The Relationship Between Body Energy Traits and Production and Fitness Traits in First-Lactation Dairy Cows

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ABSTRACT

Daily breeding values for various body energy traits were estimated from nationally recorded linear type information using random regression techniques. These traits included predicted live weight, growth rate (GR), and several measures of body energy during first lactation. The relationship between the individual linear type traits, body energy traits, and other production and fitness traits was examined by estimating the approximate genetic correlations (and standard errors) from adjusted predicted transmitting ability correlations. The relationship between fitness and body traits was further examined by calculating the partial correlation between the pairs of traits at a constant milk yield. Daily sire solutions for type traits showed that there were differences in how cows changed body shape across lactation. On average, cows lost body energy in early lactation but regained it by the end of the lactation. However, there was large variation, with the daughters of some sires still in negative energy balance by the end of lactation. The estimates of genetic correlation of linear type traits with production and fitness traits agreed with previous linear point estimates. The fertility traits were correlated across lactation with all linear type traits studied and indicated that bigger animals tend to have poorer fertility. There was an unfavorable correlation between production and GR; therefore, higher producing cows were more likely to have lower GR early in first lactation. The results also showed that higher producing animals were likely to lose body energy during the peak of first lactation. This is mirrored in the relationship of early lactation energy balance with somatic cell count and longevity, indicating that peak lactation is a critical time in terms of metabolic pressures on the dairy cow.

Key words: fitness, energy balance, type trait, correlations

INTRODUCTION

Energy balance can be described as the difference between the energy a cow expends (for lactation, growth, and reproduction) and the energy a cow gains from the intake of nutrients (Forbes, 1983). If there is a shortfall in the nutrient intake of the animal and what is required for energy expenditure, the cow will have to reduce energy expenditure (e.g., reduce milk yield) or mobilize body reserves to meet energy requirements. Many studies have shown the negative impact of high production on functional performance in the dairy cow (Wiggans, 1991; Jairath et al., 1995; Veerkamp et al., 2002). It is suggested that selection for increased milk production has resulted in the partial “shift” of nutrients away from maintaining functional fitness, as manifested through reduced BCS (Veerkamp et al., 2001; Dechow et al., 2002; Kadarmideen and Wegmann, 2003).

Wall et al. (2005) showed how random regression techniques could be used to estimate the profiles of type trait changes across lactation. The daily solutions for type traits were used to predict daily sire breeding values for daughter live weight (**LWT**) across first lactation, which showed substantial variation. A loss in bodyweight is partly indicative of the cow mobilizing body reserves and partitioning the energy released toward lactation. Previous studies have shown that cows will typically mobilize body reserves at the start of lactation, as indicated by a reduction in BCS (e.g., Jones et al., 1999). However, some cows are able to recover this lost body energy before the end of lactation or in the dry period, whereas others are not (Coffey et al., 2003). Although absolute body energy loss has been related to health and fertility problems, the profile of the body energy changes across lactation has not yet been studied for these relationships.

The contribution of body energy to milk production is thought to have an effect on dairy cows, leading to poorer health and fertility and eventually involuntary culling. This has led to the conclusion that dairy cows appear to be less “robust” or adaptable than in the past. A way to address these concerns in national breeding programs would be to determine whether increased

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lifespan, health, and welfare can be delivered more efficiently through including traits related to robustness in a broader breeding index. Harnessing early life body energy information may help improve estimates of later life performance for these fitness traits.

The aim of this study was to produce bull profiles for daughter performance for various body energy traits, including growth, using random regression techniques. The relationship between production and fitness traits with type, growth, and body energy traits was examined.

MATERIALS AND METHODS

The body type traits chosen were BCS, stature (**STAT**), angularity (**ANG**), body depth (**BD**), and chest width (**CW**) because they relate to volumetric dimension and body fatness. These traits are recorded by Holstein UK as part of the national type classification scheme. They were adjusted for field officer by scaling records so that individual officer standard deviations were equal to the mean standard deviation of all officers (Brotherstone, 1994). Type records were included in the data set if the DIM of the cow were between 10 and 290 d (Wall et al., 2005). Records for first-lactation Holstein-Friesian animals with linear type records and at least 3 monthly milk tests were taken for animals calving from 1997 until the end of April 2005. A full pedigree (up to 4 generations) for each sire was selected from a combination of the Holstein UK and milk-recording organizations' databases and fitted in the analysis for each type trait.

A random regression model using Legendre polynomial functions described by Wall et al. (2005) was used to model the change in type traits across lactation using ASREML (Gilmour et al., 2002). A total of 9 residual error classes were fitted from 10 to 290 DIM. The daily sire solutions for BD, CW, STAT, and ANG were then used to predict LWT and thereby differences in LWT of sires' daughters across first lactation (Wall et al., 2005). The random regression model fitted was as follows:

$$Y_{ijk} = \mu + hys_i + month_j + \beta_1 X_{age} + \beta_2 (X_{age})^2 + \sum_{m=0}^{n-1} \gamma_m P_m(dim) + \sum_{m=0}^{n-1} \alpha_{km} P_m(dim) + e_{ijk}$$

where Y_{ijk} = type trait record (BCS, BD, CW, STAT, ANG); hys_i = fixed effect of i th herd-by-year-by-season (3 seasons per year) of type classification visit; $month_j$ = fixed effect of the j th month of calving; β_1 and β_2 = linear and quadratic regression coefficients of

dependent variable (Y) on age effect; X_{age} = continuous variable representing age of animal (in months) at calving; dim = DIM at type classification; γ_m = fixed regression coefficients; α_{km} = random regression coefficients for sire k ; e_{ijk} = residual random error term; m = order of the polynomial (linear for BD, CW, and STAT; quadratic for ANG; cubic for BCS); and $P_m(dim)$ = m th Legendre polynomial evaluated at dim .

Coffey et al. (2003) combined predicted daily LWT and BCS to estimate energy balance across lactation for the daughters of sires by predicting body lipid and protein weight. However, the equations to predict body lipid and protein weights were derived from studies of Wright (1982) based on the body composition of Friesian cows and the equations may not be relevant to that of a modern Holstein dairy genotype. The US National Research Council (NRC, 2001) published predictions of body lipid and protein weights from LWT and BCS based on equations derived by Fox et al. (1999), which used various genotypes, including Holstein, and accounts for all classes and ages of beef and dairy cattle. The NRC (2001) net energy system was used to predict daily body lipid and protein weight and body energy content (**BEC**). Changes in daily body lipid and protein weights were used to predict the daily energy balance (**EB**) and cumulative energy balance (**CEB**) using the effective energy system of Emmans (1994). For further information see the study of Banos et al. (2006).

Each bull had a prediction of their daughter's CEB at the end of lactation. A negative value indicated that daughters of that bull were genetically predisposed to being in energy deficit by the end of their first lactation. Coffey et al. (2003) used this CEB figure to discount the sire milk PTA. The present study adapts the method of Coffey et al. (2003) to adjust sire fat and protein estimated breeding values for the energy deficit using the following steps: 1) the energetic cost of producing a kilogram of milk fat and protein for each bull was estimated (NRC, 2001); 2) the kilograms of fat and protein energy equivalent to the CEB of each bull were estimated; 3) the bull's fat and protein breeding values were then adjusted for the energetic content of the CEB.

Correlation of Type Traits, Growth Traits, and Body Energy Traits with Production and Fitness Traits

The daily estimates for the type traits, LWT, growth rate (**GR**, calculated by daily differences in daughter LWT or by daily changes in cow BW), BEC, EB, and CEB were correlated with sire breeding values for profit index (**PIN**), SCC, lifespan (**LS**), calving interval (**CI**), and nonreturn rate (**NR**) after 56 d produced in

November 2005 in the UK (Milk Development Council, 2005). The energy-adjusted milk fat and protein breeding values were also correlated with the sire breeding values for PIN, SCC, LS, CI, and NR. The PIN is an economic index for production traits combining breeding values for 305-d milk, fat, and protein using relative economic values for each. Lifespan is estimated directly from completed lactation information and indirectly from type traits (Brotherstone et al., 1997). Somatic cell count PTA are produced using an animal model and information from the first 3 lactations (Mrode et al., 1998). The minimum reliability for inclusion in the correlation estimation for PIN was 90% and for LS, SCC, and fertility was 70%. The PTA were used to estimate approximate genetic correlations by accounting for the reliability of the PTA in the estimation of the correlation (Hickman et al., 1969; Calo et al., 1973):

$$\hat{r}_{1,2} = \frac{\sqrt{\Sigma REL_1 \times REL_2}}{\Sigma (REL_1 \times REL_2)} \times r_{1,2}$$

where REL_1 and REL_2 = reliabilities of the PTA of trait 1 and trait 2, and $r_{1,2}$ = correlation between the PTA for traits 1 and 2.

The standard error of the correlation was estimated using the following equation:

$$s.e.r = \sqrt{\frac{1 - \hat{r}_{1,2}^2}{n - 2}}$$

where n is the number of data records (sires) used to estimate the genetic correlation (Sokal and Rohlf, 1995).

The partial correlation coefficients between the linear type traits and fitness traits were calculated to examine the correlation between the traits at a constant milk yield (Sokal and Rohlf, 1995). Examining the correlation between the type traits and fitness traits at a constant milk yield shows if the relationship is significant or being mediated through the relationship with milk yield:

$$\hat{r}_{1,2}^* = \hat{r}_{1,2} - \frac{r_{1,3}r_{2,3}}{\sqrt{(1 - r_{1,3}^2)(1 - r_{2,3}^2)}}$$

where $\hat{r}_{1,2}^*$ is the partial correlation coefficient between type trait and fitness trait at a constant milk yield, and $r_{1,3}$ and $r_{2,3}$ = correlation of trait 1 (type trait) with milk yield and trait 2 (fitness trait) with milk yield.

The significance of the partial correlation (if significantly different from zero) was tested by calculating the t statistic (Sokal and Rohlf, 1995):

$$t = \hat{r}_{1,2}^* \sqrt{\frac{n - 2 - m}{1 - \hat{r}_{1,2}^*^2}}$$

where m is the number of variables kept constant, which in this case is 1, milk yield.

Correlations between type traits and milk yield were taken from Brotherstone (1994), that between milk yield and lifespan was taken from Brotherstone and Hill (1991), that between milk yield and fertility were taken from Wall et al. (2003), and that between milk yield and SCC were taken from Mrode et al. (1998).

RESULTS

After editing, the data set consisted of 311,719 daughter records for 11,736 sires in 32,997 herd-year-season of inspection classes. Records were relatively evenly distributed across the 9 residual classes ranging in size from 14,466 records (1 to 29 d) to 48,932 records (90 to 119 d). Daily sire solutions and reliabilities were estimated for BCS, BD, CW, STAT, and ANG and combined with the fixed population curve from each analysis (Banos et al., 2004). These were then used to predict LWT across time (Wall et al., 2005). Daily sire values for GR were derived from daily sire LWT values by subtracting current LWT from the LWT on the previous day. The daily value for LWT was a combination of the daily solutions for ANG, BD, CW, and STAT (linear random effect), with ANG having the highest order of fit (quadratic). Using the daily (or divided) differences in the LWT to estimate the daily value for GR is equivalent to taking the first derivative of the quadratic curve for predicted LWT. Figure 1 shows that, on average, LWT breeding values increased across lactation, and GR breeding values increased linearly across lactation.

Body condition score and LWT breeding values were used to estimate daily sire breeding values for daughter body energy content (BEC, MJ); EB and CEB were derived from daily BEC values. Profiles of daughter body energy traits (BEC, EB, and CEB) were produced for sires and displayed variation across lactation with significant differences between sires. Across the lactation, BEC increased with a small dip at the start and end of lactation (Figure 1). The daily breeding value for EB was negative and rose quickly at the start of lactation to 3.52 MJ/d on d 150 before dropping at the end of lactation (d 280) to an average value of -2.66 MJ/d (Table 1). The CEB tended to increase across the

Figure 1. Average ($\pm$ SD) predicted live weight (— LWT, kg) and growth rate (---- GR, kg/d), daily body energy content (BEC, MJ), daily energy balance (EB, MJ), and cumulative energy balance (CEB, MJ). Each trait is predicted from the daily sire breeding values for angularity, body depth, chest width, stature, and BCS.

lactation with a slight decrease at the start and end of lactation (Figure 1). Figure 1 and Table 1 show that the variance in daily breeding values for CEB increased across time resulting in a large range of CEB breeding values by the end of lactation. It must be

noted that the range in EB daily breeding values increased across first lactation (Table 1), and this increase in EB values was compounded in CEB because it is a sum of adjacent EB values. A total of 36% of the bulls had a negative CEB by d 290 of lactation.

Table 1. Descriptive statistics of sire breeding values for production, fitness, and body energy traits¹

Sire breeding value	Mean	SD	Minimum	Maximum
Fat (kg)	2.2	8.7	-35.6	30.4
Protein (kg)	3.3	8.1	-28.7	40.3
PIN (£)	8.3	21.5	-69.0	72.0
LS (lactations)	0.0	0.2	-0.7	0.8
SCC	1.7	11.7	-32.0	43.0
CI (d)	1.8	3.8	-7.0	18.0
NR (0/1)	-1.0	1.2	-4.3	2.9
BEC20 (MJ)	4,931.5	262.5	4,217.5	5,993.9
BEC150 (MJ)	5,056.6	206.9	4,460.4	5,937.9
BEC280 (MJ)	5,256.9	232.7	4,510.9	6,030.7
EB20 (MJ/d)	-8.0	5.0	-19.4	26.7
EB150 (MJ/d)	3.5	2.7	-2.7	13.1
EB280 (MJ/d)	-2.7	4.2	-14.7	22.8
CEB20 (MJ)	-99.5	70.6	-313.3	297.5
CEB150 (MJ)	107.7	401.3	-1,126.3	2,102.7
CEB280 (MJ)	358.1	504.6	-1,202.2	2,152.7
Fat _{AD} (kg)	-3.2	9.0	-41.1	24.9
Prot _{AD} (kg)	-5.3	8.4	-37.0	32.8

¹PIN = production index; LS = lifespan; CI = calving interval, NR = nonreturn rate; BEC = body energy content at 20, 150, and 280 DIM; EB = energy balance at 20, 150, and 280 DIM; CEB = cumulative energy balance at 20, 150, and 280 DIM; fat_{AD} and prot_{AD} = energy-adjusted milk fat and protein.

Figure 2. Approximate genetic correlation [$r(G)$] between linear type traits: angularity (ANG), body depth (BD), chest width (CW), and stature (STAT) and production index (PIN, $\triangle$), lifespan (LS, $\square$), SCC ($\circ$), calving interval (CI, $\times$), and nonreturn rate (NR, $\blacksquare$). Standard errors of the correlations ranged from 0.035 to 0.05 across the lactation.

There was large variation in individual sire profiles for daughter body energy (not shown) indicating that some bulls' daughters finished in positive energy balance and others completed their first lactation in negative energy balance. The negative CEB profiles show that daughter body energy was lost at the start of lactation and was not regained during lactation, culminating in a negative CEB breeding value by d 290. The converse was true for positive CEB profiles, which showed that the daughters of certain sires were predicted to gain body energy over the lactation.

After setting minimum reliabilities for the traits, a total of 745 sires were used to estimate the correlation between breeding values across lactation. Figure 2 shows the approximate genetic correlation of the type traits used to predict live weight (ANG, BD, CW, and STAT) with a selection of UK production and fitness breeding values (PIN, LS, SCC, CI, and NR). The standard errors of the correlations ranged from 0.035 to 0.05 and almost all results presented were significantly different from zero. The one exception is STAT, which was not significantly correlated to PIN, LS, and SCC during first lactation before and after adjustment for the correlation with milk yield. The BD, CW, and

STAT had a consistent correlation with all traits across lactation. Body depth had a negative correlation with LS (-0.23 , or -0.30 at constant milk yield on DIM 150) suggesting that animals with deeper bodies are likely to have a shorter life. Body depth, CW, and STAT were also correlated with CI (0.19 , -0.19 , and 0.18 , respectively). However, only the correlation between CW and CI was significantly different from zero when adjusted to a constant milk yield (-0.11), which suggests that animals with narrow chests (or thin cows) are likely to have a longer interval between calvings independent of milk yield (Table 2). Body depth, CW and STAT were also correlated with NR (-0.19 , -0.26 , and 0.12 , respectively) suggesting that taller animals with deep bodies and wide chests (or big cows) are likely to return to service within 56 d of a first service. However, after adjusting to a constant milk yield, only the correlation between CW and NR remained significant, increasing to 0.34 .

The correlation of ANG with other traits varied across lactation, being lower at the start and end of lactation (Figure 2). The production index, PIN, had a low correlation with the traits apart from ANG where it rose to 0.39 on d 180 of lactation. Somatic cell count

Table 2. Correlations and partial correlation coefficients between body type traits and fitness traits at a constant milk yield at various DIM throughout first lactation

Trait ¹	DIM	Correlation ²				Correlation at constant milk			
		LS	SCC	CI	NR	LS	SCC	CI	NR
BD	50	-0.24 ^a	0.07	0.20 ^a	-0.19 ^a	-0.28 ^a	0.05	0.06	-0.03
	100	-0.27 ^a	0.08	0.21 ^a	-0.21 ^a	-0.31 ^a	0.06	0.07	-0.05
	150	-0.27 ^a	0.09 ^a	0.21 ^a	-0.21 ^a	-0.31 ^a	0.07	0.07	-0.05
CW	50	-0.12 ^a	-0.04	-0.19 ^a	-0.24 ^a	-0.09 ^a	-0.03	-0.11 ^a	-0.33 ^a
	100	-0.09 ^a	-0.04	-0.19 ^a	-0.25 ^a	-0.07	-0.03	-0.11 ^a	-0.35 ^a
	150	-0.07	-0.04	-0.19 ^a	-0.26 ^a	-0.05	-0.03	-0.11 ^a	-0.35 ^a
STAT	50	-0.06	0.03	0.18 ^a	-0.12 ^a	-0.10 ^a	0.01	0.05	0.02
	100	-0.08 ^a	0.02	0.18 ^a	-0.13 ^a	-0.11 ^a	0.00	0.05	0.02
	150	-0.04	0.01	0.17 ^a	-0.12 ^a	-0.08 ^a	-0.01	0.04	0.02
ANG	50	-0.14 ^a	0.13 ^a	0.40 ^a	-0.11 ^a	-0.21 ^a	0.10 ^a	0.12 ^a	0.21 ^a
	100	-0.25 ^a	0.21 ^a	0.45 ^a	-0.14 ^a	-0.33 ^a	0.19 ^a	0.18 ^a	0.17 ^a
	150	-0.27 ^a	0.24 ^a	0.44 ^a	-0.15 ^a	-0.35 ^a	0.21 ^a	0.17 ^a	0.16 ^a
BCS	50	0.06	-0.11 ^a	-0.33 ^a	-0.06	0.12 ^a	-0.09 ^a	-0.10	-0.32 ^a
	100	0.17 ^a	-0.21 ^a	-0.35 ^a	-0.07	0.24 ^a	-0.19 ^a	-0.12 ^a	-0.34 ^a
	150	0.18 ^a	-0.21 ^a	-0.36 ^a	-0.04	0.24 ^a	-0.19 ^a	-0.13 ^a	-0.30 ^a

^aCorrelations with superscripts are significantly different from zero ($P < 0.05$).

¹BD = body depth; CW = chest width; STAT = stature; ANG = angularity.

²LS = lifespan; CI = calving interval; NR = nonreturn rate.

did not have a strong correlation with all the traits although it had a moderate correlation of 0.23 with ANG in mid lactation, which dropped slightly to 0.2 at a constant milk yield. The correlation of ANG with CI was highest at d 120 (0.45) and indicated that more angular cows would have a longer calving interval. This correlation dropped sharply after adjustment to a constant milk yield to 0.18, which was significantly different from zero.

Figure 3 shows the approximate genetic correlations of the selected body energy traits (BCS, LWT, GR, BEC, EB, and CEB) with production and fitness breeding values (PIN, LS, SCC, CI, and NR). Body condition score had a favorable correlation with CI that was highest (-0.30 to -0.33) from d 50 to 250, indicating that fatter cows (high BCS) are associated with shorter intervals between calvings. The correlation between CI and BCS at constant milk yield was lower (0.12 in mid lactation), but significant. Live weight had low correlations with the majority of traits across lactation. However, GR, which is the first derivative of the LWT curve, displayed stronger correlations with the traits. For example, in early lactation the correlation of PIN with GR was -0.3, whereas the correlation with LWT in the same period was close to zero. This implies that higher production is associated with a lower early lactation GR, independent of overall weight. Early lactation growth was moderately correlated to increased lifespan (0.18), although the magnitude of this correlation decreased over time.

The genetic correlations of BEC with the production and fitness traits were similar (slightly smaller) to those seen with BCS and the production and fitness

traits (Figure 3). This could suggest that body energy content is highly predicted from the fatness levels (BCS) of the cow. This is further illustrated by the high correlation (0.96 to 0.99) between BEC and BCS breeding values on any particular day.

Both EB and CEB are measures of the rates of change in BEC across lactation. However, their correlation with both production and fitness traits was low and in many cases not significantly different from zero, especially compared with the relationships seen between BEC and these traits (Figure 3). The correlations of daily EB values with other traits over lactation were not stable. For example, the correlation of EB with SCC was -0.14 in early lactation and +0.17 on d 200, but was not significantly different from zero from d 110 to 170. If these significant correlations across time are a fair representation of the genetic relationship between SCC and EB, it suggests that cows gaining body energy early in lactation will have a lower SCC, whereas animals gaining later in lactation will have a higher SCC. The CEB is the cumulative measure for EB and accounts for continued days of energy loss in a cow. The relationship of CEB with production and fitness traits was relatively consistent across lactation and ranged from -0.19 with PIN to 0.13 with LS.

Deducting the body energy equivalent of kilograms of milk fat and protein from the sire breeding value for these traits resulted in a correlation of 0.92 and 0.94, respectively, between the ranking of sires before and after adjustment. Table 3 shows that the genetic correlation between adjusted milk fat and protein and fitness traits tends to be unfavorable, particularly with fertility traits, such that higher levels of fat and pro-

Figure 3. Approximate genetic correlation [r(G)] between body energy traits: BCS, live weight (LWT), growth rate (GR), body energy content (BEC), energy balance (EB), and cumulative energy balance (CEB) and production index (PIN, △), lifespan (LS, □), SCC (◇), calving interval (CI, ×), and nonreturn rate (NR, ■). Standard errors of the correlations ranged from 0.035 to 0.05 across the lactation.

Table 3. Approximate genetic correlations between fat and protein yield (kg) adjusted and unadjusted for negative energy balance and lifespan, SCC, calving interval, and nonreturn rate

	Fat (adjusted)	Protein (adjusted)	Fat (unadjusted)	Protein (unadjusted)
Lifespan	-0.11 ± 0.038	-0.12 ± 0.038	-0.13 ± 0.38	-0.14 ± 0.038
SCC	0.11 ± 0.034	0.17 ± 0.033	0.11 ± 0.034	0.17 ± 0.032
Calving interval	0.36 ± 0.029	0.43 ± 0.027	0.35 ± 0.029	0.43 ± 0.027
Nonreturn rate	-0.34 ± 0.041	-0.66 ± 0.046	-0.33 ± 0.041	-0.67 ± 0.046

tein will result in shorter lifespan, higher SCC, and poorer fertility.

DISCUSSION

Overall, LWT increased across first lactation (Figure 1) as reported in previous studies (Berry et al., 2005; Coffey et al., 2006). Growth rate increased toward mid lactation and slowed down thereafter, suggesting that cows are still maturing in their first lactation. On the whole, CEB increased across lactation. However, there was large variation in CEB breeding values by the end of lactation indicating that daughters of some sires can be in chronic negative EB and under metabolic stress whereas the daughters of another may be in favorable energy balance and able to store body lipid.

Figure 1 shows that the daughters of some bulls remained in positive CEB across the whole lactation whereas the daughters of other bulls were consistently in negative CEB. The negative CEB profiles show that the majority of this energy was lost in early lactation and not regained by d 290. The converse was true for positive CEB profiles, which showed that the daughters of certain sires were predicted to gain body energy in early lactation. This could indicate that these cows partition nutrient resources to growth early in their first lactation. On average, the lowest CEB breeding value was on d 50 of lactation when it was -191 MJ. This is a critical point in the lactation as it is close to peak lactation, but it is also when the cow requires energy to prepare for further breeding. Understanding which cows are losing large amounts of body energy in early lactation could help farmers identify which animals require more feed in the dry period and early lactation.

It is important to note the differences between results from the current study and those of Coffey et al. (2003) who found a higher level of body energy loss throughout lactation. First, different energy systems were used to predict the body lipid and protein weights in these studies. Also, the study of Coffey et al. (2003) did not convert BCS from the 9-point dairy scale to the 5-point beef scale as used by Wright (1982), resulting in an overprediction of body energy. It should also be noted that the random regression modeling might result in a slightly inflated variance at the extremities where the data are more scarce (Wall et al., 2005). However, the general trends in changes in the type traits and the body energy traits, derived from the type daily solutions, for the majority of the lactation agree with other published results.

The estimates of genetic correlation of linear type traits with production and fitness traits agree with previous linear point estimates (Pryce et al., 2000;

Caraviello et al., 2004; Haile-Mariam et al., 2004). However, only ANG (up to 0.37) and CW (up to -0.15) had a significant correlation with production traits as described by PIN. The component traits in PIN (kg of milk, fat, and protein) were also correlated with ANG. For example, at 100 DIM the correlation between ANG and PIN was 0.31 whereas the correlations with yields of milk, fat, and protein were 0.37, 0.28, and 0.12, respectively. Only BD and ANG were significantly correlated with LS (-0.27 in mid lactation for both traits). Cows with deeper bodies were more likely to have a shorter life as reported in previous studies (Short and Lawlor, 1992; Pérez-Cabal and Alenda, 2002).

Body depth, CW, and STAT were not significantly correlated to udder health (as predicted by SCC) agreeing with previous phenotypic (Collard et al., 2000) and genetic (Rogers et al., 1991) studies. However, ANG was shown to have a significant correlation with SCC (up to 0.24 in mid lactation, or 0.21 at constant milk yield), slightly lower than that seen by Berry et al. (2004) indicating that more angular cows are likely to have a higher SCC independent of milk yield. Angular cows will have a lower BCS and therefore lower body energy reserves, which could adversely affect the general health of the cow resulting in higher SCC (Berry et al., 2004).

The fertility traits were correlated with body type traits across lactation indicating that bigger animals tend to have poorer fertility. There was a moderate to strong genetic correlation between ANG and CI (up to 0.45, or 0.18 at constant milk yield) and between BCS and CI (up to -0.30 , or -0.13 at constant milk yield) agreeing with previous studies (Pryce et al., 2000; Banos et al., 2004). Angularity has been shown to be strongly correlated with milk and BCS (Haile-Mariam et al., 2004), both of which are strongly correlated to fertility traits, and it is likely that its influence on fertility is, in part, being mediated indirectly via milk. However, the correlation of CI with BCS and ANG is significant at a constant milk yield suggesting that thinner cows do have poorer fertility, independent of milk yield. Body energy content had very similar relationships with the production and fitness traits across lactation to those seen with BCS.

Other studies have shown moderate (0.26 to 0.66; Brotherstone, 1994) to high (0.81; Short and Lawlor, 1992) correlations between the BD, CW, and STAT traits. It is important to note that the body traits in this study were selected as predictors of live weight and are therefore related to overall body size. This study has shown that the traits are correlated to both production and fitness traits in their own right and therefore could be useful as indicator traits.

Live weight was correlated with production across lactation (Figure 3) indicating that higher producing cows will be lighter. However, the higher producing cows are likely to have a lower GR in early lactation (or could even be losing weight). Coffey et al. (2006) showed that the higher yielding cows had a lower GR than average-yielding cows in first lactation. Early-lactation GR was also correlated with LS. Animals with higher GR in early lactation are more likely to have a higher longevity. Animals that are still growing in early lactation may not have reached maturity by first calving and could be partitioning energy toward growth and away from milk production with favorable effects on overall survival in the herd.

The EB traits (EB and CEB), which are indicators of the loss or gain of energy from the cow's own body reserves throughout lactation, had low correlations with production and fitness traits, and these correlations were not significantly different from zero after mid lactation. Fertility was not significantly correlated with either EB trait across the whole lactation. Lifespan and SCC are correlated to EB in early lactation (approximately 0.1 and -0.15 , respectively) indicating that animals losing body energy are likely to have a reduced LS and a higher SCC. Peak lactation is a critical time of metabolic stress in the dairy cow, with feed and body energy resources being partitioned toward milk production, potentially at the expense of her own functionality (Lucy, 2001). The study of Collard et al. (2000) showed on a phenotypic level that various EB traits were unfavorably correlated to various health and reproductive disorders, which could have a reciprocal effect on the longevity of the cow, but not related to fertility traits.

The correlation between fat and protein, adjusted for loss of body energy, and LS was unfavorable but low (-0.11 and -0.12 , respectively) and similar to the study of Tsuruta et al. (2005). The correlation between SCC and adjusted fat and protein was unfavorable (0.11 and 0.17, respectively) but not as strong as the values reported by Stott et al. (2005) of 0.19 and 0.22, respectively, with unadjusted fat and protein. Energy-adjusted milk traits should, in part, account for the body energy that a cow loses during lactation. This loss of body energy has been shown to have a subsequent effect on fitness traits, particularly if large amounts of body energy are lost during the lactation (Berry et al., 2004). Adjusting the fat and protein breeding values for the body energy a bull's daughters lose during the lactation would help to account for the body energy lost toward production and away from functionality. Table 3 should therefore reflect the relationship between production and fitness traits in cows that do not give up their body energy to support lacta-

tion. If the loss of body energy does have an effect on fitness traits, we would expect that adjusting the production traits would result in a lower correlation between SCC and fat and protein.

Female fertility has caused the biggest concern to commercial milk producers as selection leads to a continued increase in production levels. Wall et al. (2003) showed that there was a strong unfavorable correlation between milk yield and CI and NR of 0.27 and -0.45 , respectively. Brotherstone et al. (2002) showed that 305-d combined fat and protein kilograms were also unfavorably correlated with CI and NR (0.40 and -0.29 , respectively). This study showed that adjusted fat had a moderate correlation with CI and NR (0.36 and -0.34 , respectively) and adjusted protein had a moderate to strong correlation with the 2 fertility traits (0.43 and -0.66 , respectively). The correlation of fertility traits with production traits did not drop after adjusting for body energy, as seen with SCC. The correlation would be expected to drop if the loss of body energy to production had a subsequent unfavorable effect on reproductive fitness. However, the adjustment to the 305-d fat and protein breeding values is based on the cumulative loss of body energy throughout the first lactation. Cows are preparing themselves for pregnancy when they are approaching, and just after, the peak of lactation. By using the cumulative loss of body energy as the adjustment factor, we may be losing information on the loss of body energy at the critical point of lactation with regards to fertility.

The majority of national indices around the world have been broadened with varying emphasis on fitness and production traits (Miglior et al., 2005). The aim of incorporating health, fertility, and longevity information in a selection index with production is to optimize the response in fitness traits relative to production traits. Incorporation of traits related to body energy into an index of production and fitness traits could have a double benefit in terms of aiding the prediction of breeding values for correlated traits (e.g., lifespan) as well as accounting for the costs of production of animals that lose body reserves to maintain production.

CONCLUSIONS

Selected body type traits were shown to be correlated with fitness traits across lactation, independent of their relationship with milk yield. These traits could be used to help in the prediction of fitness traits, including lifespan. Daily sire proofs for body energy traits including growth rate and body energy content were produced from daily solutions of linear type traits and showed differences between sires in how their

daughters grow and gain or lose body energy across lactation.

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