

## Breed and Parity Effects on Energy Balance Profiles Through Lactation: Evidence of Genetically Driven Body Energy Change

N. C. Friggens,<sup>1</sup> P. Berg, P. Theilgaard, I. R. Korsgaard, K. L. Ingvarsten, P. Løvendahl, and J. Jensen  
University of Aarhus, Faculty of Agricultural Sciences, Research Center Foulum, PO Box 50, DK-8830 Tjele, Denmark

### ABSTRACT

The aim of this study was to characterize patterns of energy balance through lactation of cows kept under constant feeding conditions. Danish Holstein, Danish Red, and Jersey cows were studied during consecutive lactations and remained on the same dietary treatment throughout. They were fed a normal (13.55 MJ of digestible energy/kg of dry matter) or a lower energy diet (12.88 MJ of digestible energy/kg of dry matter) *ad libitum* throughout lactation. Energy balance was calculated using the effective energy (EE) system in such a way that energy balance equated to body energy reserve change. In the EE system the energy values assigned to feeds are directly equivalent to the energy requirements of the animal; 1 MJ of EE supply has the same energy value as 1 MJ of lipid loss from the body. The resulting body energy change data were analyzed using a linear spline model. There was no evidence to suggest that different combinations of breed and parity required different knot placements. The Holstein mobilized significantly more body energy in early lactation than the Danish Red and Jersey breeds. Parity 1 cows mobilized significantly less than parity 2 and 3 cows. There was a significant interaction between breed and parity in the first half of lactation due to parity 1 Jersey cows having a greater mobilization than would be expected of the difference between parities in the other breeds. As lactation progressed, the differences between parities and between breeds decreased. Cows on the higher energy diet had a more positive energy balance. Within breed and parity, the following possible predictors of individual differences in body energy change were examined: fatness-corrected live weight, condition score at calving, and genotype. There was no difference in the predicted cow effect or residual energy balance profile when grouped according to quartiles of corrected live weight or according to condition score at calving. During the period of most negative energy balance (d 14) there

was no significant relationship between live weight and intake, suggesting that, within diet type, the systematic patterns of body energy change through lactation in cows that were kept under stable and sufficient nutritional conditions cannot be accounted for by environmental factors such as constrained intake or condition score at calving. Thus, these patterns appear to have a genetic basis. The proportion of the phenotypic variation (remaining after accounting for fixed effects) accounted for by additive genetic effects varied through lactation from 4.2 to 13.0%. Genetic correlations between early and late lactation energy balances were low and close to zero, suggesting that body energy changes in early and late lactation are genetically independent traits.

**Key words:** energy balance, breed, parity, dairy cow

### INTRODUCTION

Increased mobilization of body reserves in early lactation has been associated with increased health problems and a reduction in reproductive performance (Hansen, 2000; Pryce et al., 2001; Ingvarsten et al., 2003). Further, the incidence of these problems has increased substantially in recent decades (Pryce et al., 1999; Royal et al., 2000), and at the same time selection for milk production has increased usage of body reserves in early lactation (Coffey et al., 2001; Koenen et al., 2001). In this context, achieving a better understanding of the factors predisposing for mobilization of body reserves is an important step in the development of strategies to reduce the health and reproduction problems experienced by the modern dairy cow.

There is mounting support for the idea that body energy change has 2 components: environmental and genetic (for a summary of supporting evidence see Friggens et al., 2004). Genetically driven body energy change is defined as that which would occur in cows kept in an environment that was in no way constraining. It then follows that environmentally driven body energy change is defined as that which occurs in response to an environment that is constraining. The notion of genetically driven body energy change has a number of important implications. If in early lactation,

Received March 7, 2007.

Accepted July 2, 2007.

<sup>1</sup>Corresponding author: n.friggens@agrsci.dk

mobilization is genetically driven then, by definition, it cannot be eliminated by increasing nutrient availability. If some mobilization is genetically driven, then it is reasonable to suppose that the cow is adapted to this type of mobilization and that, therefore, it does not affect health and reproduction to the same extent as environmentally driven mobilization. Further, it is reasonable to expect differences between breeds or genotypes in the extent of their genetically driven mobilization (Friggens et al., 2004).

These implications indicate that improvements in rationing and management of health and reproduction could be achieved by incorporating genetically driven mobilization into systems for prediction. Although a number of studies have estimated the genetic variation in some indirect energy balance measures (Veerkamp, 1998), direct experimental evidence for genetically driven body energy change is lacking. This lack of direct evidence is reflected in the fact that surprisingly few feeding systems accommodate genetically driven body energy change (Friggens et al., 2004). To measure genetically driven mobilization experimentally it is necessary to ensure that environmental disturbances are minimized (ideally removed) and that the environment provided is not nutritionally limiting. The study reported here was designed to approximate these conditions. It also permitted the assessment of body energy change from energy inputs and outputs (i.e., by energy balance calculation). Consequently, the aims of this paper are to examine patterns of energy balance through lactation for evidence of genetically driven body energy change and to characterize breed and parity differences in body energy change profiles under constant environmental conditions.

## MATERIALS AND METHODS

The data used in this study were collected during a 5-yr experiment carried out from October 1996 to October 2001 at the Danish Cattle Breeders Organisation research farm, Ammitsbøl Skovgård. All the procedures involving animals were approved by the Danish Animal Experiments Inspectorate and complied with the Danish Ministry of Justice Law no. 382 (June 10, 1987) and Acts 739 (December 6, 1988) and 333 (May 19, 1990) concerning animal experimentation and care of experimental animals.

### *Experimental Design and Animals*

The design and methods for the production aspects of the experiment have been described in detail elsewhere (Nielsen et al., 2003). Briefly, 3 breeds were represented: Danish Holstein, Danish Red, and Jerseys. The

design included 2 genetic lines within each breed. For Danish Red and Danish Holstein the 2 lines were selected for solely milk yield or dual-purpose milk and meat production. The 2 Jersey lines were Danish Jerseys or American Jerseys. Within all levels of genetic structure, cows were equally assigned to 1 of 2 dietary treatments. The cows were studied during consecutive lactations and remained on the same dietary treatment throughout. The cows were housed throughout the year in single tie stalls. Records of 637 lactations from 322 cows from 76 sires were available. A summary of the performance of the different breeds on the 2 dietary treatments is presented in Table 1.

### *Feeding*

The cows were fed 1 of 2 TMR ad libitum throughout lactation. The normal energy diet (**NTMR**) was designed to allow the cows to meet their energy requirements. The lower energy diet (**LTMR**) was designed to be more limiting with respect to feed energy supply. In the dry period (56 d before calving) all cows were fed the LTMR ad libitum. The 2 rations used the same concentrate and had the same forage:concentrate ratio. The forages used were (kg/kg of dry TMR): whole-crop pea silage (0.08 or 0.10), whole-crop wheat silage (0.305 or 0.415), and chopped straw (0.13 or 0) in LTMR and NTMR, respectively. The concentrate composition was (kg/kg of dry TMR): rapeseed meal, 0.13; soybean meal, 0.05; sugar beet pulp, 0.16; sugar beet molasses, 0.125; mineral vitamin mix, 0.02. The composition of the 2 TMR was fixed irrespective of stage of lactation. The average digestible energy contents of NTMR and LTMR were 13.55 and 12.88 MJ/kg of DM, respectively. (The ME content of the ration components is given in Nielsen et al., 2003). The average crude protein contents of NTMR and LTMR were 153 and 145 g/kg of DM, respectively.

### *Recording of Production Data*

Fresh feed was offered 3 to 4 times a day, and the amount offered was such as to attain refusal amounts of at least 5% of predicted intake. Refusals were removed and weighed on Monday, Wednesday, and Friday. The cows were milked twice daily between 0600 and 0800 h and between 1600 and 1800 h. Milk yield and milk composition were recorded at each milking. Proportional milk samples taken from each milking were analyzed for fat, protein, and lactose. All animals were weighed on d 2, 3, and 8 after calving and then once a week until 3 mo after calving. From 3 mo after calving to the dry period they were weighed every 2 wk. During the dry period the cows were weighed once

**Table 1.** The average lactational performance according to breed and dietary treatment of the cows used in this study

Item	Breed					
	Danish Red		Danish Holstein		Jersey	
	NTMR <sup>1</sup>	LTMR <sup>1</sup>	NTMR	LTMR	NTMR	LTMR
305-d milk yield <sup>2</sup> (kg)	6,060	5,400	7,242	6,780	5,081	4,680
Milk fat (g/kg)	47.0	46.2	45.2	45.3	61.8	58.5
Milk protein (g/kg)	37.0	35.7	35.4	34.2	41.7	39.9
Mean DM intake (kg/d)	18.8	17.7	20.8	20.1	16.4	15.4
Live weight (kg)	630	587	616	615	424	401

<sup>1</sup>NTMR = normal energy density TMR; LTMR = lower energy density TMR.

<sup>2</sup>Excludes cows with records missing before 30 d in lactation.

a week. To minimize the influence from milking and feeding, the cows were always weighed at the same time of day. Body condition was scored to the nearest half unit on the Danish scale (Kristensen, 1986) derived from Lowman et al. (1976) from 1 to 5 on d 2, 14, 28, 42, 56, 84, 112, 168, and 224 after calving. Additionally, BCS was recorded on the day of drying off the cow; 35, 21, and 7 d before expected calving; and finally on the day of calving. Outside the period -14 to +14 d from calving, body condition scoring was done on 1 calendar day in the week. Trained personnel on the research farm undertook all body condition scoring, with the same person responsible for 92% of the scores. There were no significant differences between scorers. When cows required the attention of a veterinary surgeon, veterinary diagnosis and treatment were recorded. Using the treatment records, periods in which the cow was assumed to be not healthy were defined according to disease/disorder type in accordance with literature estimates of their duration (Fourichon et al., 1999; Baraille et al., 2003). On the day of treatment the cow was assigned a health status of 2; in the period surrounding the treatment day (typically  $\pm 21$  d) the cow was assigned a health status of 1. Outside these periods (i.e., when assumed healthy), health status was 0.

Milk yield, milk fat percentage, and feed intake records were checked for outliers according to the procedure used by Friggens et al. (1999). For each individual cow lactation, observations with a residual greater than +5 or less than -5 standard deviations from a cubic spline fitted curve (with 5 knots) were rejected. Extremely deviant observations, which highly influenced the residual standard deviations, were accounted for by running the spline procedure twice, the second time without the deviant observations identified in the first run. In total over both splines, 0.4% of intake records, 0.4% of milk composition records, and 0.7% of milk yield observations were rejected. Condition score and weight records for each cow and lactation number were checked for deviant observations by visual inspection relative

to days from calving. A total of 0.6% of the condition score records and 0.8% of the weight records were rejected.

### Calculation of Energy Balance

The method of calculating energy balance for this study was chosen so that energy balance equated to body energy reserve change (i.e., in this paper the 2 terms are synonymous). It was also chosen with the aim of minimizing possible bias due to the differences between breeds and parities. The energy system used was the effective energy (EE) system (Emmans, 1994). In this system, the EE values assigned to feeds are directly equivalent to the energy requirements of the animal; 1 MJ of EE supply has the same energy value as 1 MJ of lipid loss from the body. This arises because the differences that exist between metabolizable and net energies are dealt with in the EE system in a logical and consistent way across life functions. Another advantage of the EE system is that body lipid and protein retention are distinguished with the heat increments (i.e., the metabolic work energy) of gain and loss of body lipid and protein being derived in a consistent way. The EE values assigned to feeds are also largely unaffected by level of feeding. These are attractive properties for an energy system that is being used in an experiment where we may expect growth in some animals (e.g., heifers), substantial differences in intake between breeds and stages of lactation, and mobilization and deposition of body reserves.

The basic energy balance equation for calculating body energy reserve change (**EBody**; MJ/d) from the difference between feed energy input per day (**EFood**) and energy requirements per day for milk (**EMilk**), lean tissue growth (**EGrowth**), conceptus growth (**EConceptus**), maintenance (**EMaintenance**), and activity (**EActivity**) was

$$\text{EBody} = \text{EFood} - (\text{EMilk} + \text{EGrowth} + \text{EConceptus} + \text{EMaintenance} + \text{EActivity}).$$

The assumptions made for calculating the energy content are described below for each of the components of the energy balance equation. A number of the assumptions have been made to allow proper size-scaling and thus minimize between breed bias in the energy balance calculations.

**EFood.** The chemical composition of the feed components, from which the energy content was calculated, was measured monthly. It was found that the feed composition (g/kg of DM) was stable within each harvest year (Nielsen et al., 2003). Therefore, the energy content of the feed was assumed to be a constant, the average, within harvest year. The DM content of the roughages, measured weekly, was found to vary between and within harvest years. The trend in roughage DM within harvest year was characterized by a local regression smoothing function. The smoothed DM values were used to calculate DM intake from fresh intake. To account for the combined effects of feed wastage, evaporative losses in the food trough and average bias in energy value determination (see Ellis et al., 2006), DM intake values were discounted by 10% when calculating energy intake. The EE content of the feed was calculated, according to Emmans (1994), as

$$\text{EE (MJ/kg of DM)} = \text{DE} - 0.228 \text{ GE} - 4.67 \text{ DCP},$$

where digestible energy (**DE**) and gross energy (**GE**) contents are in MJ/kg of DM and digestible crude protein (**DCP**) content is expressed as kg/kg of DM. The average EE contents of the NTMR and LTMR were 9.1 and 8.5 MJ/kg of DM, respectively.

**EMilk.** Because 3 breeds (Danish Red, Danish Holstein, and Jersey) were used at all stages of lactation, there was a substantial variation in milk composition. Thus, it was decided that formulas for calculating EMilk based on assumptions about the ratios of milk components were insufficient for the present experiment. Therefore, for each milk component (i.e., fat, protein, and lactose) the energy content of and the metabolic work energy used to create the yield of that component were first calculated. The EMilk was then calculated as the sum of the energy requirements for the milk component yields. The EE needed to produce 1 kg of milk protein, milk fat, and milk lactose were assumed to be 33, 56, and 18 MJ, respectively (Coffey et al., 2001).

**EGrowth.** As the focus of this study is on the usage of body reserves in support of reproductive function, it was decided to adjust energy balance for growth. For these purposes, growth is defined as a systematic accre-

tion of lean tissue. When calculating energy balances for cows of a given breed in a given lactation it may be reasonable to assume that the energy requirements of growth are the same for all cows. However, this may introduce a bias when making comparisons between lactations as it is to be expected that first-, second-, and third-parity cows have different growth rates. The same applies to comparisons between breeds. To minimize these potential biases the following procedure was used.

In lactating animals, live weight change alone does not provide a good measure of growth because it also reflects mobilization of body reserves in early lactation and conceptus growth in late lactation. Therefore, some assumptions are necessary to estimate growth. First, it was assumed that cows in third parity were mature (i.e.,  $\text{EGrowth} = 0$  in third parity). Second, it was assumed that in all parities differences due to body mobilization and conceptus growth were negligible at wk 16 of lactation. Week 16 was chosen because it is just beyond the end of the period of early lactation body mobilization, which usually has a nadir at  $80 \text{ DIM} \pm 20$  (Coffey et al., 2001) and is sufficiently early in pregnancy for conceptus weight to be negligible (ARC, 1980) even for cows conceiving earlier than the average conception date of 90 d postcalving. Thus, the difference in live weight at wk 16 between 2 parities could be used as a measure of growth. However, if there are systematic changes in body fatness with increasing parity, this would bias this measurement of lean growth. Consequently, live weights at wk 16 were adjusted to a constant level of body condition. The final assumption made was that, within lactation, growth was linear. Given the degree of maturity of lactating cows, this simplifying assumption has a negligible effect on energy balance calculations.

The adjustment of live weight to a constant level of body condition was done assuming that there is a linear relationship between BCS and body lipid content (Wright and Russel, 1984a; NRC, 2001):

$$\text{L/EBW} = b \times (\text{BCS} - a),$$

where **L** is body lipid and **EBW** is empty body weight. Given that the lipid free empty body (**LFEB**) =  $\text{EBW} - \text{L}$ , the equation can be rearranged to

$$1/\text{EBW} = (1 + a \times b)/\text{LFEB} - (b/\text{LFEB}) \times \text{BCS}.$$

This allowed breed-parity specific coefficients to be estimated by linear regression of  $1/(\text{week 16 EBW})$  on wk 16 BCS estimates with breed  $\times$  parity effects on both the intercept and slope. Empty BW was calculated as live weight – gut fill. Gut fill was assumed to be  $6 \times$  feed intake, which is equivalent to assuming the DM

**Table 2.** The number of cows with body energy change records, their standard live weight,<sup>1</sup> and the average percentage contributions of the different components of the energy balance calculation relative to energy intake in lactations 1, 2, and 3

Item	Danish Red			Danish Holstein			Jersey		
	1	2	3	1	2	3	1	2	3
Number of cows	86	75	38	100	85	43	64	56	27
Standard BW, <sup>1</sup> kg	531	602	619	575	637	654	384	425	436
Eintake, <sup>2</sup> MJ/d	146	173	169	167	189	191	134	149	148
Emilk, <sup>3</sup> %	66	67	69	70	71	72	73	76	79
Egrowth, <sup>3</sup> %	0.7	0.6	0.0	0.7	0.5	0.0	0.5	0.4	0.0
Econceptus, <sup>3</sup> %	0.02	0.02	0.01	0.02	0.02	0.01	0.02	0.03	0.04
Emaintenance, <sup>3</sup> %	24	23	24	22	22	22	20	20	21
Eactivity, <sup>3</sup> %	4	4	4	3	3	3	3	3	3

<sup>1</sup>Live weight adjusted to a constant BCS of 3.

<sup>2</sup>Average energy intake (MJ of effective energy/d) over the period 100 to 150 d in milk.

<sup>3</sup>Energy requirement for: milk (Emilk), lean tissue growth (Egrowth), conceptus growth (Econceptus), maintenance (Emaintenance), and activity (Eactivity) expressed as percentages of energy intake averaged over the period 100 to 150 d in milk.

content of gutfill to be 16.7% (see Coffey et al., 2001). The average standardized live weights (i.e., wk 16 live weights adjusted to a condition score of 3) are given in Table 2.

Lean tissue growth rate in third parity was, by definition, 0. Lean tissue growth rate in second parity was calculated from the difference between the lipid-free empty bodyweight (**LFEB**) at the start of third parity and LFEB at wk 16 in second parity divided by the number of days between. Using the wk 16 LFEB and the lean tissue growth rate in second parity, LFEB at the start of second parity was calculated allowing lean tissue growth rate in first parity to be calculated in the same way as for second parity. To calculate LFEB, it was assumed that body lipid content is 0.25 when condition score = 3 (on a 1 to 5 scale, adapted from Wright and Russel, 1984b).

$$\text{LFEB} = (1 - 0.25) \times (\text{standardized live weight} - \text{gut fill}).$$

The protein content of lean tissue was assumed to be 0.2224 g/g, and the EE needed to accrete protein was 50 MJ/kg (Emmans, 1997); therefore,

$$\text{EGrowth} = 50 \times 0.2224 \times \text{lean tissue growth}.$$

**EConceptus.** The energy requirements for development of the fetus and associated maternal tissues were calculated as a function of the number of days since conception (AI records) and predicted size of the calf. The predicted size of the calf was adjusted according to measured mature live weight of the cow. The main purpose of this adjustment was to account for breed differences in EConceptus. For those cows that did not reach maturity (third parity), mature live weight was

estimated from their wk 16 live weight in the highest parity they reached adjusted by the average ratio between parities in wk 16 live weight. These ratios were found to be 0.85 and 0.94 for first and second parities, relative to third parity, respectively. These ratios were not affected by breed. Conceptus energy requirements were calculated from fetal growth using the following equations:

$$\text{Fetal growth} = \text{Pmat} \times \exp[-\exp(2.808 - 0.02335 * T)],$$

$$\text{Conceptus protein growth} = 2.02 \times (\text{fetal growth})^{0.737},$$

$$\text{and Conceptus lipid growth} = 0.29 \times (\text{fetal growth})^{0.812},$$

where **Pmat** is protein mass at maturity ( $0.2224 \times \text{LFEBwt}$  in parity 3) and T is days from conception scaled for mature size as (days from conception - 3.5)/( $\text{Pmat}^{0.27}$ ) according to Taylor (1980).

**EMaintenance.** The energy requirement for maintenance was assumed to be a function of the protein mass of the cow. There is good evidence that maintenance requirements of body fat are essentially zero (Kirkland et al., 2002). This equates to making EMaintenance a function of live weight adjusted to constant body fatness as described above, in this case to zero fatness. In accordance with well established scaling rules (Emmans, 1997), it was assumed that maintenance requirements per unit protein mass are a function of mature size, as follows:

$$\text{EMaintenance} = 1.63 \times P / (\text{Pmat}^{0.27}) \text{ MJ/d},$$

where P is the protein mass of the cow and Pmat is the protein mass at maturity. The P was calculated for each day from LFEBwt and lean tissue growth rate.

**EActivity.** A standard adjustment was made to the energy balance for activity. This was partly because the animals were housed in tie-stalls and thus had a rather limited scope for great variation in activity and partly because there was no means to measure the variation between animals in this quantity. EActivity was therefore assumed to be 0.01 MJ/kg of live weight/d (ARC, 1980).

The average percentage contribution of each component to the overall energy balance is given in Table 2.

### Data Manipulation and Statistical Analysis

**Smoothing of Input Data Variables.** Energy balance calculations involve the summing of a substantial number of components. This means that the uncertainties attached to the measurement of each of the components also sum, resulting in a relatively large uncertainty. Although this large uncertainty reflects the reality of measuring energy balance it makes comparison of energy balance profiles difficult. A portion of this residual variation is due to short-term random effects. Examples could be changes in level of human disturbance in the barn or random measurement error. As it was assumed that this portion of the residual variation was of no biological significance, the following procedure to reduce this noise was applied. Because an important aspect of the subsequent analysis of energy balance is how it changes through time, the procedure was chosen to reduce noise without introducing time-related bias in the process.

For each combination, ( $ijg$ ), of the 7 data variables: milk yield ( $j = 1$ ), milk protein content ( $j = 2$ ), milk fat content ( $j = 3$ ), milk lactose content ( $j = 4$ ), DM intake ( $j = 5$ ), live weight ( $j = 6$ ), and body condition score ( $j = 7$ ); and group ( $g = 1 \dots 60$ ), where  $g$  denotes a specific combination of lactation (1, 2, 3, 4, 5), breed (1, 2, 3), treatment (1, 2), and line (1, 2), a univariate analysis was carried out. The model of the variable was given by

$$Y_{it_k}^{(ijg)} = X_{it_k}^{(ijg)} \beta^{(ijg)} + u_{it_k}^{(ijg)} + e_{it_k}^{(ijg)},$$

where  $y_{it_k}^{(ijg)}$  denotes the observed value of animal  $i$ ,  $i = 1, \dots, I$ , at time  $t_k$ ,  $k = 1, \dots, n_i^{(ijg)}$ , where  $n_i^{(ijg)}$  is the number of observations of animal  $i$  (of the  $j$ th variable in the  $g$ th group). In the model, the average curve for each variable was assumed to be piecewise constant on predefined intervals specified as described below. Thus,  $\beta^{(ijg)}$  is a vector of parameters describing the average curve, and  $X_{it_k}^{(ijg)}$  is the corresponding design vector.  $(u_{it_k}^{(ijg)})_{i=1, \dots, I; k=1, \dots, n_i^{(ijg)}}$  are time-dependent random cow ef-

fects, and the  $u_{it_k}^{(ijg)}$  were assumed to be  $N(0, \sigma_u^2(ijg))$  distributed with a covariance structure given by

$$\text{Cov}(u_{it_k}^{(ijg)}, u_{it_{k'}}^{(ijg)}) = \sigma_u^2(ijg) (\rho^{(ijg)})^{|t_k - t_{k'}|}.$$

This is a generalization of the autoregressive process of order 1 (AR(1)) [i.e., had the observations been equally spaced, then the time-dependent cow effects would follow an AR(1) process]. The cow effects of different animals were assumed to be independent. Finally,  $e_{it_k}^{(ijg)}$  is a random error term. All error terms were assumed to be independent and  $N(0, \sigma_e^2(ijg))$  distributed, and the random error terms were assumed to be independent of the random cow effects. The average curve for milk yield was assumed to be piecewise constant on intervals  $[\tau_{q-1}, \tau_q)$ ,  $q = 1, \dots, 41$  with  $(\tau_0 \dots \tau_{41}) = (0, 1, 2, 3, 6 \dots 27, 30, 35, 42 \dots 91, 98, 112, 126 \dots 350, 364 \text{ DIM})$ . Note, the length of the first 3 intervals is 1 and then the length of the intervals gradually increases to 3, 7, and 14. The average curves for milk protein, milk fat, and milk lactose were assumed to be the same as for milk except that the first 3 intervals (0, 1, 2) were pooled. The intervals for DM intake were assumed to be  $(\tau_0 \dots \tau_{33}) = (0, 7, 14, \dots 91, 98, 112, 126 \dots 350, 364 \text{ DIM})$ . The intervals for live weight were assumed to be piecewise constant on intervals  $q = 1, \dots, 17$  with  $(\tau_0 \dots \tau_{17}) = (0, 14, 28 \dots, 98, 112, 140 \dots 364 \text{ DIM})$ . The intervals for body condition score were assumed to be  $(\tau_0 \dots \tau_4) = (0, 21, 49, 98, 364)$ . The choice of intervals reflected both the shape of the lactation profile and the requirement for sufficient data within each interval to permit the model to converge. Variance and covariance parameters,  $\sigma_u^2(ijg)$ ,  $\sigma_u^2(ijg) (\rho^{(ijg)})^{|t_k - t_{k'}|}$ , and  $\rho^{(ijg)}$  were estimated using REML (restricted maximum likelihood as implemented by SAS software (SAS Institute, 2001) and predicted values,  $\hat{y}_{it_k}^{(ijg)}$ , of animal  $i$  at time points  $t = 0 \dots 364$  were the empirical BLUP values  $\hat{y}_{it_k}^{(ijg)} = X_{it_k}^{(ijg)} \hat{\beta}_{it_k}^{(ijg)} + \hat{u}_{it_k}^{(ijg)}$ .

Twenty lactations were excluded, for all variables, because of insufficient data due to early exit from the experiment. Also, in 43 cases (out of 4,368) the model could not estimate predicted values.

Body energy change (EBody, MJ of EE/d) was calculated for each individual from the predicted values, as described in the preceding section. In this process, for each lactation, all predicted values outside the range of the raw data were deleted (i.e., no extrapolation beyond the original period of records was allowed). Likewise, predicted values were set to missing if the gap between adjacent records was greater than 6 d for milk yield and milk composition, 14 d for feed intake, and 42 d for live weight and condition score. The resulting numbers of cows according to breed and lactation are

given in Table 2. The process of deriving smoothed data for input into, and the assumptions involved in, calculation of the energy balance were validated by visual inspection of average curves of predicted values relative to original data and by comparison of cumulative energy balance across lactation with live weight and condition score changes from start to end of lactation. No marked deviations were found.

**Analysis of Body Energy Change.** The resulting body energy change data were analyzed using a linear spline model. This simplified function for body energy change has been shown to generate realistic curves of body condition score through lactation (Friggens et al., 2004). Further, by virtue of their knots, splines eliminate autocorrelations between different parts of lactation, and they provide a simple function for describing relatively complex curve shapes (e.g., a rapid dip in energy balance immediately postcalving). The analyses were carried out in two steps, based on the following model

$$y_{jk} = s_i + \beta^{dfc} \cdot x_{jk}^{dfc} + \sum_{m=1}^6 \beta_m^r \cdot l_j^m + \sum_{m=1}^6 \beta_m^h \cdot l_j^m + \sum_{m=1}^6 \beta_m^l \cdot l_j^m + \sum_{m=1}^3 \varphi_{mk}^r \cdot l_j^m + \sum_{m=1}^3 \varphi_{mk}^a \cdot l_j^m + e_{jk},$$

where  $y$  is the body energy change (EBody) of cow  $k$  on day  $j$  ( $j = 1, \dots, 305$ ), which is influenced by the  $i$ th interaction of season (quarter of the calendar year) and harvest ( $s$ ), a regression ( $\beta^{dfc}$ ) on days from conception ( $x^{dfc}$ ),  $\beta_m^r$ ,  $\beta_m^h$ , and  $\beta_m^l$ . These are the  $m$ th regression coefficients of breed, line, and lactation interactions ( $r$ ), health status ( $h$ ), and lactation and feeding treatment interaction ( $l$ ), respectively, on the  $m$ th linear spline coefficients,  $l^m$  (Misztal, 2006). Similarly  $\varphi^r$  and  $\varphi^a$  are random regression coefficients of permanent cow and additive genetic effects respectively on linear spline coefficients, and  $e$  are residuals assumed to be identical and independently distributed  $N(0, \sigma_e^2)$ . Fitting a permanent cow effect across parity resulted in lack of convergence; thus only a within parity cow effect was fitted. Visual inspection of residuals indicated that homogeneous residual variance was an acceptable assumption.  $\varphi^r$  and  $\varphi^a$  are assumed independent and multivariate distributed  $N(0, I \otimes R)$  and  $N(0, A \otimes G)$ , respectively, where  $R$  and  $G$  are (co)variance matrices,  $I$  is an identity matrix, and  $A$  is the numerator relationship matrix. The pedigree included a total of 2,638 animals of which 299 had energy balance records.

In the first step, the number of knots and knot placement in the linear spline were chosen based on a model ignoring additive genetic effects ( $\varphi^a$ ). Theoretical considerations (Friggens et al., 2004) suggested 4 knots,

visual inspection suggested that extra knots might be needed in early lactation. Accordingly, models containing from 4 to 6 knots were compared. Likewise, the placement of each knot was evaluated by comparing models in which the knot was placed at a range of different days from calving. This was done by repeatedly (100 replicates) fitting the model to a random subset of 90% of the observations, predicting the remaining 10% and computing the prediction error. Knots were iteratively chosen to minimize the mean squared prediction error, except for knots at d 1 and 305, which were always included. For the random effects, knots at d 1, 145, and 305 were selected. This was done because convergence problems occurred when knots for the fixed and random effects were the same.

In the second step the full model was fitted, conditional on the knots selected in the first step, estimating variance components by an average information REML algorithm using DMU (Madsen and Jensen, 2006). Standard errors of functions of variance components were computed by a Taylor series expansion. Fixed effects were tested by comparing Akaike's information criterion (AIC) in nested models including a random cow effect but ignoring additive genetic effects (for computational feasibility), using PROC MIXED (SAS Institute, 2001). Differences in AIC between 2 models greater than 3 indicate that there is good evidence that the model with the smaller AIC is significantly better than the model with the larger AIC (Burnham and Anderson, 2002) and was used to justify inclusion of fixed effects.

Further analyses to explore possible sources of variation between individuals in body energy change were carried out. To avoid confounding these individual differences with breed and parity differences, the predicted cow effects (3 knot linear spline for additive genetic plus permanent cow) and the overall residual energy balance after fitting the fixed effects were used in these analyses. To assess if there was an association between size and energy balance, fatness corrected live weight (BWstd) was used as a proxy for size. The average BWstd was calculated for each cow lactation, and then cow lactations were classified according to quartiles of the distribution of average BWstd. For each quartile class, the average energy balance and associated variance for each knot of the random cow spline was calculated. The resulting average energy balances for the different quartiles of the BWstd distribution were examined for systematic differences according to quartile using  $t$ -test to assess the significance of the differences. The same procedure was used to see if there was an association between BCS at calving and energy balance.

**Table 3.** Effect of breed, genetic line, and parity on the estimates of energy balance at the knots of the spline function used to describe the lactation curve of energy balance<sup>1,2</sup>

DFC	Danish Red		Danish Holstein		Jersey	
	Milk	Dual	Milk	Dual	American	Danish
Parity 1						
1	-39.1 (5.9)	-45.1 (6.2)	-75.5 (5.8)	-58.6 (6.0)	-60.0 (6.4)	-48.2 (6.3)
7	-50.9 (5.0)	-34.4 (5.3)	-70.1 (4.9)	-50.2 (5.1)	-55.9 (5.3)	-57.9 (5.3)
20	-37.3 (4.8)	-22.7 (5.0)	-54.4 (4.7)	-39.5 (4.9)	-45.5 (5.1)	-53.7 (5.0)
60	-17.0 (4.4)	-13.4 (4.6)	-25.5 (4.4)	-13.4 (4.5)	-24.1 (4.7)	-26.2 (4.3)
115	-22.4 (4.5)	-10.0 (4.6)	-18.5 (4.4)	-14.3 (4.5)	-26.1 (4.7)	-21.1 (3.9)
305	-7.4 (4.0)	-5.5 (4.4)	-1.2 (3.9)	-2.9 (4.1)	-17.9 (4.5)	-9.8 (1.1)
Parity 2						
1	-63.1 (5.9)	-89.1 (6.1)	-103.1 (5.8)	-85.1 (6.2)	-51.7 (6.5)	-66.4 (6.4)
7	-72.1 (5.0)	-84.6 (5.2)	-98.7 (4.9)	-92.3 (5.1)	-59.4 (5.3)	-63.6 (5.3)
20	-60.2 (4.8)	-64.2 (5.0)	-75.8 (4.7)	-75.8 (4.9)	-52.4 (5.1)	-63.4 (5.0)
60	-25.3 (4.4)	-29.8 (4.6)	-34.2 (4.4)	-30.4 (4.5)	-28.3 (4.7)	-33.8 (4.3)
115	-16.6 (4.4)	-12.2 (4.6)	-21.7 (4.4)	-18.6 (4.5)	-27.6 (4.6)	-26.7 (3.9)
305	12.5 (4.0)	13.5 (4.4)	9.5 (3.9)	7.8 (4.1)	-5.0 (4.5)	-1.2 (1.0)
Parity 3						
1	-113.0 (6.5)	-132.7 (7.3)	-133.6 (6.3)	-104.1 (6.9)	-63.6 (7.0)	-51.1 (6.9)
7	-83.3 (5.1)	-89.7 (5.4)	-94.8 (5.0)	-108.8 (5.3)	-73.8 (5.4)	-61.6 (5.5)
20	-65.7 (4.8)	-72.9 (5.0)	-73.4 (4.7)	-63.4 (5.0)	-72.2 (5.1)	-67.0 (5.1)
60	-29.9 (4.4)	-37.0 (4.6)	-19.8 (4.4)	-14.4 (4.5)	-28.5 (4.7)	-37.7 (4.4)
115	-19.9 (4.5)	-17.3 (4.6)	-18.9 (4.4)	-23.7 (4.5)	-27.7 (4.7)	-30.3 (4.0)
305	27.5 (4.1)	21.3 (4.4)	28.5 (4.0)	16.9 (4.3)	-10.4 (4.6)	0.0 (0.0)

<sup>1</sup>The knots correspond to days from calving (DFC): 1, 7, 20, 60, 115, and 305. The standard errors of the estimates are shown in parentheses. Actual energy balance values at each knot can be calculated by adjusting the values in this table with values for the intercept, average season  $\times$  harvest effect and other effects given in Table 4.

<sup>2</sup>The Danish Red and Danish Holstein lines were selected for solely milk yield (Milk) or dual-purpose milk and meat production (Dual). The Jersey lines were Danish Jerseys or American Jerseys.

## RESULTS

The method of calculating energy balance for this study was chosen so that energy balance equated to body energy reserve change (i.e., in this paper the terms energy balance and body energy change are synonymous). Estimates for the fixed effects of breed, line, parity, feeding treatment, and health status on the knots of the spline function are given in Tables 3 and 4. The fixed part of the spline model for body energy change used six knots at 1, 7, 29, 60, 115, and 305 d from calving. There was no evidence to suggest that different combinations of breed and parity required different knot placements.

### Breed and Parity

The fixed spline functions for each combination of breed and parity, all other effects being equal, are shown in Figure 1. Body energy change profiles through lactation for each combination of breed and parity including the random effects of cow, averaged over all cows, are shown in Figure 2. There were substantial differences in mobilization and deposition of body energy among breeds and also among parities ( $P < 0.001$ ; Table 3). On average the Danish Holstein mobilized significantly more body energy in early lactation than

the Danish Red and Jersey breeds. First-parity cows mobilized significantly less than second- and third-parity cows. However, there was a significant interaction between breed and parity in the first half of lactation. This was largely due to parity 1 Jersey cows having a greater mobilization than would be expected of the difference between parities in the other breeds (Figure 1). As lactation progressed, the differences between parities and between breeds decreased, although the effect of the breed-parity interaction was still significant (Table 3).

### Feed, Genetic Line, and Health Status

There were small but significant effects of feeding treatment (Table 4) and genetic line (Table 3) on body energy change. Omitting genetic line or feeding treatment from the model caused the AIC values to increase by 2,587 and 748, respectively. The cows on the higher energy diet (NTMR) had a more positive energy balance. There was also a significant interaction between feeding treatment and parity. The difference in energy balance between the 2 feeding treatments is shown for each lactation in Figure 3. The difference was greater in early lactation and, by late lactation (knots 5 and 6), there was no significant difference between feeds in

**Table 4.** Effect of feeding treatment,<sup>1</sup> as affected by parity, and health status<sup>2</sup> on the estimates of energy balance at the knots of the spline function used to describe the lactation curve of energy balance<sup>3</sup>

DFC	Feeding treatment <sup>1</sup>											
	LTMR						NTMR					
	Parity 1		Parity 2		Parity 3		All	Health status <sup>2</sup>				
							0	1	2			
Intercept	35.9*	(3.6)										
Season × harvest	-6.1*	(0.5)										
1	-14.1*	(2.8)	-7.2	(2.9)	12.1*	(3.8)	0.0	-5.0	(3.2)	-7.1	(3.2)	0.0
7	-16.3*	(2.3)	-7.9*	(2.3)	-9.5*	(2.5)	0.0	-5.0*	(1.9)	-3.4	(1.9)	0.0
20	-13.6*	(2.1)	-3.6	(2.1)	-3.2	(2.2)	0.0	-2.7	(1.6)	-2.7	(1.6)	0.0
60	-8.2*	(1.7)	-4.3	(1.8)	-12.4*	(1.8)	0.0	-7.4*	(1.5)	-4.2*	(1.5)	0.0
115	-2.5	(1.6)	-2.2	(1.6)	-1.0	(1.6)	0.0	-3.4*	(1.2)	-3.6*	(1.2)	0.0
305	-4.7	(2.3)	-5.6	(2.3)	-5.8	(2.4)	0.0	-10.0*	(1.7)	-7.5*	(1.7)	0.0

<sup>1</sup>NTMR is a normal energy density TMR; LTMR is a lower energy density TMR.

<sup>2</sup>Health status: 0 = healthy, 1 = period around a veterinary treatment, 2 = day of treatment.

<sup>3</sup>Effects are presented relative to cows in health status 2 and on the normal energy density TMR. The model intercept and the average season × harvest effect are also given. The knots correspond to days from calving (DFC): 1, 7, 20, 60, 115, and 305. The standard errors of the estimates are shown in parentheses.

\*Values are significantly different from 0 ( $P < 0.01$ ).

body energy change. Despite being a significant component of the model for fixed effects, genetic line had only small effects on the body energy change profiles. There was no consistent pattern to the line effects between breed or between lactations within breed (Table 3). The average difference between lines was only 1.45 MJ/d.

There was an overall significant effect of health status on energy balance (4 out of 6 knots; reduction in AIC with inclusion of health status: 274). Cows in health status 2 (i.e., the day of veterinary treatment) had a 5.6 MJ/d greater energy balance (average across all knots) than healthy cows (health status = 0; Table 4). There was no significant difference between health status 0 and 1 in energy balance. The greater energy balance of the sick cows is most likely an artifact of the different recording frequencies of feed intake (twice weekly) and milk yield (daily). Because of this, the drop in milk yield caused by illness would always be more pronounced than that of feed intake, resulting in a transitory positive energy balance.

### Sources of Variation Between Individuals in Body Energy Change

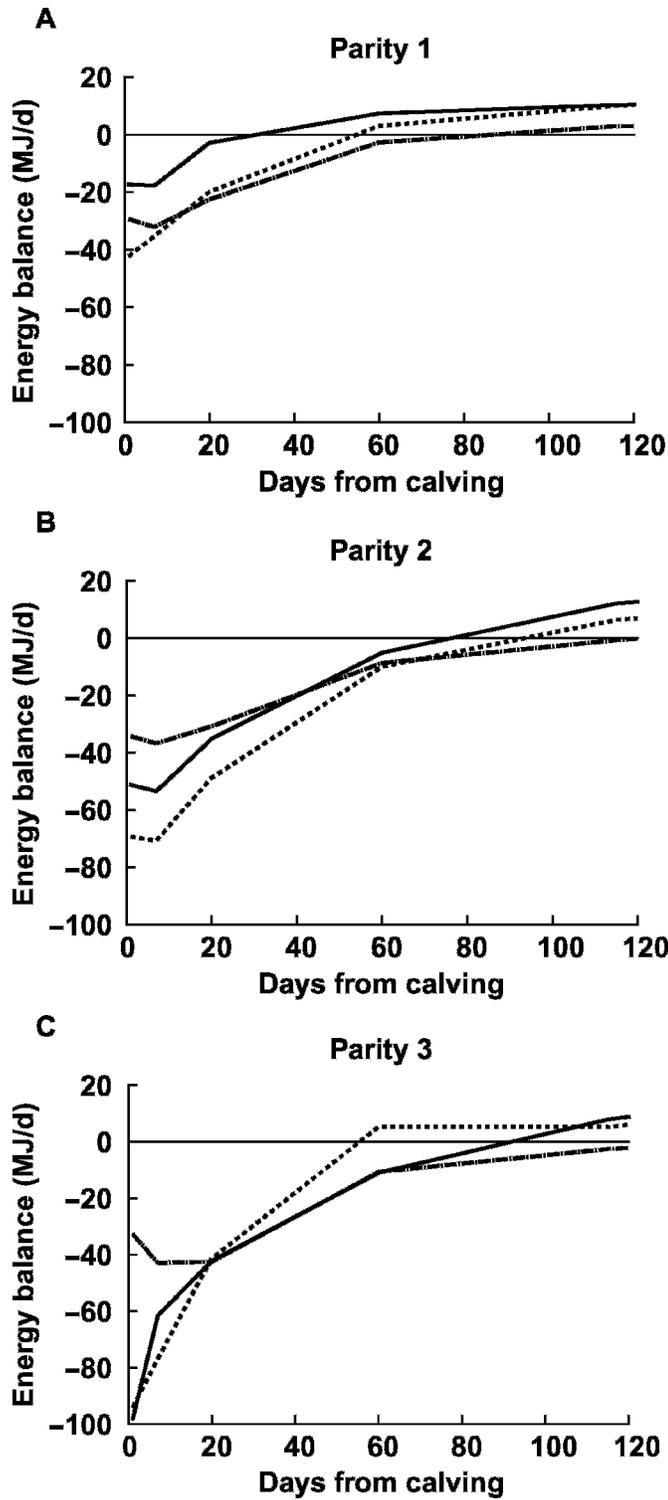
The following possible sources of individual differences in body energy change were examined: fatness-corrected live weight (BWstd), body fatness at calving (CScalv), and genotype. There was no systematic difference in the random cow effect or residual energy balance profile when grouped according to quartiles of BWstd. This was the same within each breed parity combination. There were no systematic differences in random cow effect when grouped according to quartiles of CScalv. The same was true for the residual energy bal-

ance profile. Further, there was no significant relationship between CScalv and body energy change on d 14 of lactation (Figure 4). This was the case within all breed parity combinations.

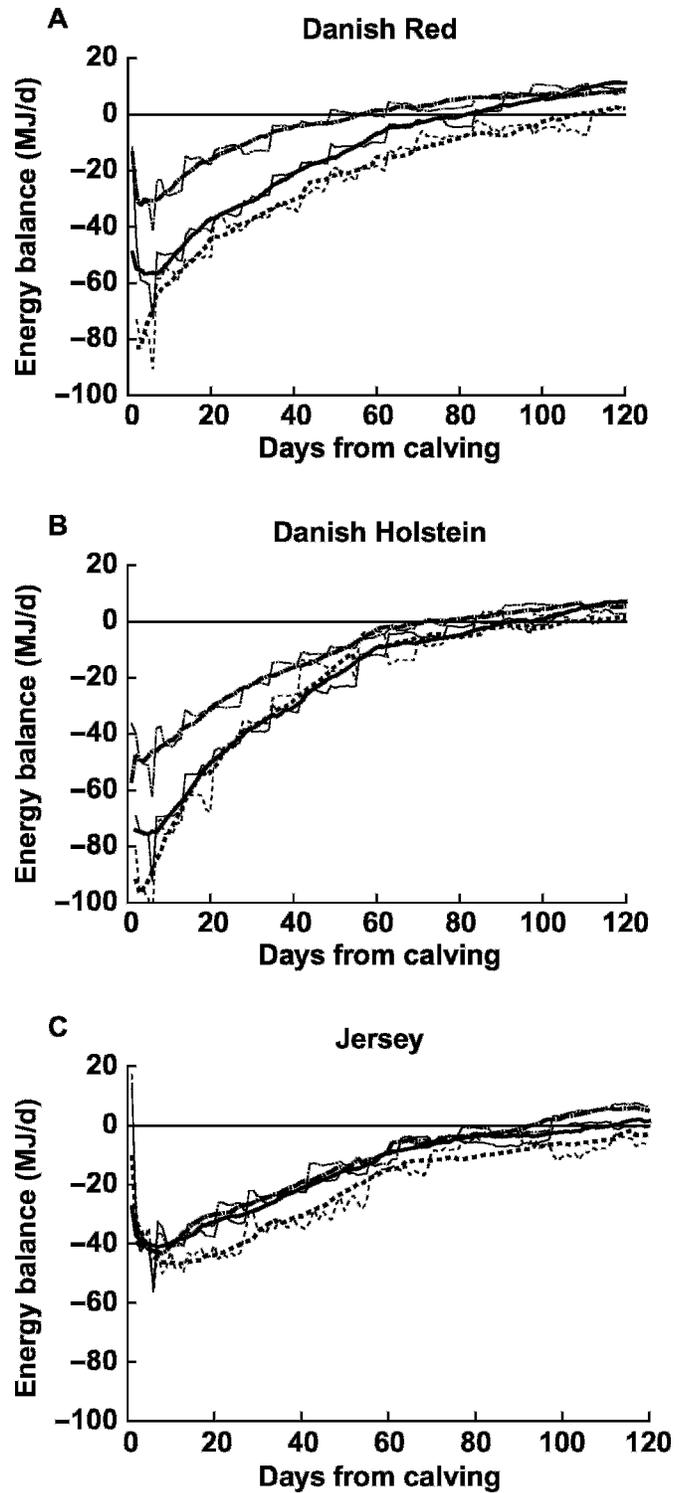
To assess the genetic contribution to the variation in body energy change, pedigree information was included in the statistical analysis. The total phenotypic variation was largest in early and late lactation, decreasing in midlactation (Table 5). The proportion of the total phenotypic variation accounted for by genotype varied through lactation from 4.2 to 13.0% (Table 5). However, this was not significantly different from zero at any time point. Similarly, the genetic variance was not significantly different from zero at any time point, although the estimates (Table 5) were relatively large compared with the average energy balance curves (Figures 1 and 2). Repeatability within lactation, the proportion of total phenotypic variance accounted for by permanent cow and additive genetic effects, accounted for 45 to 65% of the total phenotypic variation, and it was largest in early and late lactation (Table 5). Genetic and phenotypic correlations between energy balances at different days in lactation were generally intermediate to high within part lactations (less than 100 d apart), but low and close to zero between early and late lactation (Table 5), suggesting that body energy change in early and late lactation are genetically independent traits. However, due to large sampling variances these estimates should be interpreted with caution.

### Relationship Between Intake and Size

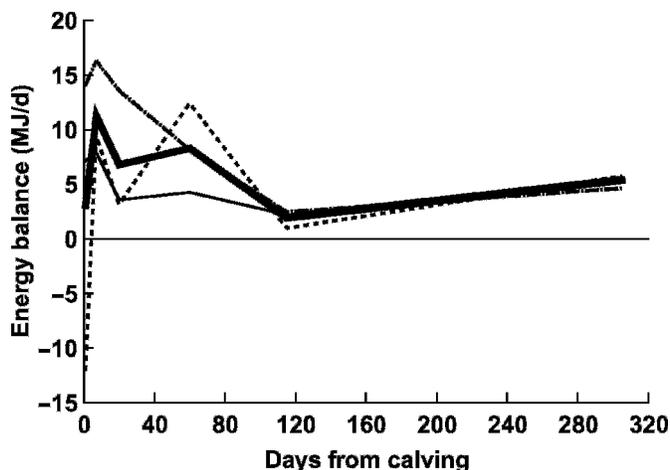
The relationship between intake, expressed as individual deviations within breed and parity, and fatness



**Figure 1.** Linear splines for fixed effects describing energy balance relative to days from calving for Danish Red (solid lines), Danish Holstein (dotted lines), and Jersey (stippled lines) cows in parities 1, 2, and 3 fed a normal energy density TMR and in health status 0.



**Figure 2.** Average predicted (thick lines) and observed (thin lines) energy balance relative to days from calving for Danish Red, Danish Holstein, and Jersey cows in parities 1 (stippled lines), 2 (solid lines), and 3 (dotted lines). Predicted linear spline values include random effects.

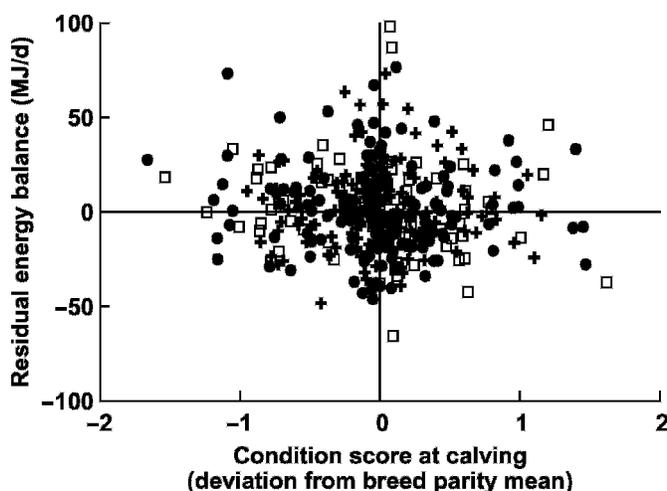


**Figure 3.** The average difference (thick line) between linear splines due to the fixed effects of feeding treatments (NTMR – LTMR). The differences within parity 1 (stippled line), 2 (solid thin line), and 3 (dotted line) are also shown. There was no significant interaction with breed.

corrected live weight (BWstd) on d 14 of lactation is shown in Figure 5. There was no significant relationship between BWstd and intake. This was the case within all breed parity combinations.

## DISCUSSION

In addition to characterizing breed and parity differences in body energy change through lactation, the aim of this paper was to examine the patterns of body energy



**Figure 4.** Individual differences in energy balance at 14 d from calving relative to individual differences in condition score at calving for first (+), second (●), and third (□) parity cows. Individual differences in energy balance are the residuals after fitting fixed spline effects including breed and parity (see Materials and Methods).

change through lactation for evidence of genetically driven mobilization. The notion of genetically driven body energy change has a number of important implications. First, in early lactation, if body mobilization is genetically driven then, by definition, it cannot be eliminated by improved feeding. Second, if some mobilization is genetically predetermined then it may be reasonable to suppose that the cow has adapted to this type of mobilization and that it therefore does not affect health and reproduction (or at least, has a different effect than that of mobilization caused by inadequate feed energy supply). This assumes that genetically predetermined mobilization, which has arisen through natural selection and is thus part of a successful reproductive strategy, should be benign; otherwise it would not have been favored. The extent to which this assumption is violated under artificial selection is ultimately a very important issue for sustainable genetic progress and for managing modern highly selected dairy cows. In this context, it seems plausible that the greater the contribution of body energy change to milk production the more sensitive modern dairy genotypes may be to a decrease in the quality of the nutritional environment. Identifying the component of body energy change that is under genetic control is an important first step in tackling this issue.

Although the finding of significant genetic variation is evidence for genetic control of a given trait, the opposite is not true. Conversely, observing a significant time trend in energy balance when possible environmental causes of this time trend have been eliminated does provide evidence for a genetic basis to these body energy changes. This of course depends upon being able to convincingly eliminate environmental effects. In any given situation, the observed changes in body energy reserves will consist of genetically driven and environmentally driven body energy change in proportions that vary according to the environmental conditions and physiological state. The observed body energy change will be 100% genetically driven only when the environment does not limit energy intake. Because doubts can always be raised about whether a given environment is truly nonconstraining, particularly in ruminants, it is necessary to demonstrate that indications of environmentally driven mobilization are absent to provide evidence of genetically driven mobilization.

Environmentally driven mobilization occurs when there is an inadequate feed energy supply due to a constrained intake. By far the most common constraints on intake in ruminants are due to low digestibility of the feed. Under these circumstances, intake of a given food is related to body size (Mertens, 1987; NRC, 2001). However, in the present experiment during the period of body energy mobilization, there was no significant

**Table 5.** Phenotypic and genetic variance for energy balance [(MJ/d)<sup>2</sup> corrected for fixed effects], repeatability ( $r^2$ ), and heritability ( $h^2$ )<sup>1</sup>

Item	Days from calving (DFC)				
	1	50	100	200	305
Phenotypic variance	575	383	330	358	514
Genetic variance	45 ± 59	23 ± 33	18 ± 26	15 ± 29	67 ± 55
$r^{2*}$	0.65	0.50	0.45	0.48	0.61
$h^2$	0.08 ± 0.10	0.06 ± 0.09	0.06 ± 0.08	0.04 ± 0.08	0.13 ± 0.11
DFC					
1	—	0.92 ± 0.13	0.49 ± 0.68	-0.10 ± 1.15	-0.13 ± 0.73
50	0.64	—	0.78 ± 0.36	0.18 ± 1.13	-0.23 ± 0.83
100	0.38	0.50	—	0.58 ± 0.69	-0.30 ± 0.95
200	0.05	0.24	0.46	—	0.47 ± 0.60
305	-0.04	0.07	0.20	0.49	—

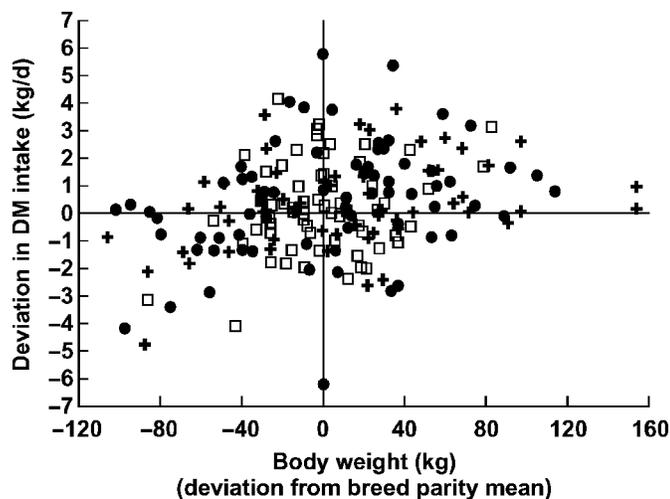
<sup>1</sup>The lower portion of the table presents correlations between energy balance at different days from conception, genetic correlations above the diagonal and phenotypic correlations below the diagonal.

\*Standard errors for repeatabilities were 0.02.

relationship between intake and size (as measured by fatness-corrected live weight) for cows on the more energy dense feed (NTMR; Figure 5). Thus, intake was not constrained by any size-related factor. Two other known constraints on intake, heat stress and competition for feed, are not relevant in the present experiment because the cows were individually housed (in tie stalls), had unlimited access to feed and water, and were housed at a latitude of 55.43N. Standardized management procedures were used, and they remained the same throughout the experiment. Likewise, cows remained on the same feed throughout lactation. Thus, the patterns of body energy change through lactation were not a consequence of management or dietary

changes. Furthermore, it should be noted that the greatest energy mobilization occurred in the first 2 wk of lactation (Figure 2), and during this time intake was on average no more than 80% of maximum intake (in the same lactation). Even if there were some constraint at the time of maximum intake, it is difficult to argue, given that these cows were on the same feed throughout their productive life, that intake was constrained when there was substantial energy mobilization. In this experiment, in early lactation, it seems likely that there was not any significant environmentally driven mobilization. Thus, the highly significant changes with time from calving in energy balance found in this study provide evidence for genetically driven body energy reserve change.

Body fatness at calving is another factor that has previously been shown to affect patterns of body energy change even under constant feeding conditions (post-calving). In experiments where cows have been nutritionally manipulated to have different levels of body fatness at calving, there was a strong negative correlation between body fatness at calving and body energy change in lactation (see Broster and Broster, 1998). Fat cows mobilized more body energy. In contrast, in the present experiment, there was no relationship between condition score at calving and subsequent energy mobilization (Figure 4). The disparity between the present experiment and the experiments reviewed by Broster and Broster (1998) can be attributed to the nature of the differences in body fatness at calving. In the present experiment the variation in BCS at calving was not the result of any prior nutritional manipulation (because all cows stayed on the same feeding treatment throughout their productive life). Other studies that have examined body mobilization relative to the natural variation in body fatness at calving have similarly found no relation-



**Figure 5.** Individual differences in DM intake at 14 d after calving relative to individual differences in live weight (adjusted to constant body fatness) for Danish Red (+), Danish Holstein (●), and Jersey (□) cows feed a normal energy density TMR. Individual differences presented as deviations from breed parity means.

ship between the 2 (Pedron et al., 1993; Koenen et al., 2001). Those experiments that have found a strong relationship between BCS at calving and subsequent mobilization are all experiments in which differences in fatness at calving were the result of a prior nutritional insult (Broster and Broster, 1998), and there is a consequent compensatory mobilization occurring (Friggens et al., 2004).

In the present experiment, the temporal patterns of body energy change were not affected by body fatness at calving. Also, there was no strong evidence of significant environmentally driven mobilization, and environmental conditions were kept as stable as possible through time. Such conditions are favorable with respect to estimating the heritability of the shape of the energy balance curve. However, the heritability of body energy change was found to be low and not significantly different from zero throughout lactation, ranging from 4.2 to 13.0% (Table 5). This means that within breed, only 4 to 13% of the phenotypic variation was associated with differences in genotype.

There are very few estimates of heritability made directly on energy balance (Svendsen et al., 1994; Veerkamp et al., 2000). In addition, heritabilities have been reported for indirect measures of energy balance such as residual feed intake (Veerkamp, 1998) and change in BCS (Berry et al., 2002; Dechow et al., 2002). Unfortunately for the purpose of comparison with the present study, the heritabilities made directly on energy balance come from studies where the definition of energy balance included growth as well as body energy reserve change and was determined on heifers, in which significant growth is expected. Not surprisingly, these studies reported higher heritabilities [0.33 (Veerkamp et al., 2000) and 0.09 to 0.43 (Svendsen et al., 1994)] than values found in the present study where the body energy change was adjusted for growth. The heritability estimates reported for residual feed intakes are also generally higher than values found in the present study (0.19 to 0.69; see Veerkamp, 1998). Although residual feed intake calculations account for growth (as well as maintenance and milk energy requirements), there are still computational difficulties involved. When Veerkamp (1998) adjusted the heritability of residual feed intake using the genetic variance-covariance matrix for the component traits, the heritability was reduced from 0.34 to 0.05. This suggests that when the environment influences performance (e.g., if intake is constrained and thus is related to size), these correlations can inflate the heritability estimate. When these correlations were accounted for, the heritability estimate was similar to that found in the present study where such correlations were minimized by designing the experiment to be in a stable and nonlimiting environment. The heritability

in the present study was also in agreement with those studies that have reported heritabilities for BCS change, a more direct measure of body energy change (Berry et al., 2002; Dechow et al., 2002). An alternative explanation for the low heritability is that the number of cows was limited for genetic analysis and there is a relatively high degree of random error associated with this type of rate data. However, this does not seem a sufficient argument on its own given the smoothing applied to the input data variables and the repeatability values reported in Table 5.

The low heritability of body energy change can seem, at first sight, contradictory to the finding that the patterns of body energy change in this study are largely genetically driven. However, the extent to which a particular trait (e.g., body energy change) is heritable is not a measure of whether that trait has a genetic basis but is instead a measure of how much genetic variation there is in that trait relative to the phenotypic variance. An example of this is the length of pregnancy (mean 280 d), which is clearly genetically determined yet within breed is highly repeatable [i.e., has very low variability (SD 6.2 d; Jamrozik et al., 2005)]. It has generally been found that traits that make a major direct contribution to fitness have lower heritability than other [e.g., morphological traits (Falconer and Mackay, 1996)]. In this context, it could be argued that the low heritability of energy balance indicates that the rate of change in body energy reserves (i.e., mobilization and accretion) provides a better description of the fitness value of body reserves than measures of the size of these reserves such as cumulative energy balance (Coffey et al., 2003), total body energy content (Banos et al., 2005a), and BCS, which has a much higher heritability (Pryce et al., 2001; Dechow et al., 2002). Two recent studies (Pryce and Harris, 2006; Beerda et al., 2007) support this hypothesis in that the same characteristic shape of the body energy change profiles was found across a wide range of conditions and breeds despite significant differences in BCS, suggesting that the profile of body energy change has a common underlying form. Although this common underlying form is an obvious feature of the body energy change curves in this study, there were significant differences between breeds in the curve parameters. Similarly, Coffey et al. (2003) reported small but significant differences between sires in the shape of the cumulative energy balance curve. This suggests that, despite the low heritabilities reported for body energy change, selection can affect body energy change profiles.

As can be seen from Figure 2, the spline functions used to model the temporal patterns of body energy change fitted the observed data well. Because different periods of lactation are modeled independently by

splines, they did not generate spurious end effects that are frequently an undesired property of those models that use a number of correlated coefficients that each affect all time-points in lactation (Banos et al., 2005b). Further, when using splines to model body energy change we found very low phenotypic and genetic correlations between early and late lactation (Table 5). This suggests that the genetic control of body energy mobilization in early lactation is different from that of body energy accretion in later lactation. It has been postulated that body reserve usage in early lactation is an adaptation in support of the current calf, whereas subsequent body reserve accumulation is an adaptation in support of the future calf (Friggens, 2003; Friggens et al., 2004). The current findings are in accordance with this.

The disadvantage of using splines is that they are dependent on the number and placement of knots. We chose to use 6 knots for the fixed effects based on consideration of the biological properties of energy balance curves (Friggens et al., 2004) and then evaluated the consequences of varying the position of the knots in terms of prediction error. No evidence was found for an effect of breed and parity on the time-points of the knots. This is in agreement with other studies (Dillon et al., 2003a; Friggens and Badsberg, 2007). There were, however, significant breed and parity effects on the temporal patterns of body energy change. Breed and parity effects have been reported by others (Dillon et al., 2003a; Coffey et al., 2004). In first parity, there was a clear difference between the dual-purpose Danish Red and the 2 dairy-only breeds, with these 2 breeds having a more negative energy balance in early lactation (Figure 1). There was a reranking of breeds in parity 2 such that Jersey had the smallest and Danish Holstein had the greatest negative energy balance in early lactation. This was because there was relatively little effect of parity on the energy balance profiles of Jersey cows, especially between first and second parities. This breed-parity interaction suggests that there could be different consequences for the effects of early life selection for lactation performance on later performance in different breeds (see also Dillon et al., 2003b).

## CONCLUSIONS

There were systematic patterns of body energy change through lactation in cows that were kept under stable and sufficient nutritional conditions. These could not be accounted for by environmental factors such as constrained intake or differences in BCS at calving. Thus, these patterns appear to be genetically driven. Further, there were significant differences between

breeds and parities in their patterns of body energy change, especially in early lactation.

## ACKNOWLEDGMENTS

We gratefully acknowledge the valuable contribution of Hanne Marie Nielsen, Peter Trier, Connie Middehede, Gitte Munch, and the farm staff at Ammitsbøl Skovgård. This study was part of the MEMO project funded by the Danish Ministry of Food, Agriculture and Fisheries and the Danish Cattle Industry via Finance Committee Cattle.

## REFERENCES

- ARC. 1980. The nutrient requirements of ruminant livestock. 1st ed. CAB, Farnham Common, UK.
- Banos, G., S. Brotherstone, and M. P. Coffey. 2005a. Genetic profiles of total body energy content of Holstein cows in the first three lactations. *J. Dairy Sci.* 88:2616–2623.
- Banos, G., M. P. Coffey, and S. Brotherstone. 2005b. Modeling daily energy balance of dairy cows in the first three lactations. *J. Dairy Sci.* 88:2226–2237.
- Bareille, N., F. Beaudeau, S. Billon, A. Robert, and P. Faverdin. 2003. Effects of health disorders on feed intake and milk production in dairy cows. *Livest. Prod. Sci.* 83:53–62.
- Beerda, B., W. Ouweltjes, L. B. J. Šebek, J. J. Windig, and R. F. Veerkamp. 2007. Effects of genotype by environment interactions on milk yield, energy balance, and protein balance. *J. Dairy Sci.* 90:219–228.
- Berry, D. P., F. Buckley, P. Dillon, R. D. Evans, M. Rath, and R. F. Veerkamp. 2002. Genetic parameters for level and change of body condition score and body weight in dairy cows. *J. Dairy Sci.* 85:2030–2039.
- Broster, W. H., and V. J. Broster. 1998. Body score of dairy cows. *J. Dairy Res.* 65:155–173.
- Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference. 2nd ed. Springer Verlag, New York, NY.
- Coffey, M. P., G. C. Emmans, and S. Brotherstone. 2001. Genetic evaluation of dairy bulls for energy balance traits using random regression. *Anim. Sci.* 73:29–40.
- Coffey, M. P., G. Simm, W. G. Hill, and S. Brotherstone. 2003. Genetic evaluations of dairy bulls for daughter energy balance profiles using linear type scores and body condition score analysed using random regression. *J. Dairy Sci.* 86:2205–2212.
- Coffey, M. P., G. Simm, J. D. Oldham, W. G. Hill, and S. Brotherstone. 2004. Genotype and diet effects on energy balance in the first three lactations of dairy cows. *J. Dairy Sci.* 87:4318–4326.
- Dechow, C. D., G. W. Rogers, and J. S. Clay. 2002. Heritability and correlations among body condition score loss, body condition score, production and reproductive performance. *J. Dairy Sci.* 85:3062–3070.
- Dillon, P., F. Buckley, P. O'Connor, D. Hegarty, and M. Rath. 2003a. A comparison of different dairy cow breeds on a seasonal grass-based system of milk production. 1. Milk production, live weight, body condition score and DM intake. *Livest. Prod. Sci.* 83:21–34.
- Dillon, P., F. Snijders, F. Buckley, B. Harris, P. O'Connor, and J. F. Mee. 2003b. A comparison of different dairy cow breeds on a seasonal grass-based system of milk production. 2. Reproduction and survival. *Livest. Prod. Sci.* 83:35–42.
- Ellis, J. L., F. Qiao, and J. P. Cant. 2006. Evaluation of net energy expenditures of dairy cows according to body weight changes over a full lactation. *J. Dairy Sci.* 89:1546–1557.
- Emmans, G. C. 1994. Effective energy: A concept of energy utilization applied across species. *Br. J. Nutr.* 71:801–821.
- Emmans, G. C. 1997. A method to predict the food intake of domestic animals from birth to maturity as a function of time. *J. Theor. Biol.* 186:189–199.

- Falconer, D. D., and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. 4th ed. Longman Limited, Harlow, UK.
- Fourichon, C., H. Seegers, N. Bareille, and F. Beaudeau. 1999. Effects of disease on milk production in the dairy cow: A review. *Prev. Vet. Med.* 41:1–35.
- Friggens, N. C. 2003. Body lipid reserves and the reproductive cycle: Towards a better understanding. *Livest. Prod. Sci.* 83:219–226.
- Friggens, N. C., and J. H. Badsberg. 2007. The effect of breed and parity on lactation curves of body condition estimated using a non-linear function. *Animal* 1:565–574.
- Friggens, N. C., G. C. Emmans, and R. F. Veerkamp. 1999. On the use of simple ratios between lactation curve coefficients to describe parity effects on milk production. *Livest. Prod. Sci.* 62:1–13.
- Friggens, N. C., K. L. Ingvarstsen, and G. C. Emmans. 2004. Prediction of body lipid change in pregnancy and lactation. *J. Dairy Sci.* 87:988–1000.
- Hansen, L. B. 2000. Consequences of selection for milk yield from a geneticist's viewpoint. *J. Dairy Sci.* 83:1145–1151.
- Ingvarstsen, K. L., R. J. Dewhurst, and N. C. Friggens. 2003. On the relationship between lactational performance and health: Is it yield or metabolic imbalance that cause production diseases in dairy cattle? A position paper. *Livest. Prod. Sci.* 83:277–308.
- Jamrozik, J., J. Fatehi, G. J. Kistemaker, and L. R. Schaeffer. 2005. Estimates of genetic parameters for Canadian Holstein female reproduction traits. *J. Dairy Sci.* 88:2199–2208.
- Kirkland, R. M., T. Yan, R. E. Agnew, and F. J. Gordon. 2002. Efficiency of use of body tissue energy for milk production in lactating dairy cows. *Livest. Prod. Sci.* 73:131–138.
- Koenen, E. P. C., R. F. Veerkamp, P. Dobbelaar, and G. De Jong. 2001. Genetic analysis of body condition score of lactating Dutch Holstein and Red-and-White heifers. *J. Dairy Sci.* 84:1265–1270.
- Kristensen, T. 1986. Method for estimation of body condition of dairy cows. Pages 59–75 in Rep. no. 615. *Natl. Inst. Anim. Sci., Fredrik-sberg, Denmark.*
- Lowman, B. G., N. Scott, and S. Somerville. 1976. Condition scoring of cattle. Pages 1–29 in *East of Scotland College of Agriculture, Edinburgh, UK.*
- Madsen, P., and J. Jensen. 2006. A user's guide to DMU. A package for analyzing multivariate mixed models. Danish Institute of Agricultural Sciences. <http://dmu.agrsci.dk> Accessed Sep. 14, 2006.
- Mertens, D. R. 1987. Predicting intake and digestibility using mathematical models of ruminal function. *J. Anim. Sci.* 64:1548–1558.
- Misztal, I. 2006. Properties of random regression models using linear splines. *J. Anim. Breed. Genet.* 123:74–80.
- Nielsen, H. M., N. C. Friggens, P. L. Løvendahl, J. Jensen, and K. L. Ingvarstsen. 2003. The influence of breed, parity and stage of lactation on lactational performance and the relationship between body fatness and live weight. *Livest. Prod. Sci.* 79:119–133.
- NRC. 2001. *Nutrient Requirements of Dairy Cattle*. 7th ed. *Natl. Acad. Press, Washington, DC.*
- Pedron, O., F. Cheli, E. Senatore, D. Baroli, and R. Rizzi. 1993. Effect of body condition score at calving on performance, some blood parameters, and milk fat composition in dairy cows. *J. Dairy Sci.* 76:2528–2535.
- Pryce, J. E., M. P. Coffey, and G. Simm. 2001. The relationship between body condition score and reproductive performance. *J. Dairy Sci.* 84:1508–1515.
- Pryce, J. E., and B. L. Harris. 2006. Genetics of body condition score in New Zealand dairy cows. *J. Dairy Sci.* 89:4424–4432.
- Pryce, J. E., B. L. Nielsen, R. F. Veerkamp, and G. Simm. 1999. Genotype and feeding system effects and interactions for health and fertility traits in dairy cattle. *Livest. Prod. Sci.* 57:193–202.
- Royal, M. D., A. O. Darwash, A. P. F. Flint, R. Webb, J. A. Woolliams, and G. E. Lamming. 2000. Declining fertility in dairy cattle: Changes in traditional and endocrine parameters of fertility. *Anim. Sci.* 70:487–501.
- SAS Institute. 2001. *SAS version 8.e.* SAS Inst. Inc., Cary, NC.
- Svendsen, M., P. Skipenes, and I. L. Mao. 1994. Genetic correlations in the feed conversion complex of primiparous cows at a recommended and a reduced plane of nutrition. *J. Anim. Sci.* 72:1441–1449.
- Taylor, S. C. S. 1980. Genetic size-scaling rules in animal growth. *Anim. Prod.* 30:161–165.
- Veerkamp, R. F. 1998. Selection for economic efficiency of dairy cattle using information on live weight and feed intake: A review. *J. Dairy Sci.* 81:1109–1119.
- Veerkamp, R. F., J. K. Oldenbroek, H. J. Van der Gaast, and J. H. J. Van der Werf. 2000. Genetic correlation between days until start of luteal activity and milk yield, energy balance, and live weights. *J. Dairy Sci.* 83:577–583.
- Wright, I. A., and A. J. F. Russel. 1984a. Estimation in vivo of the chemical composition of the bodies of mature cows. *Anim. Prod.* 38:33–44.
- Wright, I. A., and A. J. F. Russel. 1984b. Partition of fat, body composition and body condition score in mature cows. *Anim. Prod.* 38:23–32.