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Genetic Profile of Body Energy and Blood Metabolic Traits Across Lactation in Primiparous Holstein Cows

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ABSTRACT

The objectives of this study were to characterize the changes of body condition score (BCS), energy content (EC), cumulative effective energy balance (CEEB), and blood serum concentrations of glucose, β -hydroxybutyrate (BHBA), and nonesterified fatty acids (NEFA) across the first lactation of Holstein cows, and to estimate variance components for these traits. Four hundred ninety-seven cows kept on a commercial farm in Greece that had calved during 2005 and 2006 were used. Body condition score, estimated live weight, and blood metabolic traits were recorded weekly for the first 3 mo of lactation and monthly thereafter until the end of lactation. Body condition score and estimated live weight records were used to calculate EC and CEEB throughout the first lactation. Estimates of fixed curves and genetic parameters for each trait, by week of lactation, were obtained with the use of random regression models. The estimated fixed curves were indicative of changes in the metabolic process and energy balance of the cows. Significant genetic variance existed in all studied traits, and was particularly high during the first weeks of lactation (except for the genetic variance of CEEB, which was not significant at the beginning of lactation). Significant heritability estimates for BCS ranged from 0.34 to 0.79, for EC from 0.19 to 0.87, for CEEB from 0.58 to 0.93, for serum glucose from 0.12 to 0.39, for BHBA from 0.08 to 0.40, and for NEFA from 0.08 to 0.35. Genetic correlations between different weeks of lactation were near unity for adjacent weeks and decreased for weeks further apart, becoming practically zero for measurements taken more than 3 to 4 mo apart, especially with regard to blood metabolic traits. Significant heritability estimates were also obtained for BCS recorded before first calving. Results suggest that genetic evaluation and selection of dairy cows for early-lactation body energy and blood metabolic traits is possible.

Key words: body energy, dairy cow, energy balance, genetic profile

INTRODUCTION

Genetic selection for increased milk production has led to an increase in the energy requirements of the dairy cow, especially at the beginning of lactation. This increase has not been accompanied by a proportionate increase in DMI (van Arendonk et al., 1991). Furthermore, genetic selection for greater milk production as well as improved dairy form or angularity may have favored cows with greater propensity for intense lipid mobilization (Dechow et al., 2003). Hence, the modern Holstein cow usually experiences an extended period of negative energy balance after calving. The magnitude and duration of this phenomenon has been proven, in many studies, to be related to health and fertility problems and is now considered one of the main problems that the dairy industry has to solve (Collard et al., 2000; de Vries and Veerkamp, 2000). Most previous studies focused on establishing phenotypic or environmental relationships between body energy and functional traits. However, there is evidence of substantial genetic variation in the way dairy cows mobilize their energy reserves (Coffey et al., 2003; Banos et al., 2005). Substantial genetic correlation between energy balance traits and reproductive performance has also been reported (Veerkamp et al., 2000). Thus, there is a growing interest to investigate the possibility to address the negative energy balance problem through genetic selection.

The direct calculation of cow energy balance from estimates of feed intake and milk yield is quite difficult under field conditions, usually because feed intake records at the individual cow level are mostly unavailable. Thus, the use of various energy balance indicator traits has been proposed for the study of negative energy balance and its effect on health and fertility.

Evaluation of body condition is a subjective yet reliable and widely accepted method of the assessment of a cow's fat tissue and body mass reserves (Edmonson et al., 1989; Fox et al., 1999) and, therefore, BCS can

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be viewed as an indicator trait to energy balance. In addition, total body energy content (**EC**) and cumulative effective energy balance (**CEEB**), calculated from BCS and live weight records, have been proposed for the study of energy balance (Banos et al., 2006). Furthermore, various metabolic traits have been associated with energy balance. Blood serum concentrations of glucose, BHBA, and NEFA are examples of such traits (Reist et al., 2002; Clark et al., 2005).

Before genetic selection for any of the above mentioned energy balance-related traits becomes feasible, their genetic variation and heritability must be studied. Body condition score has already been genetically analyzed in several studies (e.g., Coffey et al., 2001; Berry et al., 2003; Banos et al., 2005). Banos et al. (2006) also reported genetic parameters for EC and CEEB derived from research farm data. However, to the best of our knowledge, the genetic profile of blood serum glucose, BHBA, and NEFA throughout a lactation period, or even for a part of this period, has not been reported.

The objective of this study was to obtain a deeper understanding of the genetic variation in energy balance and metabolic regulation during lactation by a) characterizing the systematic change of BCS, EC, CEEB, and blood serum glucose, BHBA, and NEFA concentrations just before first calving and throughout the first lactation of cows kept on a commercial farm setting and b) estimating genetic parameters for these traits.

MATERIALS AND METHODS

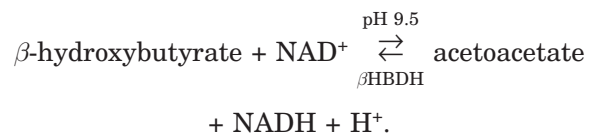
Data

Data were collected on a large commercial dairy farm located in northern Greece (41°2' N, 25°15' E, altitude 20 m). The cows were housed in 4 free-stall barns and fed, twice daily, a total mixed ration to meet their energy and protein requirements. Ration formulation was based on US National Research Council recommendations (NRC, 2001). Four hundred ninety-seven primiparous Holstein cows that calved between January 2005 and July 2006 were considered in this study. Cows were daughters of 210 sires. The average number of progeny per sire was 2.4 with a standard deviation of 2.7 and a range from 1 to 19. All cows had known pedigree information. Considering all pedigree available and tracing it for 3 generations added 2,809 ancestor animals to the data set.

Cows calved at an average age of 27.6 ± 2.6 mo. These animals were either born on the farm or had been imported as pregnant heifers from 3 other European countries. The latter is a common practice among many commercial dairy farms in Greece.

Body condition score of these cows was assessed after the morning milking, by the same trained veterinarian, weekly from calving to wk 13 of lactation and thereafter monthly until the end of a 305-d lactation. A 5-point scale (1 = emaciated, 5 = obese, scored in 0.25-point intervals) and the method described by Ferguson et al. (1994) were used. At the same time, the cows' live weight was estimated using a heart girth tape.

Blood was drawn from the coccygeal vein or artery in a subset of 365 randomly selected cows. Blood samples were left to clot at room temperature for approximately 30 min and then centrifuged at $2,000 \times g$. The obtained serum samples were stored at -20°C until analyzed for glucose, BHBA, and NEFA. Serum glucose and NEFA were assayed colorimetrically using commercial kits (Glucose GOD-PAP method, P. Zafropoulos S.A., Attiki, Greece, and Wako NEFA C kit, Wako Chemicals GmbH, Neuss, Germany, respectively). The serum concentration of BHBA was assayed with the use of an enzymatic kinetic method based on the oxidation of β -hydroxybutyrate to acetoacetate by β -hydroxybutyrate dehydrogenase (Bruss, 1997):



The intraassay coefficient of variation was 1 to 3% for glucose and 1.5 to 3% for NEFA whereas the interassay coefficient was 3 to 5% for both glucose and NEFA. For BHBA, the intra- and interassay coefficients were 2 to 4% and 4 to 8%, respectively.

The final data set consisted of 8,094 BCS, 8,087 estimated live weight, and 6,015 blood serum glucose, BHBA, and NEFA concentration records. Some cows did not complete the 305-d lactation because they were involuntarily culled. However, all animals in the data set had at least one BCS and estimated live weight record. Body condition score and estimated live weight records were used for the calculation of body EC and CEEB according to the procedure described in detail by Banos et al. (2006). Briefly, empty body weight and total lipid and protein weights were predicted using the method of the National Research Council (NRC, 2001) and were then combined to calculate EC. The latter was an estimate of the total energy in a cow's body at any given time of lactation. Changes in predicted lipid and protein weights from one week of lactation to the next were converted to effective energy as described by Banos et al. (2006), yielding estimates of CEEB. The latter represented body energy changes as accumulated throughout lactation.

Table 1. Descriptive statistics of BCS, estimated live weight (ELW), energy content (EC), cumulative effective energy balance (CEEB), and blood serum concentration of glucose, BHBA, and NEFA measured throughout first lactation

Item	Records, n	Cows, n	Mean	SD	Minimum	Maximum
BCS (1–5)	8,094	497	2.47	0.44	1.25	5.00
ELW (kg)	8,087	497	549.6	66.5	350.0	803.0
EC (MJ)	8,087	497	4,465	947	2,329	9,928
CEEB (MJ)	8,087	497	–424	974	–3,690	5,984
Glucose (mg/dL)	6,015	365	74.3	19.7	12.0	190.0
BHBA (mmol/L)	6,015	365	0.79	0.28	0.19	4.42
NEFA (mmol/L)	6,015	365	0.32	0.30	0.02	4.00

Single measurements of BCS, estimated live weight, EC, and serum glucose, BHBA, and NEFA concentrations taken approximately 2 mo before first calving were also available for a subgroup of the studied animals.

Statistical Analysis

Repeated cow BCS, EC, CEEB, glucose, BHBA, and NEFA records taken throughout first lactation were analyzed with the following random regression model; each trait was analyzed separately:

$$Y_{ijkmn} = YS_i + C_j + a_1 \cdot \text{age} + \sum_{n=0}^3 b_n P_n W_m + \sum_{n=0}^3 c_{kn} P_n W_m + \sum_{n=0}^1 d_{kn} P_n W_m + e_{ijkmn},$$

where Y_{ijkmn} = record of cow k in week of lactation m , YS_i = fixed effect of year-season of calving i (4 levels), C_j = fixed effect of country of origin j (4 levels), a_1 = linear regression coefficients on age at calving (age), W_m = week of lactation m (44 levels), b_n = fixed regression coefficient on week of lactation, c_{kn} = random regression coefficient on week of lactation associated with the genetic effect of cow k including the full animal pedigree relationship matrix, d_{kn} = random regression coefficient on week of lactation associated with the permanent environment effect of cow k , $P_n = n$ th orthogonal polynomial of week m ($n + 1 =$ order of polynomial), and e_{ijkmn} = random residual term (4 classes as described below).

In the model the fixed regression coefficient was associated with an overall, average lactation curve for each trait, whereas the random regression was associated with each individual cow's deviation from the overall curve. The full model was applied to the analysis of BCS, EC, and CEEB. For the analysis of blood serum glucose, BHBA, and NEFA concentration, the effects of country of origin and age at calving were not included because preliminary analyses showed that they were not significantly different from zero ($P > 0.05$).

Fourth-order orthogonal polynomial was chosen to model the genetic effect following preliminary analyses of different (lower) orders and comparisons between models using the log-likelihood, until the latter stopped changing significantly ($P > 0.05$) with increasing polynomial order. This was true for all traits except BHBA, where third-order was the maximum significant.

Permanent environment was modeled with second-order orthogonal polynomial. Efforts to increase the order were unsuccessful as they led to convergence problems. This may be a function of the data size, although the number of observations is not deemed too small for a controlled study. Another explanation can be that higher order regression might have actually over fitted first-lactation permanent environment effects. For the analysis of CEEB, glucose, and NEFA, a first-order permanent environment polynomial was the highest significant.

Depending on lactation stage, 4 measurement error classes were defined as follows: wk 1 to 4, 5 to 9, 10 to 21, and >21. Different residual variances were estimated for each measurement error class, while covariances between classes were zero.

The REML estimates of (co)variance components from the model were used to calculate heritabilities for each trait and week of lactation as well as genetic correlations between different weeks of lactation. All analyses were performed with the use of the ASREML software package (Gilmour et al., 2002). Single records, taken on heifers before calving, were analyzed with a similar model that included the effect of days to calving but excluded the fixed and random regressions on week of lactation. Product-moment correlations among estimated animal breeding values for all studied traits were calculated to derive estimates of the relationship between these traits.

RESULTS

Descriptive statistics of the studied traits are shown in Table 1 and Table 2. Estimated fixed curves for each trait by week of lactation are shown in Figure 1 (BCS,

Table 2. Descriptive statistics, genetic variance, and heritability (h^2) of BCS, estimated live weight (ELW), energy content (EC), and blood serum concentrations of glucose, BHBA, and NEFA measured on pregnant heifers

Item	Heifers, n	Mean	SD	Minimum	Maximum	Genetic variance	h^2	<i>P</i> -value
BCS (1–5)	192	3.24	0.47	2.25	5.00	0.19 ± 0.08	0.88 ± 0.37	0.02
ELW (kg)	143	606.0	66.8	463.0	772.0			
EC (MJ)	143	5,559	951	3,752	7,720	379,300 ± 315,400	0.50 ± 0.41	0.22
Glucose (mg/dL)	174	70.6	19.8	20.0	122.0	123.9 ± 72.8	0.37 ± 0.21	0.08
BHBA (mmol/L)	175	0.55	0.19	0.24	1.57	0.010 ± 0.007	0.25 ± 0.18	0.16
NEFA (mmol/L)	142	0.49	0.41	0.05	2.50	0.018 ± 0.012	0.29 ± 0.20	0.15

EC, and CEEB) and Figure 2 (blood serum glucose, BHBA, and NEFA concentrations). These curves illustrate the average value for each trait at specific times of lactation as well as changes throughout lactation, adjusted for all other effects included in the model.

Estimated genetic variances for BCS, EC, CEEB, and blood concentrations of glucose, BHBA and NEFA by week of lactation are illustrated in Figure 3 and Figure 4, respectively. Furthermore, heritability estimates for all traits by week of lactation are presented in Figure 5.

Genetic variance for BCS (Figure 3) was greater at the beginning and the end of lactation. Standard errors indicated that all genetic variances were significantly different from zero ($P < 0.05$). Weekly heritabilities derived from these estimates ranged from 0.34 (±0.19) to 0.79 (±0.20) (Figure 5). Genetic variance trends were similar for EC (Figure 3). All estimates were significantly different from zero ($P < 0.05$) except for wk 6 to 10 ($P = 0.08$ to 0.12), which were associated with the

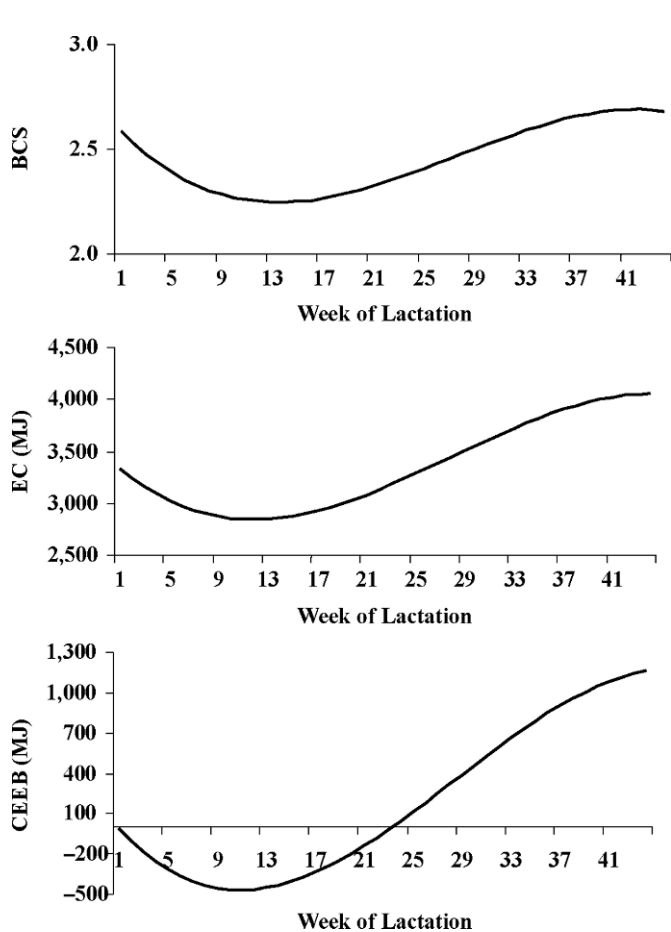


Figure 1. Estimated fixed curves of BCS (SE = 0.009 to 0.034), energy content (EC; SE = 19.3 to 71.7), and cumulative effective energy balance (CEEb; SE = 24.7 to 96.3) by week of lactation.

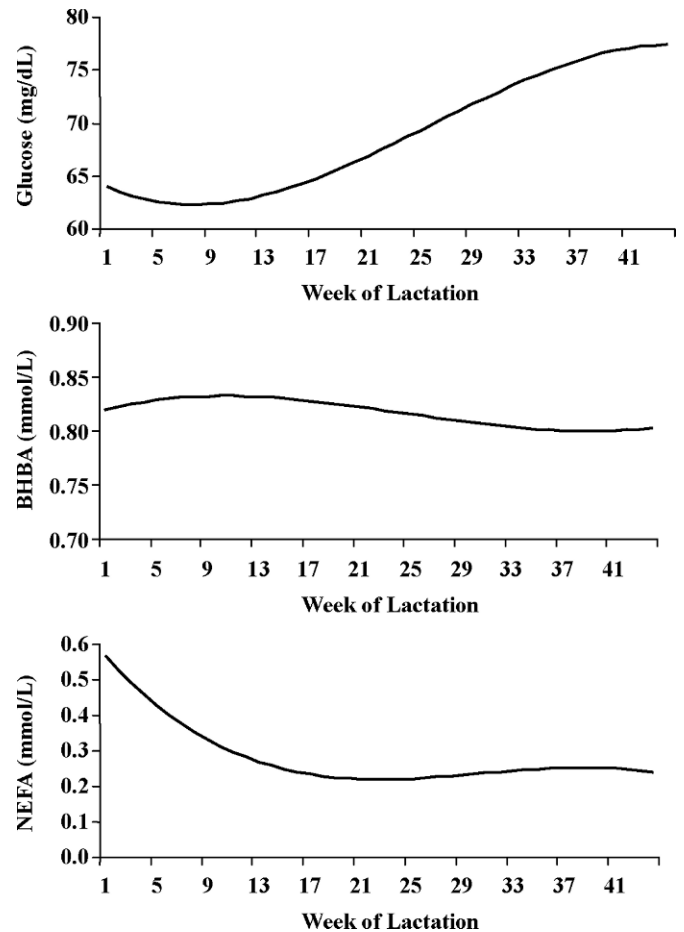


Figure 2. Estimated fixed curves of blood serum concentrations of glucose (SE = 0.63 to 1.80), BHBA (SE = 0.008 to 0.023), and NEFA (SE = 0.008 to 0.023) by week of lactation.

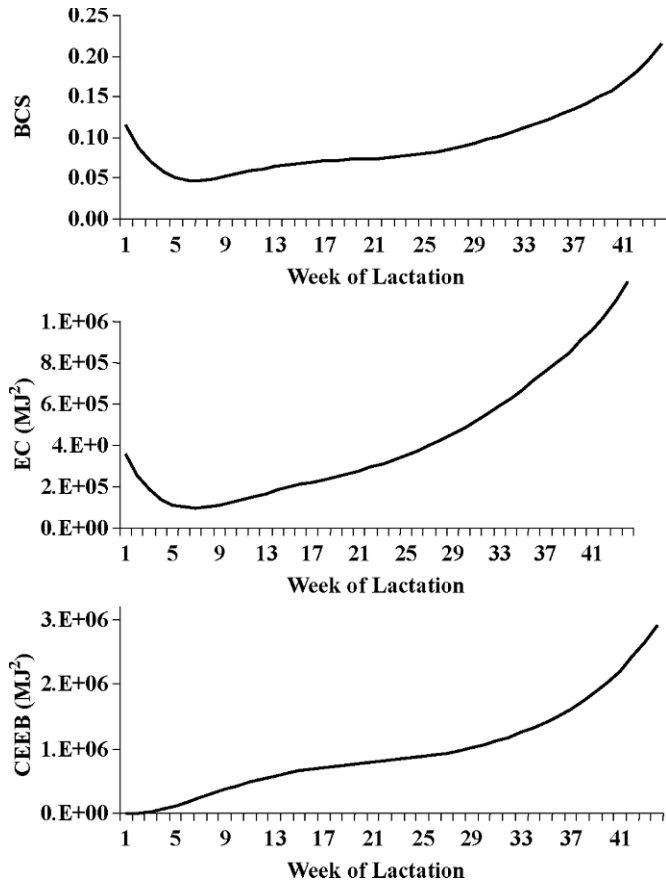


Figure 3. Estimated genetic variance of BCS (SE = 0.023 to 0.038), energy content (EC; SE = 58,872 to 157,216 MJ²), and cumulative effective energy balance (CEEb; SE = 67,683 to 122,124 MJ²) by week of lactation.

lowest levels of EC (Figure 1). Heritability estimates for the periods when genetic variance was significantly different from zero ranged from 0.19 (± 0.11) on wk 4 of lactation to 0.87 (± 0.19) at the end of lactation (Figure 5). Genetic variance of CEEb (Figure 3) was not significantly different from zero ($P > 0.05$) during the first 6 wk of lactation, which is expected given the definition of the trait. Thereafter, genetic variance estimates steadily increased and were always significantly different from zero ($P < 0.05$). Corresponding heritability estimates ranged from 0.58 (± 0.26) on wk 7 of lactation to 0.93 (± 0.08) at the end of lactation (Figure 5).

Estimated genetic variance of serum glucose levels was greater at the beginning and the end of lactation (Figure 4). All estimates were significantly different from zero ($P < 0.05$) while heritability ranged from 0.12 (± 0.04) on wk 38 to 0.39 (± 0.11) at the end of lactation (Figure 5). In this particular trait, there was a sharp increase of the genetic variance estimate toward the very end of the trajectory, which may be due to fitting a

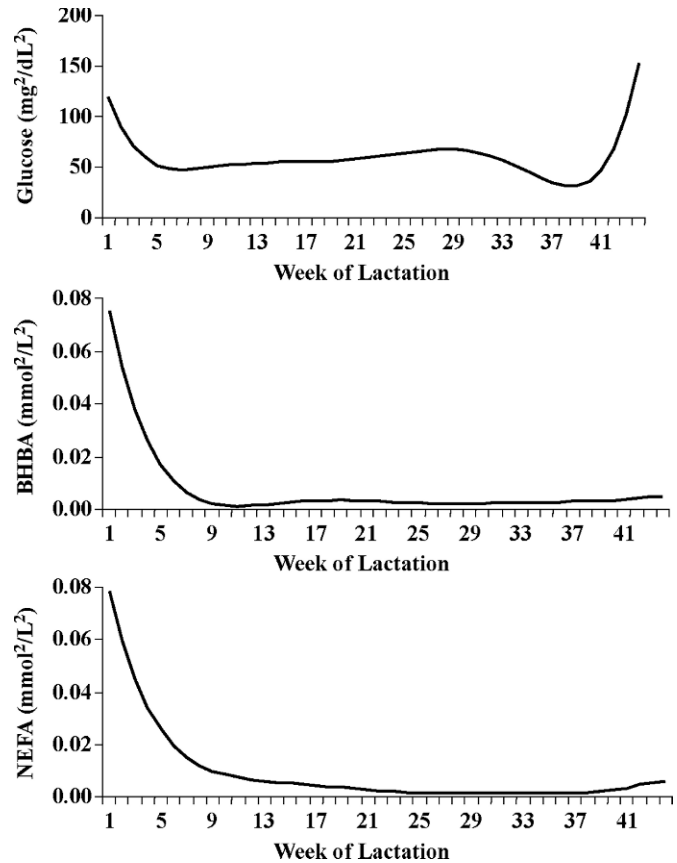


Figure 4. Estimated genetic variance of blood serum concentrations of glucose (SE = 10.05 to 39.69 mg²/dL²), BHBA (SE = 0.002 to 0.007 mmol²/L²), and NEFA (SE = 0.001 to 0.004 mmol²/L²) by week of lactation.

high-order polynomial. Estimates at the end of lactation were associated with relatively greater standard errors (0.003–0.004) compared with other lactation stages (0.001–0.002) but were still significantly different from zero ($P < 0.05$). Despite this observation, fitting a fourth-order polynomial was justified by the significant ($P < 0.05$) increase in the log-likelihood.

Genetic variance estimates for BHBA serum concentration were significantly greater than zero ($P < 0.05$) during the first 7 wk of lactation (Figure 4). Heritability estimates for this period ranged from 0.08 (± 0.04) to 0.40 (± 0.06) (Figure 5).

Estimated genetic variance of serum concentration of NEFA was significantly different from zero ($P < 0.05$) until wk 24 of lactation (Figure 4). Heritability estimates for this period ranged from 0.08 (± 0.04) to 0.35 (± 0.05) in the beginning of lactation (Figure 5).

Genetic correlations of the above traits in different weeks of lactation were near unity for adjacent weeks and decreased for weeks further apart. Compared with the onset of lactation, genetic correlations decreased

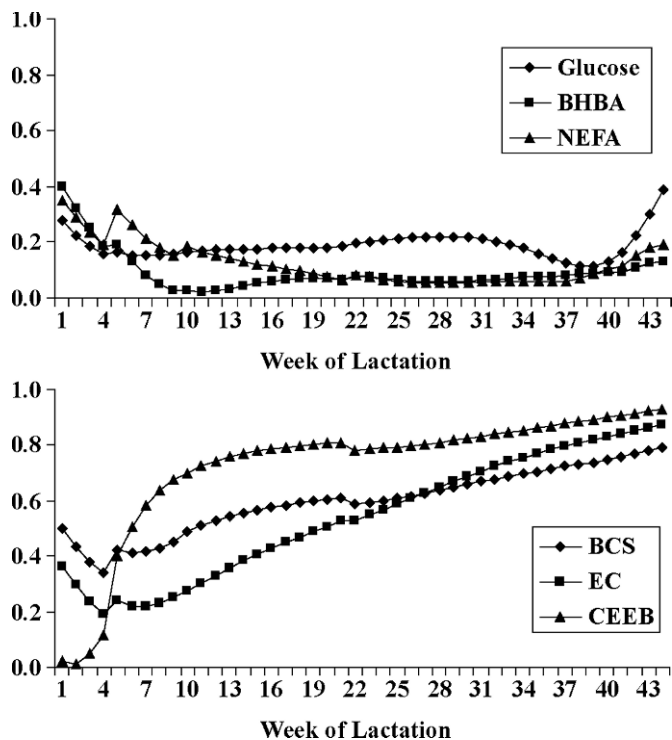


Figure 5. Heritability estimates for BCS (SE = 0.19 to 0.30), energy content (EC; SE = 0.20 to 0.33), cumulative effective energy balance (CEE; SE = 0.05 to 0.34), and blood serum concentrations of glucose (SE = 0.03 to 0.10), BHBA (SE = 0.03 to 0.14), and NEFA (SE = 0.02 to 0.14) by week of lactation.

most rapidly for BHBA, followed by glucose, NEFA, and the body energy traits. This is illustrated in Figure 6 presenting genetic correlations of each studied trait measured on wk 4 of lactation with subsequent week measurements. Average genetic correlation of body energy traits measured in the first 4 wk and last 4 wk of lactation was 0.25 and 0.10 for BCS and EC, respectively. Also, the average genetic correlation between the first 4 wk and all remaining weeks for the same 2 traits were 0.42 and 0.34, respectively. For CEEB, where genetic variation in the first 6 wk was not statistically significant ($P > 0.05$), genetic correlations of records in wk 7 to 10 with all remaining and the last 4 wk of lactation were 0.71 and 0.56, respectively. Genetic correlations of the blood serum concentration traits in different weeks of lactation were, in general, lower than those of the other traits. These correlations became practically zero for measurements taken more than 3 to 4 mo apart. For example, glucose measurements in the first 4 wk of lactation had significant ($P < 0.05$) positive genetic correlations with measurements up to wk 16 with an average estimate of 0.54. Thereafter, genetic correlations were not significantly different from zero. For BHBA, serum levels in the first 4 wk

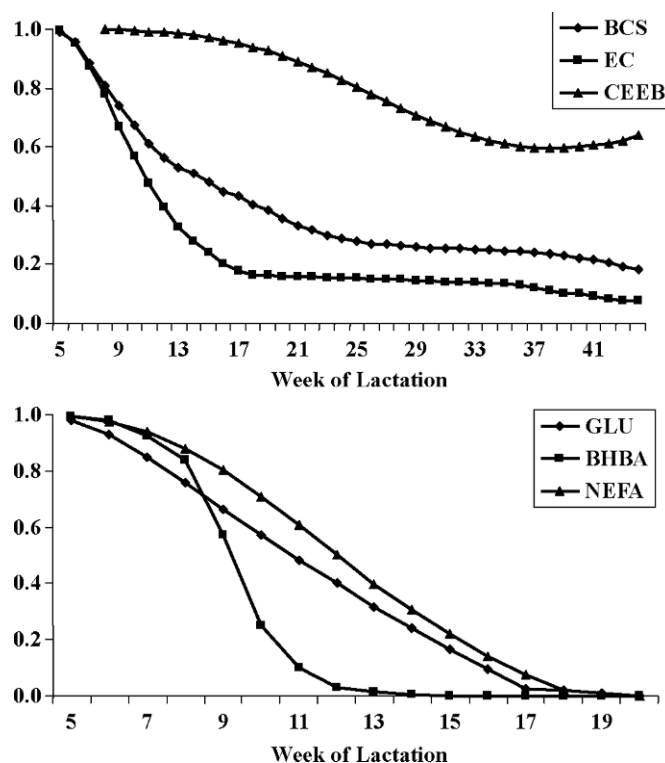


Figure 6. Genetic correlations of BCS, energy content (EC), cumulative effective energy balance (CEE), and blood serum concentrations of glucose, BHBA, and NEFA measured in the fourth week of lactation with subsequent week measurements.

were significantly correlated with measurements until wk 9 (average estimate 0.72) and for NEFA the corresponding values were 15 wk and an average genetic correlation of 0.58.

Genetic variance and heritability estimates were also obtained for BCS, EC, and blood serum glucose, BHBA, and NEFA concentrations measured on heifers once before calving. These results are presented in Table 2. Genetic parameters were significantly greater than zero ($P < 0.05$) only for BCS.

Finally, average product-moment correlations among animal breeding values for the studied traits are presented in Table 3. These are averages of correlations pertaining to the first 3 mo (13 wk) of lactation.

DISCUSSION

Estimated fixed curves for the 6 studied traits are clearly indicative of changes in the metabolic process and energy balance of cows during lactation. The negative energy balance period in the beginning of lactation is characterized by a decrease of BCS, EC, and CEEB. This situation is reversed in later stages of lactation. Furthermore, lower glucose levels and increased BHBA

Table 3. Average product-moment correlation estimates¹ between animal breeding values for BCS, energy content (EC), cumulative effective energy balance (CEEB), and blood serum concentrations of glucose, BHBA, and NEFA measured in the first 13 wk of lactation

Item	EC	CEEB	Glucose	BHBA	NEFA
BCS	0.81*	0.30*	0.09*	0.00	0.05
EC		0.49*	0.10*	0.02	0.06
CEEB			0.13*	0.00	-0.27*
Glucose				-0.04	-0.14*
BHBA					0.44*

¹SE = 0.04.

* $P < 0.05$.

and NEFA levels were observed during the first weeks of lactation compared with mid or late lactation. Fixed curves of EC and CEEB calculated in the present study are similar to those presented by Banos et al. (2006). Wathes et al. (2007a) investigated the phenotypic change of BHBA and NEFA levels during the first 7 wk of lactation. Their results, although not derived from a genetic analysis and the use of random regression models, were still relatively comparable to results from the present study that showed BHBA and NEFA levels to be greater during the first weeks of lactation.

The genetic profile of BCS has been investigated in several previous studies. Our results are quite similar to those from studies conducted on single farms using observations on a few hundreds cows. For example, Coffey et al. (2001) reported heritability estimates for BCS across the first lactation that ranged from 0.38 to 0.81, using data from an experimental research station. In another study with similar data, Veerkamp and Brotherstone (1997) found that the heritability estimate was 0.43 for the first 26 wk of the first lactation. In the present study, data were from a commercial rather than a research farm, and the fact that results were consistent with the literature suggests that the type of farm may not be the crucial factor in a genetic analysis, as long as all other sources of systematic variation are properly recorded and accounted for.

Lower BCS heritability estimates have, in general, been reported in studies conducted using large numbers of cows raised in many different herds. This is expected because, in single farm studies, more controlled environmental conditions can lead to greater heritability estimates. Body condition score heritability estimates from large-scale studies have been reported to range from 0.23 to 0.28 (Jones et al., 1999), 0.39 to 0.51 (Berry et al., 2003), 0.22 to 0.38 (Banos et al., 2004), and 0.23 to 0.37 (Koenen et al., 2001).

Genetic variance and heritability estimates for EC and CEEB were very similar to those reported by Banos et al. (2006) using data from an experimental farm in Scotland. Among body energy traits measured in

pregnant heifers, only BCS had a significant heritability estimate, suggesting possible utility in a genetic evaluation and selection program. Its genetic correlation with postpartum energy balance levels still needs to be established.

As has already been mentioned, genetic parameters for glucose, BHBA, and NEFA serum concentrations throughout lactation were not found in the literature. Therefore, no direct comparisons can be made with the results of this study. Ingvarstsen and Friggens (2005) reported significant between-cow variation for glucose, BHBA, and NEFA concentrations. Although not a genetic analysis, this was an indication of genetic variation in these traits. Furthermore, genetic selection for milk yield has been found to affect these traits (Veerkamp et al., 2003), which is another indication of the existence of genetic variation. Such indications were confirmed and quantified in the present study. More comparable to our results were heritability estimates of blood serum glucose and NEFA concentration that were reported by Hayhurst et al. (2007) using data on Holstein male calves that were approximately 9 mo old. These estimates were 0.15 for both traits and were close to the lower limit of our results. The greater heritability values that were observed in our study during the first week of lactation are probably related to the metabolic challenges a dairy cow faces immediately after calving that may be connected to a different expression of her genetic component for the specific traits. This could also explain the greater heritability estimates for BHBA levels that were observed in our study during the first week of lactation.

Heritability estimates of blood metabolic traits in pregnant heifers were not statistically significant. From these estimates, only glucose approached significance ($P = 0.08$) and was slightly greater than the estimate reported for male calves in the study by Hayhurst et al. (2007).

Genetic correlations of the body energy traits studied here (BCS, EC, CEEB) in different weeks of lactation were very high for adjacent weeks and decreased for weeks further apart. This pattern was expected and consistent with that reported by Banos et al. (2005) for a trait associated with body energy balance accumulated throughout lactation. These results indicate that the way cows start accumulating lipid and protein changes at the first stages of lactation sets the pace for energy changes in the remainder of lactation. The utility of this result lies in the ability to predict future energy balance indicators, especially CEEB, from values obtained early in lactation, potentially assisting farm management practices. Furthermore, it could enable the estimation of CEEB at the first stages of lactation from values obtained in mid to late lactation.

Genetic correlations of the blood serum concentration traits in different weeks of lactation were, in general, lower than those of the other traits. These correlations became practically zero for measurements taken more than 3 to 4 mo apart. Results suggest that although early-lactation body energy measurements are decent genetic predictors of late lactation, this is not necessarily true for blood serum concentration traits, whose predictive capacity ends 11 to 16 wk later. For BHBA and NEFA, this is consistent with near-zero genetic variance levels observed at mid to late lactation. However, it is important to note that a genetic evaluation for the early-lactation profile of these traits is possible with a single measurement obtained at any time during the first 2 to 3 mo of lactation.

Product-moment correlations among animal breeding values for the studied traits were calculated as the minimum values of the genetic correlation between these traits. Average correlation estimates of the first 3 mo of lactation ranged from weak to strong. This early stage of lactation is the period when weekly phenotypic measurements were available. This period is also of interest to farm management because it precedes the onset of inseminations. Body condition score had a considerable correlation with the other body energy traits (EC and CEEB) but its correlation with metabolic traits was very low or close to zero. This result may have implications in the use of such traits for selection aiming at improving cow health and fertility. In the presence of significant genetic correlations with the latter, measuring only BCS will not provide as much information as measurement of more than one of the studied traits.

Previous studies on the genetic profile of BCS, EC, and CEEB, and their genetic correlation with economically important traits such as fertility or somatic cell count, have already alluded to the opportunity for genetic selection of dairy cows for these traits (Pryce et al., 2000; Banos et al., 2004, 2006). Results presented here support this argument. Furthermore, new selection opportunities arise with the genetic characterization of metabolic traits related to dairy cow energy balance. Genetic selection of cows that have more desirable metabolic profiles, especially at the critical early postpartum period, seems to be possible because the heritabilities of glucose, NEFA, and BHBA concentration, at least during the first weeks of lactation, were found to be significantly greater than zero. Heritability estimates of BCS before first calving suggest that the genetic evaluation of heifers could be possible, giving useful information early in the animal's life. Validation of these data with similar studies that could also involve observations on multiparous cows would be desirable, while estimates of genetic correlations between these

metabolic traits and health and fertility traits are largely missing from the literature. On the other hand, phenotypic relationships of metabolic energy balance indicators with health (LeBlanc et al., 2005; Hammon et al., 2006) and fertility (Reist et al., 2000; Westwood et al., 2002; Reist et al., 2003; Walsh et al., 2007; Wathes et al., 2007b) have already been reported. The substantial genetic variation presented here for these metabolic traits enhances the importance of an attempt to quantify the proportion of these phenotypic relationships that is due to genetic factors. If significant genetic correlations of blood metabolic traits with health and fertility are established, then measurements of the former can be used to facilitate genetic improvement of health and fertility traits, which are known to have low heritability.

Arguably, recording blood metabolic traits in a commercial dairy cattle population can be difficult. It requires a properly equipped laboratory, and the cost for consumables is not negligible. In our case, the consumables cost for the measurement of glucose, BHBA, and NEFA was approximately €3.5 (US\$5.20) and analysis took 7 to 9 min per sample. An additional cost is required for the acquisition of blood samples. In this regard, possible first applications of such trait recording and monitoring may be restricted to selected herds, where elite breeding animals are principally identified and evaluated.

At the same time, metabolic profiles during the transition period are considered to be very useful tools for the refinement of nutrition and health management procedures, especially in high production herds (Herdt, 2000; Oetzel, 2004). This fact, together with the development of more automated techniques for frequent sampling and biochemical analyses and probably the reduction of the cost of consumables, could present a possibility for the introduction of metabolic profiles in dairy herd improvement schemes and the use of these measurements for management and selection purposes.

CONCLUSIONS

Results presented in this study show that there is significant genetic variation in body energy and metabolic traits throughout lactation and, specifically and perhaps more importantly, in the early stages of lactation. Genetic evaluation of dairy cows for these traits, based on records taken in the first 2 to 3 mo of lactation, is possible. This can contribute to the selection of animals that are more capable of coping with the metabolic stress of the postpartum period, as manifested, for example, by their lower blood BHBA concentration during early lactation, potentially leading to an improvement of their health and reproductive performance.

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