Effect of genetic merit for energy balance on luteal activity and subsequent reproductive performance in primiparous Holstein-Friesian cows

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ABSTRACT

Postpartum energy status is critically important to fertility. However, studies dealing with the relationship between both traits are rare and most refer only to the phenotypic level. In this study, random regression models were used to generate cow-specific lactation curves for daily breeding values (BV) of energy balance (EB) to assess the effect of genetic merit for energy status on different traits derived from progesterone profiles and on subsequent reproductive performance of high-producing dairy cows. Individual feed intake, milk yield, and live weight were recorded for lactation d 11 to 180, and EB was estimated on a daily basis. The results provided the basis for the estimation of BV for 824 primiparous Holstein-Friesian cows. For a subset of these cows ($n = 334$), progesterone profiles for the resumption of ovarian activity were available. Four different traits describing the genetic merit for EB were defined to evaluate their relationship with fertility. Two EB traits referred to the period in which the average daily EB across all cows was negative (d 11 to 55 postpartum), and 2 parameters were designed considering only daily BV for d 11 to 180 in lactation that were negative. We found that cows with a high genetic merit for EB had a significantly earlier resumption of ovarian activity postpartum. Thus, an EB (indicator) trait should be included in future breeding programs to reduce the currently prolonged anovulatory intervals after parturition.

Key words: dairy cow, energy balance, luteal activity, reproductive performance

INTRODUCTION

Milk production per cow has been considerably improved over the last decades (Lucy, 2001), but the success in breeding for milk yield has been accompanied by negative side-effects, especially in terms of an

aggravated negative energy balance (EB) in early lactation. Cows require sufficient energy intake to support all physiological functions; that is, to produce milk and grow while maintaining fitness and reproducing (Banos et al., 2006). However, DMI is insufficient to cover the demand in early lactation and, according to Collard et al. (2000), selection for milk traits has resulted in a partial shift of available energy toward milk production at the cost of other biological pathways. Additional energy for milk production is made available by mobilization of body fat and skeletal muscle (Butler and Smith, 1989; Bell, 1995). Bauman and Currie (1980) demonstrated that the average EB of high-yielding dairy cows was negative during the first 100 DIM. Beever et al. (1998), studying cows fed a high-quality diet at an intake level >28 kg of DM/d, reported that the period of negative EB can even persist for 20 wk after parturition. During this critical period (~ 80 d after calving), the majority of farmers aim to get their cows pregnant again to achieve a calving interval of approximately 1 yr. This situation has given cause for concern but studies dealing with EB and fertility traits are rare, mainly because recording of individual feed intake is costly and difficult to apply in practice (Hüttmann et al., 2009). Available data sets are generally small. Nevertheless, several studies have reported negative effects of an energy deficit or losses of body energy on the reproductive performance of dairy cows. Reist et al. (2003) found that cows exhibiting a severe or prolonged negative EB remained open for longer. This was in line with the results of Patton et al. (2007), who stated that cows not experiencing a pronounced energy deficit have an increased likelihood of conception at first service. A few studies also investigated the genetic association of directly measured body energy and reproductive performance: Veerkamp et al. (2000) reported negative genetic correlations between measures of EB and the interval from calving to first luteal activity (commencement of luteal activity; CLA). This is in line with Banos and Coffey (2010), who reported negative genetic correlations between the interval from calving to the first observed estrus and daily EB, energy content, cumulative effective energy, and BCS. For EB, this was true only for the first 105

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DIM, whereas for the other traits, all daily estimates (DIM 4 to 311) were significant. Significant correlations with CLA were found only for the first 107 d of energy content and the first 222 d of BCS. These results substantiate the need to accomplish further investigations on the genetic association between traits for body energy and reproductive performance.

The objectives of this study were (1) to define adequate parameters characterizing cow-specific lactation curves for daily breeding values (BV) of EB, and (2) to estimate the effect of these parameters on the resumption of first luteal activity postpartum as well as on subsequent reproductive performance. To the best of our knowledge, no comparable research has been done on this issue to date.

MATERIALS AND METHODS

Energy Balance Raw Data and Estimation of Daily Breeding Values

Data were collected from primiparous Holstein-Friesian cows. Data recording was done between March 2006 and December 2012 on the dairy research farm Karkendamm (Bimöhlen, Germany). This farm runs a bull dam performance test, and all Karkendamm bull dam candidates had to complete a test period under commercial conditions in a freestall barn until DIM 180. Nonqualified primiparous cows left the herd afterward. Therefore, only records between 11 (start of feed intake recording) and 180 DIM were used in the present investigation. Animals were milked twice a day and milk yield was recorded at every milking. Milk composition was analyzed weekly based on samples collected from 2 consecutive milkings. Milk was corrected for energy following the formula of Kirchgeßner (1997):

$$\text{ECM (kg)} = (0.39 \times \text{fat \%} + 0.24 \times \text{protein \%} + 0.17 \times \text{lactose \%}) \times \text{milk yield (kg)} / 3.17.$$

For this purpose, milk composition per day was obtained by weighting the respective or previous analysis values per day with the respective milk yield. Cows were weighed after every milking and the daily value was derived by averaging morning and evening BW. Animals were fed a TMR ad libitum, and daily intake was recorded for each animal via single feeding troughs. As cows were generally housed separately during the first 10 DIM, no feed intake data were available for this period. The average NE_L of the TMR was 7.1 MJ/kg of DM. Fixed amounts of concentrates were dispensed via concentrate feeders. Energy balance was calculated as described by Buttchereit et al. (2010). Animals were discarded from the analyses if the number of EB estimates per cow across the entire period was fewer than 4. This resulted in 824 primiparous cows and an average of 83 EB estimates per cow.

A pedigree file was created by tracing the pedigree of cows with data 3 generations back. The resulting file consisted of 5,683 animals. Energy balance BV (EBBV) were estimated via ASReml 3.0 (Gilmour et al., 2009) using a random regression animal model. Test-day, age at first calving, and stage of lactation were considered as fixed effects. Age at first calving was divided into 5 classes (21 to 25, 26, 27, 28, and 29 to 38 mo). The general lactation curve was modeled by the function according to Ali and Schaeffer (1987), and random regression coefficients for permanent and additive genetic effects were modeled applying Legendre polynomials of 2 degrees:

$$y_{ijklm} = TD_i + AFC_j + \sum_{n=1}^4 b_n x_{ijklmn}(d) + \sum_{n=0}^2 p_{kn} x_{ijklmn}(d) + \sum_{n=0}^2 a_{ln} x_{ijklmn}(d) + e_{ijklm},$$

where y_{ijklm} is the m th observation of EB, TD_i represents the fixed effect of the test-day i ($i = 1$ to 1,714), and AFC_j is the fixed effect of age at first calving ($j =$

Table 1. Descriptive statistics for ECM, fat content, protein content, lactose content, energy balance (EB), DMI, BCS, and BW ($n = 824$ primiparous dairy cows, DIM 11 to 180)

Trait	No. of observations	Mean	SD	Minimum	Maximum
Age at first calving (mo)	824	27.36	2.33	21.00	38.00
ECM (kg/d)	165,805	32.72	4.69	2.50	53.64
Fat (%)	24,138	3.64	0.59	1.22	8.68
Protein (%)	24,138	3.24	0.24	1.96	6.01
Lactose (%)	24,237	4.88	0.15	3.17	5.38
EB (MJ of NE_L /d)	68,436	5.16	35.86	-141.80	185.59
DMI (kg/d)	93,797	20.17	4.83	1.99	45.45
BCS	5,662	2.95	0.33	1.50	3.90
BW (kg)	130,452	600.03	54.48	404.00	847.00

Table 2. Overview of group assignment according to the difference between energy balance breeding values (BV) for DIM 11 and 55 ($n = 334$ primiparous cows)

Difference between BV for DIM 11 and 55		Class limit ¹	Frequency, % (no.)
Positive difference (downward sloping BV curve)	Greater than mean + 1/2SD	$i \geq 7.16$	29.04 (97)
Low to moderate difference (flat BV curve)	Mean $\pm$ 1/2SD	$-2.96 < i < 7.16$	55.99 (187)
Negative difference (rising BV curve)	Less than mean - 1/2SD	$i \leq -2.96$	14.97 (50)

¹Where class limit i is the difference between BV for DIM 11 and 55.

1 to 5), b_n are the fixed regression coefficients on lactation day d with $x_{ijklm1}(d) = d/190$, $x_{ijklm2}(d) = (d/190)^2$, $x_{ijklm3}(d) = \ln(190/d)$, and $x_{ijklm4}(d) = [\ln(190/d)]^2$, p_k represents the random regression coefficients for the permanent environmental effect of animal k , and a_l are the random regression coefficients for the additive genetic effect of the l th animal with $x_{ijklm0}(d) = 1$, $x_{ijklm1}(d) = -1 + 2(d - 11/d_{\max} - 11)$ and $x_{ijklm2}(d) = 0.5\{3[-1 + 2(d - 11/d_{\max} - 11)]^2 - 1\}$ ($k = 1$ to 824, $l = 1$ to 5,683), and e_{ijklm} is the random error term.

Table 1 provides an overview of means, standard deviations, minima, and maxima of age at first calving, ECM, fat, protein, and lactose contents, EB, DMI, BCS, and BW.

Characterization of Cow-Specific Lactation Curves for Daily EBBV

Cow-specific lactation curves for EBBV showed considerable variation. Either early lactation BV were initially positive and decreased approximately linearly over time to become negative or BV were negative in the beginning and increased approximately linearly over time to become positive. Over the whole period, curves for daily BV were concave, convex or showed no such remarkable pattern. These characteristics of the daily EB BV curves were used to define 4 different parameters describing the genetic merit for energy status. According to these parameters, cows were assigned to different groups. A detailed explanation is given below.

Difference Between BV for DIM 11 and 55

This parameter characterizes the change of genetic merit for EB from DIM 11 to 55. Using this parameter,

3 groups were defined. Class limits were obtained by adding 1/2 standard deviation (SD) to the mean and subtracting 1/2 SD from the mean, respectively (Table 2). For example, the difference between BV for DIM 11 and DIM 55 was positive if cows had a positive BV at 11 DIM and a negative BV at 55 DIM. Cows with a concave or convex cow-specific lactation curve for daily EBBV were correctly classified, because the reverse occurred in a later stage of lactation (after 55 DIM).

Average BV from DIM 11 to 55

This parameter also refers to the period in which the average daily EB across all cows was negative (DIM 11 to 55). The average level of genetic merit for EB was calculated for this period and 3 groups were formed using the same procedure as described above (Table 3).

Sum and Number of Negative BV from DIM 11 to 180

The sum of negative EBBV from DIM 11 to 180 was calculated to describe the genetic disposition for the magnitude of the energy deficit postpartum. In total, 234 cows had negative EBBV throughout the whole observation period. Three groups were defined using the same procedure as described before (Table 4).

The number of negative EBBV from DIM 11 to 180 was calculated to describe the genetic predisposition for a prolonged negative EB. As described before, 3 subgroups were defined (Table 5).

Progesterone Measurements

For a subset of cows with EBBV, progesterone records were available from April 2007 to December

Table 3. Overview of group assignment according to the average energy balance breeding value (BV) across DIM 11 to 55 ($n = 334$ primiparous cows)

Average BV for DIM 11 to 55		Class limit ¹	Frequency, % (no.)
High mean BV	Greater than BV mean + 1/2SD	$i \geq 10.44$	31.44 (105)
Medium mean BV	Mean BV $\pm$ 1/2SD	$-7.04 < i < 10.44$	44.61 (149)
Low mean BV	Less than mean BV - 1/2SD	$i \leq -7.04$	23.95 (80)

¹Where class limit i is the average BV for DIM 11 to 55

Table 4. Overview of group assignment according to the sum of negative energy balance breeding values (BV) from DIM 11 to 180 (n = 234 primiparous cows)

Sum of negative BV across the entire period (DIM 11 to 180)		Class limit	Frequency, % (no.)
Low negative	Greater than mean sum of negative BV + 1/2SD	$i \geq -617.43$	43.59 (102)
Moderate negative	Mean sum of negative BV $\pm$ 1/2SD	$-617.43 > i > -2,170.64$	33.33 (78)
High negative	Less than mean sum of negative BV - 1/2SD	$i \leq -2,170.64$	23.08 (54)

¹Where class limit i is the sum of negative BV across the entire period (DIM 11 to 180).

2008 and from February 2010 to December 2011. Milk samples (about 5 mL of foremilk) were taken twice a week on Monday morning and Thursday afternoon. Sampling period was about 6 d after parturition to 30 d after a positive ultrasonographic pregnancy diagnosis. Milk samples were stored with no preservatives at -18°C until enzyme immunoassays for progesterone were conducted. Progesterone quantification was done from aliquots of 20 μL of skim milk applying the ELISA procedure, which uses a monoclonal progesterone antibody bound to the surface of a 96-well microplate. Horseradish peroxidase was used as conjugate and tetramethylbenzidine as chromogen. The reaction was stopped by addition of 50 μL of 2 M H_2SO_4 /well. Optical density was measured and plotted against the mass of conjugate with a wavelength of 450 nm using an SLT Spectra photometer (Tecan, Männedorf, Switzerland). To determine the measuring accuracy, the accuracy in duplicates approach by Doerffel (Renner, 1970) was applied. The accuracy was defined as follows:

$$\text{Accuracy} = \sqrt{\frac{\sum (x_1 - x_2)^2}{2 \times n}},$$

where x_1 and x_2 was one pair of duplicates and n was the number of pairs. For this purpose, milk samples from 2 cows in heat (low progesterone concentration) and 1 pregnant cow (high progesterone concentration) were used. The degree of accuracy for the low concentration was $\pm 0.034\%$ and $\pm 0.027\%$, for the 2 cows, respectively, and was $\pm 0.012\%$ for the high concentration. Thus, there was a discrepancy of $\pm 0.034\%$ between x_1 and x_2 for low concentrations. Cows were included in this study if the first progesterone measurement was before 10 DIM. Cows with fewer than 12 subsequent

observations in 42 d were excluded. In addition, cows were excluded if there were gaps in the time series greater than 14 d. Finally, 334 first-lactation dairy cows remained for this study.

Characterization of Luteal Activity Based on Progesterone Profiles

Data preparation of progesterone measures was done in R (R Development Core Team, 2012). The R package “stinepack” with the included subfunction “scaledstine-man” (Johannesson et al., 2009) was used to interpolate the time series. The black dashed line in Figure 1 illustrates the interpolation. First luteal activity was determined by the first postpartum progesterone value above the threshold value of 0.8 ng of progesterone/mL of skim milk, preceded by low progesterone. The threshold (0.8 ng/mL) for identifying the presence of luteal activity was chosen based on a preliminary study (von Leesen et al., 2013).

The function “rle” was used to calculate a step function based on run length encoding. The step function was applied to compute the anestrus period (progesterone values < 0.8 ng/mL of skim milk) and the length of luteal phases (values > 0.8 ng/mL). The detectable amount of progesterone in skim milk per luteal phase was calculated by summarizing all interpolated values within a luteal phase (values > 0.8 ng/mL). This presents the area under the curve (AUC).

Reproductive Management, Data on Insemination, and Pregnancy Diagnoses

Primiparous cows had a voluntary waiting period of about 100 d. All insemination data were recorded, and there was no defined breeding season for the test

Table 5. Overview of group assignment according to the number of negative energy balance breeding values (BV) from DIM 11 to 180 (n = 234 primiparous cows)

Number of negative BV across the entire period (DIM 11 to 180)		Class limit	Frequency, % (no.)
Small	Less than mean number + 1/2SD	$i \leq 91.2$	43.16 (101)
Moderate	Mean number $\pm$ 1/2SD	$91.2 < i < 143$	26.07 (61)
Large	Greater than mean number - 1/2SD	$i \geq 143$	30.77 (72)

¹Where class limit i is the number of negative BV across the entire period (DIM 11 to 180).

Figure 1. Typically interpolated progesterone profile with step function.

population. Visual detection of estrus supported by activity meter specification (GEA Farm Technologies, Kenilworth, UK) was used to determine time of AI. Experienced AI technicians performed the AI. The herd manager had no insight into the progesterone measurements and veterinarians verified ultrasonographic pregnancy diagnoses 35 d after insemination or later. For the subset of cows ($n = 255$) that did not receive hormonal treatments for superovulation, data on insemination and pregnancy diagnoses were used for further investigations.

Effect of Genetic Merit for EB on First Luteal Activity and Subsequent Reproductive Performance

The effects of genetic merit for energy status on the first luteal activity and subsequent reproductive performance, respectively, were tested using PROC GLM of SAS (SAS Institute, 2004). When subgroups within parameters differed ($P < 0.05$), post hoc tests by Scheffé (PROC GLM) were used to compare the different groups.

RESULTS

Figure 2 shows the trend of the mean EB (MJ of NE_L/d) and the range of the trait from 11 to 180 DIM. All cows were in a negative EB until DIM 20. Energy balance stabilized around DIM 55, switching from positive to negative and vice versa until DIM 63. The mean EB increased slightly as lactation proceeded, but some cows suffered from a prolonged energy deficit and did not change into a state of positive EB throughout the entire observation period.

A summary of the EB data for 4 specific DIM is given in Table 6. The mean EB increased by 43.18 MJ of NE_L from 11 to 55 DIM (i.e., 0.98 MJ/d). At 180 DIM, the mean EB was approximately 8 times higher compared with that at 63 DIM. Table 7 summarizes the estimated EBBV on 11, 55, and 180 DIM.

Table 8 illustrates the traits for the resumption of ovarian activity postpartum, which included the time of resumption, the duration of first luteal activity, and the AUC of first luteal activity. All traits were skewed to the right and had high standard deviations.

Table 6. Descriptive statistics for energy balance (MJ of NE_L/d) at DIM 11, 55, 63 and 180 ($n = 824$ primiparous cows)

DIM	No.	Mean	Minimum	Maximum	SD
11	820	-42.67	-133.83	39.54	34.58
55	802	0.51	-80.22	102.90	34.20
63	799	2.29	-91.83	137.90	36.98
180	686	18.83	-86.91	120.76	33.61

Table 7. Descriptive statistics for the estimated energy balance breeding values at DIM 11, 55, and 180 ($n = 824$ primiparous cows)

DIM	Mean	Minimum	Maximum	SD
11	1.06	-64.14	81.26	19.51
55	-0.10	-67.10	44.09	14.46
180	1.44	-101.11	84.02	16.03

Table 9 shows the effect of the difference between EBBV for DIM 11 to 55 and the average BV from DIM 11 to 55, respectively, on resumption of ovarian activity. The change in genetic merit from DIM 11 to 55 had a significant effect on the duration of first luteal activity ($P = 0.02$) and on AUC ($P = 0.01$), whereas no significant effect on time of resumption was observed ($P = 0.07$). The average genetic merit for EB in early lactation had only a significant effect on time of resumption of first ovarian activity ($P = 0.03$).

The effect of the genetic disposition for the magnitude and duration of the negative EB on fertility traits is presented in Table 10. Both traits considering only negative BV for DIM 11 to 180 had a significant effect on time of resumption of first ovarian activity.

Table 11 provides an overview of the effect of genetic merit for EB on the subsequent reproductive performance. For the analyses performed using the 2 parameters “differences between EBBV for DIM 11 and 55” and “average EBBV for DIM 11 to 55,” 255 cows with insemination data were available. Only 129 cows became pregnant during the observation period. The first 2 parameters did not have a significant effect on interval from calving to first AI or on days open.

For the analyses performed using the other 2 parameters, which described the genetic disposition for magnitude and duration of negative EB, AI records from 177 cows were available. Of these, 94 cows became pregnant during the study. The genetic disposition for the duration of the energy deficit postpartum had a significant effect on days open. Furthermore, the genetic disposition for the magnitude of the negative EB was significantly associated with interval to first AI ($P = 0.02$), but the post hoc Scheffé test showed no significant differences between the groups.

DISCUSSION

In early lactation, a mismatch exists between DMI and energy required for milk yield and maintenance (i.e., there is a negative EB). Compensation through increased mobilization of body fat and skeletal muscle is necessary (Butler and Smith, 1989; Bell, 1995). Energy status is driven mainly by individual DMI (Villa-Godoy et al., 1988; Banos and Coffey, 2010). Banos and Coffey (2010) stated that cows in the first week postpartum produced about 92% of their maximum milk yield, but their feed intake amounted to only 80% of their highest DM consumption. de Vries and Veerkamp (2000) reported that EB was negative during the first 41.5 DIM, on average. Moreover, Bauman and Currie (1980) found that the average EB was negative within the first 100 DIM. Beever et al. (1998) determined that EB was negative throughout the first 20 wk postpartum. In this study, average EB was negative until 55 DIM. Buttchereit (2011a) reported that primiparous Karkendamm

Figure 2. Means and range (error bars) of energy balance from DIM 11 to 180 ($n = 824$ primiparous cows).

Table 8. Traits for the resumption of ovarian activity postpartum (n = 334 primiparous cows)

Trait	No.	Mean	SD	Minimum	Maximum
Time of resumption of ovarian activity (d)	334	34.14	23.26	3.0	146.0
Duration of first luteal activity (d)	334	20.05	13.91	7.0	123.0
Area under curve of first luteal activity	334	47.04	43.62	7.0	377.0

cows exhibited a negative EB during the first 42 DIM, on average. Thus, the duration of the energy deficit postpartum has increased for the Karkendamm herd since that time. In addition, a decline in average daily EB from 8.00 MJ of NE_L (Buttchereit et al., 2011b; including data from March 2006 to October 2010) to 5.16 MJ of NE_L could be observed for the primiparous Karkendamm cows, which is notable because of the short time elapsing between these studies. Figure 2 illustrates that some cows (42.1%) did not revert to balanced energy status during the first 180 DIM. Likewise, Villa-Godoy et al. (1988) announced that, by the end of the study (DIM >100 or new pregnancy, respectively), 69% of the cows could not recuperate their body energy content from the beginning of lactation. In contrast to these results, de Vries and Veerkamp (2000) reported that only 17.5% of the cows did not reach balanced energy status during the first 180 DIM.

The main objective of this study was to gain a better understanding of how genetic merit for EB influences fertility. Random regression models were applied to derive cow-specific information for every day (daily EBBV) from 11 to 180 DIM. Thereafter, the relationship between fertility and the genetic merit for EB across lactation was studied. The lactation curves for daily EBBV were described by 4 parameters with 3 subgroups each. The first parameter (differences between BV for DIM 11 and 55) indicated whether or not the genetic merit was subject to change in early lactation and, if so, also described the direction or amount of change. The second parameter (average BV from DIM 11 to 55) referred to the average genetic merit for EB

within the period in which cows were in a negative EB, on average. Two further parameters (sum and number of negative EBBV from DIM 11 to 180) referred to the whole observation period and were used to describe the genetic disposition for the magnitude and duration of the energy deficit. On a phenotypic level, similar traits were studied by Villa-Godoy et al. (1988) and Reist et al. (2003).

Three parameters were extracted from progesterone profiles and used to assess the effect of differing genetic merit for EB on fertility. These parameters described the time of resumption of first ovarian activity, the duration and the AUC of first luteal activity. On average, the first luteal activity was at DIM 34.14 (± 23.26 d). The current results are in agreement with Petersson et al. (2006). Those authors observed CLA on DIM 33.5 (± 22.3 d) for Swedish Red breed and on DIM 34.5 (± 23.7 d) for Swedish White breed. Opsomer et al. (1998) found slightly longer CLA for Belgian dairy cattle (37 ± 27 DIM), whereas Holstein-Friesian dairy cows in Northern Ireland showed CLA on DIM 30.1 (± 0.46 d; McCoy et al., 2006). The duration of first luteal activity (mean = 20.05 d) was in line with physiological expectations (Lamming and Darwash, 1998). However, it should be noted that there were also atypical progesterone profiles such as shortened and prolonged luteal phases. These results are in agreement with Lamming and Darwash (1998), Opsomer et al. (1998), Royal et al. (2000), Shrestha et al. (2004), Hommeida et al. (2011), and Ranasinghe et al. (2011).

All 4 parameters describing the genetic merit for EB had a distinct effect on time of resumption of first

Table 9. Effect of the difference between energy balance breeding values (BV) for DIM 11 and 55 and the average BV from DIM 11 to 55, respectively, on the resumption of ovarian activity postpartum (n = 334 primiparous cows)

Trait	Time of resumption			Duration of first luteal activity			Area under the curve of first luteal activity		
	No.	Mean	SD	No.	Mean	SD	No.	Mean	SD
Difference between BV for DIM 11 and 55									
Positive	97	30.15 ^a	17.69	97	23.09 ^a	16.72	97	57.59 ^a	58.36
Low to moderate	187	34.88 ^a	25.50	187	18.38 ^b	12.92	187	41.33 ^b	35.62
Negative	50	39.10 ^a	23.39	50	20.42 ^{ab}	10.41	50	47.94 ^{ab}	33.63
Average BV for DIM 11 to 55									
High	105	30.74 ^a	18.18	105	20.66 ^a	14.74	105	48.48 ^a	48.22
Medium	149	33.58 ^{ab}	22.93	149	19.38 ^a	13.33	149	44.46 ^a	36.15
Low	80	39.64 ^b	28.65	80	20.53 ^a	14.05	80	49.96 ^a	50.09

^{a,b}Means with different superscripts within a column and trait are significantly different ($P < 0.05$).

Table 10. Effect of genetic disposition for magnitude and duration of negative energy balance on the resumption of ovarian activity postpartum (n = 234 primiparous cows)

Trait	Time of resumption			Duration of first luteal activity			Area under the curve of first luteal activity		
	No.	Mean	SD	No.	Mean	SD	No.	Mean	SD
Sum of BV ¹ from DIM 11 to 180									
Low negative	102	30.96 ^a	18.55	102	21.08 ^a	9.15	102	49.11 ^a	45.85
Moderate negative	78	33.26 ^{ab}	21.85	78	18.06 ^a	17.03	78	41.26 ^a	26.27
High negative	54	43.33 ^b	33.01	54	20.44 ^a	14.49	54	51.17 ^a	55.49
Number of negative BV ¹ from DIM 11 to 180									
Small	101	39.05 ^c	29.41	101	18.60 ^a	11.38	101	44.58 ^a	42.48
Moderate	69	27.07 ^d	15.47	69	22.07 ^a	18.19	61	50.84 ^a	45.22
Large	72	34.43 ^{cd}	20.15	72	19.97 ^a	14.04	72	47.03 ^a	42.47

^{a,b}Means with different superscripts within a column and trait are significantly different ($P < 0.01$).

^{c,d}Means with different superscripts within a column and trait are significantly different ($P < 0.05$).

¹BV = energy balance breeding values.

ovarian activity. We found that the subgroups “high average BV for DIM 11 to 55” and “low negative sum of negative BV across the entire period” with the highest genetic merit for EB were superior to the other subgroups. These cows exhibited their first luteal activity significantly earlier (9 and 13 d, respectively) than cows that had the lowest genetic merit for EB. Cows in the subgroups “positive difference (downward sloping BV curve)” also showed their first luteal activity about 9 d earlier compared with cows in the subgroup “negative difference (rising BV curve),” although the difference was not statistically significant. In contrast to the other results, cows with a small number of negative EBBV were significantly inferior in terms of reproductive performance. On the other hand, the subgroup with

a moderate number of negative EBBV was superior to the subgroup of cows genetically inclined to suffer from a prolonged negative EB, but this difference was not significant.

Villa-Godoy et al. (1988), Spicer et al. (1990), and Reist et al. (2003) did not find phenotypic relationships between anovulatory periods postpartum and average EB. However, Staples et al. (1990) reported that cows showing their first luteal activity after DIM 63 had a lower feed intake and greater loss of BW and, therefore, a higher magnitude of negative EB. This is consistent with Patton et al. (2007), who indicated that the average daily EB within the first 4 wk postpartum is positively related to the likelihood of fewer days to resumption of ovarian activity. Banos and Coffey

Table 11. Effect of parameters describing the genetic merit for energy balance on the subsequent reproductive performance

Trait	Interval from calving to first AI			Days open		
	No.	Mean	SD	No.	Mean	SD
Difference between BV ¹ for DIM 11 and 55						
Positive	74	141.49 ^a	66.39	44	162.02 ^a	78.17
Low to moderate	140	137.64 ^a	58.52	66	143.55 ^a	53.21
Negative	41	146.56 ^a	82.76	19	153.58 ^a	83.82
Average BV ¹ for DIM 11 to 55						
High	79	136.71 ^a	65.58	39	148.41 ^a	59.22
Medium	114	143.53 ^a	67.07	59	159.51 ^a	83.24
Low	62	138.48 ^a	61.18	31	139.42 ^a	35.89
Sum of negative BV ¹ across the entire period (DIM 11 to 180)						
Low negative	77	151.82 ^a	73.14	43	169.84 ^a	96.60
Moderate negative	60	125.12 ^a	46.07	32	141.75 ^a	39.85
High negative	40	157.85 ^a	76.94	19	149.26 ^a	55.65
Number of negative BV ¹ across the entire period (DIM 11 to 180)						
Small	75	140.91 ^a	66.17	33	158.37 ^{ab}	57.57
Moderate	47	145.28 ^a	62.12	30	133.12 ^a	34.86
Large	55	147.55 ^a	73.72	31	178.42 ^b	107.16

^{a,b}Means with different superscripts within a column and trait are significantly different ($P < 0.05$).

¹BV = energy balance breeding value.

(2010) investigated the genetic association between fertility and direct and indirect body energy traits recorded across lactation. They reported that the interval from calving to resumption of ovarian activity showed a negative genetic correlation (r_g) with BCS ($r_g = -0.50$ to -0.74), in particular within the first 25 to 50 DIM. Days of negative EB, rate of recovery of EB during the postpartum period of negative EB, sum of negative EB, nadir of energy content, as well as days from calving to nadir of energy content were negatively but not significantly correlated with the onset of first ovarian activity. Veerkamp et al. (2000) also reported a negative genetic correlation ($r_g = -0.60$) between resumption of ovarian activity and EB, but this correlation was associated with a high standard error as well.

Regarding the parameters “duration of first luteal phase” and “area under curve of first luteal activity,” the subgroup with a “positive difference between BV from DIM 11 to 55” had a significantly longer luteal phase and a greater AUC, respectively, than cows with a low to moderate or negative difference. This result is in contrast to our aforementioned results; therefore, it remains unclear whether the shape of EBBV curve is an adequate selection criterion.

Considering the parameter AUC, Spicer et al. (1990) reported similar results. Cows with negative EB during the first 12 wk postpartum had a smaller progesterone area during first and second estrous cycle compared with cows that had a positive EB during the first 12 wk postpartum ($P < 0.01$). This is not, however, in line with Villa-Godoy et al. (1988), who did not find a phenotypic association between AUC and EB; that is, regarding the detectable amount of progesterone in skim milk (area) of the first estrous cycle and the mean EB (DIM 1 to 9). Nevertheless, they found a relation for the second and third estrous cycle. Those authors also reported that the time from parturition to EB nadir and the magnitude of EB nadir were associated with progesterone in skim milk (AUC) within second and third estrous cycle. Other studies indicated that the detectable amount of progesterone in milk is important for embryo survival after AI (Stronge et al., 2005; McNeill et al., 2006). Thus, further investigations are needed to assess the effect of genetic merit for EB on reduced embryo survival due to decreased progesterone concentrations.

A subset of cows did not receive hormonal applications for superovulation. For these cows, insemination data were available, and the influence of genetic merit for EB on the interval to first AI was assessed. Cows genetically inclined to a prolonged or severe negative EB had a longer interval from calving to first AI, but although the global F -test showed a significant effect of both traits on fertility, differences between single

groups were not statistically significant ($P > 0.05$). This could be due to the small sample size, but it is more likely due to the bull dam performance test that was run at the Karkendamm farm within the observation period. Cows that passed the performance test were not inseminated until DIM 100. Thus, the effect of the genetic merit for EB on the interval to first AI might be reduced and should be re-evaluated on an independent data set. However, Berry et al. (2003) investigated the genetic relationships between BCS and fertility and found a negative genetic correlation between mean BCS and days to first service of -0.37 . This is also in accordance with de Haas et al. (2007) who estimated a genetic correlation between BCS and days to first service ranging from -0.14 to -0.45 across lactation.

Regarding days open, parameters describing the genetic merit for EB showed no distinct effects. We had expected that cows with a high and medium genetic merit for EB would be superior in days open (lower number) compared with cows with a low genetic merit for EB. However, all we found were significant longer days open for cows with the lowest genetic merit expressed through many days with negative EBBV compared with cows that had moderate numbers of days with negative EBBV. The small number of animals ($n = 94$) might explain these results. However, this result is comparable with the findings of Reist et al. (2003) to a certain extent. They reported that cows with a lower severity of EB nadir were more likely to have fewer days open.

CONCLUSIONS

Cows with a higher genetic merit for early lactation EB had significantly fewer days to first luteal activity. Thus, selection on above average EBBV from 11 to 55 DIM would reduce the calving interval and therefore has the potential to enhance productivity. Likewise, a comparatively small number of days with negative EBBV from 11 to 180 DIM is favorable. Furthermore, evidence indicates that the genetic merit for EB determines the amount of detectable progesterone in skim milk but this should be re-evaluated on a more comprehensive data set. Moreover, further investigations are needed to assess the effect of genetic merit for EB on reduced embryo survival by decreased progesterone concentrations. It must be taken into account that (up-to-date) EBBV can only be estimated for research herds, because recording of individual cow feed intake is not feasible under commercial conditions. Nevertheless, international networking; for example, within in the framework of the project gDMI (global Dry Matter Initiative), and the use of genomic tools might allow identification of positive QTL variance in specifically

designed data sets and to use this knowledge in advanced breeding programs.

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