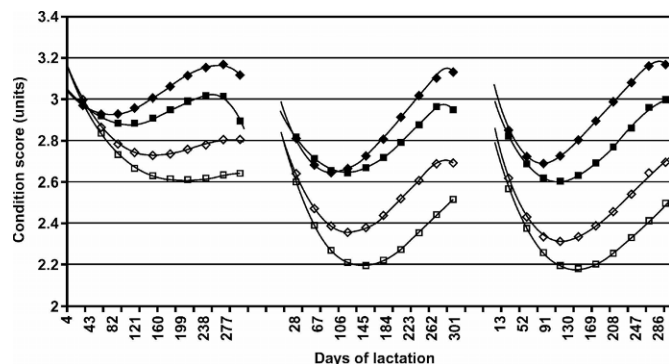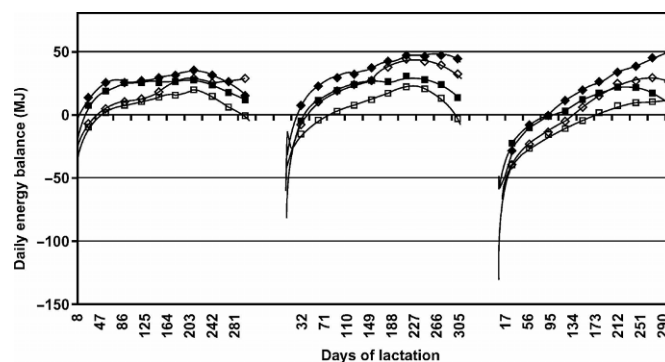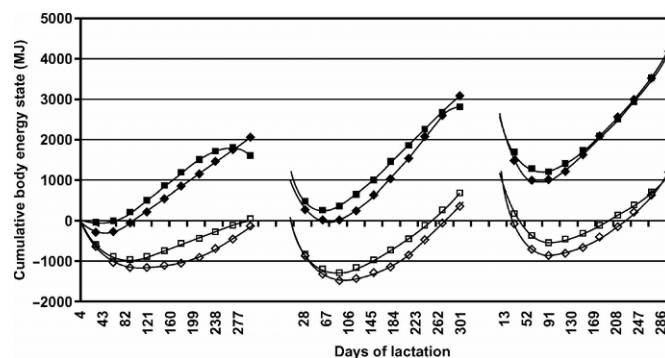

Figure 4. Average BCS (units) by day of lactation for lactations 1, 2, and 3 for cows in groups: low-concentrate control (■), low-concentrate selected for maximum production (□), high-concentrate control (◆), and high-concentrate selected for maximum production (◇).

Figure 6. Average cumulative energy balance from first calving (MJ) calculated from body energy changes by day of lactation for lactations 1, 2, and 3 for cows in groups: low-concentrate control (■), low-concentrate selected for maximum production (□), high-concentrate control (◆), and high-concentrate selected for maximum production (◇).

in early lactation (Figure 2). The SL cows on the high concentrate diet appeared to have a more persistent FI curve. The SL cows were heavier at calving in all 3 lactations but lost more weight than the CL cows on both diets (Figure 3) in all 3 lactations such that all cows were similar in weight at d 305 of each lactation. All cows, except the CL cows on a high-concentrate diet, continued to lose BCS throughout the 3 lactations with the SL cows on the high-concentrate diet having lost the most by the end of the third lactation. The magnitude of maximum BCS loss was similar in lactations 2 and 3 and both had greater loss than in lactation 1.

The change in shape of the NEB curve in lactation 3 may be explained by the alteration in shape of milk production curves for these animals. The milk production peak is reached much earlier in successive lactations (results not shown) but the rise in FI is similar in each lactation. In the absence of a rise in the rate of increase in FI over lactations, multiparous animals will be in increasing NEB in early lactation due (mostly) to their more rapid output of milk. Both the rate of output and the acceleration in the rate of output of milk may be an important issue in relation to disease because rate and acceleration are seen as stressors (Ingvartsen et al., 2003).

Both genetic lines of cows on the low-concentrate diet typically have a later return to positive energy balance than cows on the high-concentrate diet. The SL cows on the low-concentrate diet were in the lowest energy balance state (i.e., the most negative) throughout the 3 lactations (Figure 5), although this is not evident from Figure 6, which shows the predicted cumulative body energy content (lipid and protein). The SL cows on a high-concentrate diet appear to accumulate less body energy over 3 lactations despite being in a more positive daily energy balance (Figure 5). This may be explained by the calculation of body energy being related to empty body weight. Cows on a low-concentrate diet are predicted to have higher gut fill. This may be overestimated leading to a lower predicted body weight (Figure 3) and lower body energy content despite the higher BCS (Figure 4). The SL cows on both diets accumulate the least amount of energy over their lifetimes and at the end of the third lactation have approximately 3200 MJ less body energy than the CL cows even though they are of a similar weight. This is because they have significantly less body lipid (Figure 4).

Daily energy balance calculated from FI and milk output indicates that cows return to positive energy balance faster after each calving than when estimated from body lipid changes. Although in part this may be explained by BCS being an incomplete assessment of body lipid content or a delay in subcutaneous body lipid being mobilized, an additional explanation might be

that the calculation of EB1 is biased upwards. All food recorded as eaten is assumed to be consumed by the cow whereas, in practice, some is wasted such that actual FI is lower than that recorded.

At the time when diet composition changes, there is a large effect on the prediction of gut fill and hence body lipid content, leading to aberrant values for body energy change on a daily basis. Future work should attempt to smooth the transition from one stage to the next. A method to do this would be to convert all inputs and outputs to energy equivalents before analysis using a random regression model and to use the smoothed values to calculate energy balance. This technique of analysis was used by Schwager-Suter et al. (2001), who used the Net Energy system and polynomials to smooth the resulting energy balance. We chose not to conduct this type of analysis because fixed effects were thought to affect each trait differently. In particular, the effect of pregnancy operates at the individual animal level and its influence on energy balance varies throughout lactation. The fixed effects of pregnancy stage were added back to the daily solution for each cow to adjust energy balance at the phenotypic level.

Adjustments for the effects of pregnancy on body weight and energy used by conceptus were considered separately for EB1 and EB2. For EB1, the energy utilized by the growing fetus was subtracted from energy intake because it is an energetic cost to the cow but the energy required for the gravid uterus was not included because this is retained by the cow postpartum and returns to the nutrient pool. The energy requirement of the fetus is small compared with daily energy requirements for milk yield; at d 281 of pregnancy, the fetus is utilizing around 5 MJ of effective energy per day if fetal and maternal usage of energy are the same. This is likely to be an underestimate because the fetus uses maternal amino acids as an energy source creating additional heat to be lost by the mother. For EB2, the whole predicted conceptus weight was subtracted from empty body weight and body lipid content was calculated from the remainder.

The effect of NEB on reproduction has been studied extensively. Taylor et al. (2003) found a significant and unfavorable relationship between NEB and time of ovulation in primiparous high-yielding cows. Veerkamp et al. (2000) demonstrated that the commencement of luteal activity predicted from milk progesterone levels was unfavorably correlated to NEB and suggested that a selection index containing FI would allow selection for yield at a constant commencement of luteal activity. However, Riest et al. (2003) have shown that resumption of ovulation postpartum was not affected by NEB but conception rate was. Those authors suggest that NEB mediates an effect on reproduction at the concep-

tion stage due to a change in the physiological state of the cow with regard to metabolic hormones such as thyroxine and steroid precursors such as cholesterol. This is supported by a meta-analysis by Lopez-Gatius et al. (2003) who suggested that, within the normal range of body energy gain and loss, follicular activity appears to be unaffected by NEB. However, they too noted that days open increase when NEB is large.

There is an intimate relationship between body energy content, milk yield, and profitability in dairy cows in part due to the cost of producing the body energy and in part due to the effect that changes in body energy have on traits such as health and fertility. Body energy, or a parameter of its change, is therefore a suitable candidate for inclusion in future selection indices. Given the high genetic correlation between BCS and angularity or dairy form (Lassen et al., 2003), it further suggests that pending the availability of breeding values for energy balance profiles, breeding companies should place at least no emphasis on increased angularity and perhaps even select for lower angularity. Incorporating body energy into an overall index would enable the selection of cows that have a suitable profile of body energy content at a given yield level. Concurrent selection for yield and reduced body lipid loss in early lactation is, in effect, selection for increased energy intake; it is predicted to improve health and welfare of cows but does have an economic cost. Veerkamp and Brotherstone (1997) suggest that a restricted index in which BCS is maintained at its (then) current level is predicted to reduce overall economic gain by 5%. The most appropriate combination of yield and body lipid and an economic value for use in an overall profit index are worthy of future investigation.

CONCLUSIONS

Selection primarily for yield perhaps exacerbated by additional selection for angularity (or dairy form) has led to cows that mobilize more of their body energy in early lactation and do not replenish all lost body lipid later in their productive life. For high genetic merit animals, this results in a net loss of body lipid particularly when fed a low-concentrate diet. These findings have implications for management systems required for cows highly selected for yield or alternatively, for selection objectives for cows to be kept in a low concentrate management environment. Future selection indices could include body lipid content in an attempt to limit loss of body condition, negative energy balance, and concomitant health and fertility problems.

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