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Genetic relationships between weight loss in early lactation and daily milk production throughout the lactation in Holstein cows

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ABSTRACT

After calving, high-yielding dairy cows mobilize body reserves for energy, sometimes to the detriment of health and fertility. This study aimed to estimate the genetic correlation between body weight loss until nadir and daily milk production (MY24) in first- (L1) and second-lactation (L2) Holstein cows. The data set included 859,020 MY24 records and 570,651 daily raw body weight (BWR) phenotypes from 3,989 L1 cows, and 665,361 MY24 records and 449,449 BWR phenotypes from 3,060 L2 cows, recorded on 36 French commercial farms equipped with milking robots that included an automatic weighing platform. To avoid any bias due to change in digestive content, BWR was adjusted for variations in feed intake, estimated from milk production and BWR. Adjusted body weight was denoted BW. The genetic parameters of BW and MY24 in L1 and L2 cows were estimated using a 4-trait random regression model. In this model, the random effects were fitted by second-order Legendre polynomials on a weekly basis from wk 1 to 44. Nadir of BW was found to be earlier than reported in the literature, at 29 d in milk, and BW loss from calving to nadir was also lower than generally assumed, close to 29 kg. To estimate genetic correlations between body weight loss and production, we defined BWL5 as the loss of weight between wk 1 and 5 after calving. Genetic correlations between BWL5 and MY24 ranged from -0.26 to 0.05 in L1 and from -0.11 to 0.10 in L2, according to days in milk. These moderate to low values suggest that it may be possible to select for milk production without increasing early body mobilization.

Key words: genetic parameters, test-day model, body weight loss, milking robot, dairy cows

INTRODUCTION

After calving, dairy cows experience a negative energy balance when initiating milk production, and mobilize body reserves, mostly fat, to compensate. This usually results in weight loss during the first few weeks of lactation. During this period, feed intake by the cow progressively increases, and the energy ingested begins to offset the energy cost of milk production, so that body reserves can be replenished.

This cyclical pattern is normal, and reflects the fact that the change in feed intake is slower than the increase in energy demand for milk production. It also reflects the change in the mother's energy priorities between ensuring the survival of the newborn calf and preparing for the next gestation (Friggens, 2003). At the level of the individual animal, excessive mobilization of body reserves can lead to health problems such as metabolic troubles (e.g., ketosis), low immune response, and high risk of infectious disease (mastitis, metritis, claw disease, etc.), as well as low fertility (Veerkamp et al., 2001), and hampers cow longevity and economic profitability. At the population level, selection focused predominantly on high milk production—as was the case in the Holstein breed in France until the 1990s—probably tended to favor animals with a large negative energy balance after calving (Van Arendonk et al., 1991), which is a probable cause of the deterioration in fertility and mastitis resistance observed at that time. Nowadays, breeding objectives are more balanced, with positive weights on functional traits (Miglior et al., 2017), and unfavorable trends for functional traits are no longer observed. Nevertheless, the question of selecting against body weight loss after calving (i.e., in favor of a rapid adaptation of feed intake) remains of high interest because it could be more efficient than selecting for antagonistic traits. In addition, regarding feed efficiency, a high body weight loss followed by recovery is not as efficient as a rapid adaptation of feed intake,

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due to the cost of multiple chemical reactions. However, this option is possible only if milk production and body weight mobilization are not too strongly correlated. One aim of this paper is to estimate this genetic correlation, at the beginning but also all along the lactation.

Historically, the assessment of body composition and the energy balance status of dairy cows has generally been performed through visual and tactile appraisal of body fat reserves in the back and pelvic regions of the cow, generating a BCS. However, this type of assessment suffers from a high degree of subjectivity, and tends to vary from one assessor to another. For this reason, in France, scoring is performed by trained external scorers. However, this is conducted on only a fraction of farms, cannot be performed on a fixed day in milk for all cows due to the wide distribution of calving dates, and generates additional costs. Most critically, BCS is recorded only once for primiparous cows, which gives a snapshot of their adiposity at a given moment but yields no information on the rate and magnitude of body mobilization, which is a major part of the phenomenon (Lefebvre et al., 2022). Despite its potential utility, then, BCS does not typically play a significant role in French dairy selection programs.

In recent years, a growing proportion of French commercial dairy farms have been equipped with milking robots with weight plates, which automatically record the daily milk production and raw body weight (**BWr**) of lactating cows. In these farms, it is therefore possible to monitor the weight of all lactating cows throughout their productive period and, in particular, to focus on weight loss in early lactation to infer the corresponding body mobilization.

The objective of this study was to exploit the high-throughput data generated by a group of farms equipped with milking robots to estimate the evolution of genetic parameters of daily milk yield and body weight throughout lactation, as well as the genetic relationship between early body weight loss—reflecting body mobilization—and daily milk yield. Our main goal was to use these data to evaluate the possibility of decoupling production and mobilization in future dairy selection programs.

MATERIALS AND METHODS

This study was based on data routinely collected in commercial farms. We did not perform any experiment on animals; therefore, no ethical approval was required.

The data used for this study originated from 36 commercial dairy farms located in western France. The average herd size was 92 cows (range: 46–189). These herds are all members of the INNOVAL DHIS network (<http://www.innoval.com>).

In total and before any editing, data were recorded for 5,372 Holstein cows [4,464 and 3,364 cows in first (**L1**) and second lactation (**L2**), respectively; 2,456 cows had data in both L1 and L2], who calved from July 2014 to July 2018. Barns were equipped with A3 and A4 Lely milking robots (Lely; <https://www.lely.com>) that included an automatic weighing platform.

At each visit of a cow to the milking unit, the robot recorded the date and time of the visit, the weight of milk collected (MILK), and the BWr of the cow at the end of the visit. In total, more than 4.5 million visits were recorded for the 5,372 cows.

Daily Milk Yield

Consider a cow i in lactation j (1 or 2). At day in milk t , this cow goes to the milking unit k_{it} times, and the robot records its k_{it} milk yields, called $MILK_{i,j,t,k}$, respectively. Then, for each cow i in lactation j , the sum of the k_{it} milk yields of the day was calculated and standardized as a 24-h milk yield (**MY24r**):

$$MY24r(i, j, t) = \sum_{k=1}^{k_{it}} (MILK_{i,j,t,k}) \times 1,440 / \Delta_{time},$$

where Δ_{time} is the time interval (in minutes) between the last milking of the previous day and the last milking of the current day.

Because MY24r data were rather noisy, the following cleaning procedure was used. A third-order polynomial was fitted to the MY24r data within each 30-d period of each lactation of each animal, and outlier phenotypes deviating from the prediction by more than 3 standard deviations (SD) were discarded. This procedure was complemented by a visual inspection of the discarded data.

Using monthly data on fat content (**FC**) and protein content (**PC**) obtained from the national database CTIG INRAE (6.7 records on average per cow and lactation from calving to 316 DIM), we predicted for each animal i in lactation j the $FC(i,j,t)$ and $PC(i,j,t)$ at DIM t using Wilmink's lactation models:

$$FC(i,j,t) = a_{i,j} + b_{i,j} \times t + c_{i,j} \times \exp(-0.05 \times t)$$

and

$$PC(i,j,t) = d_{i,j} + e_{i,j} \times t + f_{i,j} \times \exp(-0.05 \times t),$$

where t is the DIM, and $a_{i,j}$, $b_{i,j}$, $c_{i,j}$, $d_{i,j}$, $e_{i,j}$, and $f_{i,j}$ are coefficients to be estimated for each lactation of each cow. The median of the R^2 of these models was 0.67 for FC and 0.83 for PC. These daily FC and PC predic-

tions were then used to convert MY24r(i,j,t) into fat- and protein-corrected MY24, based on 4.0% fat and 3.3% protein content and following the FAO formula (FAO, 2010):

$$\text{MY24}(i, j, t) = \text{MY24r}(i, j, t) \times \left[0.337 + 0.116 \times \frac{\text{FC}(i, j, t)}{100} + 0.06 \times \frac{\text{PC}(i, j, t)}{100} \right].$$

Daily Body Weight

For each cow i in lactation j (1 or 2) and each test-day t , the average BWr(i,j,t) of all raw body weight (BWr) measurements of a given day was calculated as

$$\text{BWr}(i, j, t) = \sum_{k=1}^{k_{it}} (\text{BWr}_{i,j,t,k}) / k_{it}.$$

Outlier phenotypes for BWr were discarded using the same procedure as described above for MY24r.

Changes in BWr reflect both variations in body reserves as well as short-term changes in digestive content related to feed intake, which, for our purposes, represent noise that must be corrected. Indeed, feed intake typically increases markedly in early lactation, which would lead to underestimation of body mobilization during this key period if not taken into account. Unfortunately, the farms participating in this study did not monitor the feed intake of their cows, which meant that our only option was to predict it throughout the course of lactation for each cow using its own data.

The prediction equation for DMI(i,j,t) of cow i in lactation j at DIM t was established from another experimental data set of 689 first-lactation and 481 second-lactation Holstein cows, each of which had weekly records of daily BWr, MY24r, and DMI for 44-wk-long lactations (Martin et al., 2021). The farming conditions (very intensive system with high production levels) were comparable to those of the 36 farms in our study. First, the regression coefficients of the following equation were estimated using this data set within lactation j and for each week in milk w :

$$\begin{aligned} \text{DMI}(i, j, w) \\ = \mu_{j,w} + \alpha_{j,w} \times \text{BWr}(i, j, w) + \beta_{j,w} \times \text{MY24r}_{j,w} + e_{i,j,w}. \end{aligned}$$

Second, the estimates $\hat{\mu}_{j,w}$, $\hat{\alpha}_{j,w}$, and $\hat{\beta}_{j,w}$ were modeled as second-order polynomials as functions of DIM t , so as to be able to predict

$$\begin{aligned} \text{DMI}(i, j, t) \\ = \hat{\mu}(j, t) + \hat{\alpha}(j, t) \times \text{BWr}(i, j, t) + \hat{\beta}(j, t) \times \text{MY24r}(i, j, t) \end{aligned}$$

for each cow of our study from $t = 0$ to $t = 305$. The prediction equations obtained were

$$\begin{aligned} \text{DMI}(i, 1, t) = & \left[6.31 - 1.07\text{E}^{-3} \times t + 9.44\text{E}^{-6}t^2 \right] \\ & + \left[0.010 + 3.07\text{E}^{-5} \times t - 9.61\text{E}^{-8}t^2 \right] \times \overline{\text{BWr}}(i, 1, t) \\ & + \left[0.111 + 1.19\text{E}^{-3} \times t - 2.76\text{E}^{-6}t^2 \right] \times \overline{\text{MY24r}}(i, 1, t) \end{aligned}$$

for L1 cows, and

$$\begin{aligned} \text{DMI}(i, 2, t) = & \left[6.77 - 1.19\text{E}^{-2} \times t + 5.03\text{E}^{-5}t^2 \right] \\ & + \left[0.008 + 1.06\text{E}^{-4} \times t - 3.32\text{E}^{-7}t^2 \right] \times \overline{\text{BWr}}(i, 2, t) \\ & + \left[0.205 - 1.59\text{E}^{-4} \times t + 9.07\text{E}^{-7}t^2 \right] \times \overline{\text{MY24r}}(i, 2, t) \end{aligned}$$

for L2 cows, where $\overline{\text{BWr}}(i, 1, t)$ and $\overline{\text{MY24r}}(i, 1, t)$ are the means, for animal i in lactation 1, of its BWr and MY24r records from DIM $t - 5$ to DIM $t + 5$. Moving averages were used instead of the daily records at DIM t to exclude daily variability, mostly for BWr, and to obtain smoother DMI predictions.

Finally, BWr(i,j,t) was corrected for the change in feed intake between DIM t and calving, assuming a digestive content change of 4.5 kg per kilogram of DMI change (Faverdin et al., 2017):

$$\begin{aligned} \text{BW}(i, j, t) = & \text{BWr}(i, j, t) - 4.5 \\ & \times [\text{DMI}(i, j, t) - \text{DMI}(i, j, 0)]. \end{aligned}$$

Estimates of genetic parameters were obtained using WOMBAT software (Meyer, 2007) by applying random regression models across the lactation and considering 3 generations of ancestors for the cows. Pedigrees and dates of insemination of the animals were extracted from the French national database (SIG, INRAE CTIG). For each test date of a cow, the corresponding number of days in milk (DIM = test date - calving date) and of days carried calf [DCC = test date - date of conception (if the cow became pregnant during lactation)] were calculated. The test dates that occurred between the dates of calving and successful insemination were assigned DCC values of 0.

Phenotypes in L1 and L2 were considered different traits. Due to the high number of records, it was not possible to directly perform 4-trait random regressions

Table 1. Numbers of daily phenotypes and cows considered in the single-trait analyses

Trait ¹	Lactation 1		Lactation 2		Total cows
	Daily phenotypes	Cows	Daily phenotypes	Cows	
MY24	859,020	3,988	665,361	3,060	4,898
BW	570,651	3,439	449,449	2,660	4,349
Total cows		3,989		3,060	4,899

¹MY24 = fat- and protein-corrected daily milk yield standardized for a 24-h production period; BW = daily body weight corrected for feed intake variation compared with the first DIM.

on daily data for MY24 and BW in L1 and L2. Therefore, a 2-step approach was applied. First, single-trait random regressions were performed on each of the 4 traits, the estimates of which were used to adjust the daily phenotypes for the nongenetic effects of the model. Second, a 4-trait random regression was performed on weekly means of adjusted MY24 and BW data per cow in L1 and L2.

Single-Trait Analyses on Daily Data for BW and MY24 in L1 and L2

Only records with values of DIM lower than 305 d and DCC lower than 242 d were considered. Records from animals with unknown parents, from cows older than 3.5 yr at first calving, and from animals with fewer than 30 daily records available were discarded. Herd–test date contemporary groups with fewer than 4 records were discarded. The numbers of phenotypes and cows remaining after filtering are presented in Table 1.

The following model was used for the single-trait analyses:

$$y_{iqlmmtz} = \text{HTD}_{lq} + \text{MN}_{nq} + \sum_{d=1}^6 x_{dmq} \theta_{dt} + \sum_{d=1}^6 u_{dpq} \theta_{dt} + \sum_{f=1}^4 v_{fq} \delta_{fz} + \sum_{r=1}^3 p_{irq} \varphi_{rt} + \sum_{r=1}^3 a_{irq} \varphi_{rt} + e_{iqlmmtz},$$

where

- $y_{iqlmmtz}$ is the observation for the q th trait (1 to 4) of animal i recorded on DIM t and DCC z , in the l th contemporary group, the m th calving month, the p th level of calving age, and the n th level of milking times per day;
- HTD_{lq} is the fixed effect of the l th level of the herd \times test-day effect on the q th trait (33,746 to 38,894 levels, depending on the trait);
- MN_{nq} is the fixed effect of the n th level of number of milkings per day (1, 2, 3, more than 3 times;

this effect was only considered in the model for MY24);

- θ_{dt} is the d th covariate at DIM t of cubic splines with 6 knots located at DIM 1, 15, 40, 90, 200, and 305 ($d = 1$ to 6);
- x_{dmq} and u_{dpq} are the d th regression coefficient that describes the average lactation or BW curve for trait q of the cows in the m th calving month or in the p th level of calving age (<25, 25–27, 28–30, 31–33, >33 mo of age in L1, and <37, 37–39, 40–42, 43–45, >45 mo of age in L2), respectively;
- δ_{fz} is the f th covariate at DCC z of cubic splines with 4 knots located at DCC 0 (before successful insemination), 99, 174, and 242 ($f = 1$ to 4);
- v_{fq} is the f th regression coefficient that describes the average effect of DCC on the lactation or BW curve for trait q ;
- a_{irq} and p_{irq} are the r th random regression coefficients that describe the trajectory of the additive genetic effect and permanent environmental effects, respectively, of the i th cow for the q th trait (second-order Legendre orthogonal polynomials were used to model the additive genetic and permanent environmental effects);
- φ_{rt} is the r th covariate at DIM t of Legendre orthogonal polynomials for additive genetic and permanent environmental effects;
- $e_{iqlmmtz}$ is the residual random effect associated with $y_{iqlmmtz}$.

The residual variance was considered heterogeneous throughout the lactation period. Seven periods were defined during which the residual variance was assumed to be constant: DIM 1–7, 8–20, 21–50, 51–100, 101–150, 151–230, and 231–305. These intervals were chosen from prior analyses with shorter intervals, and classes with similar residual variances were grouped.

Multitrait Analyses on Preadjusted Weekly Means

Daily phenotypes for MY24 and BW in L1 and L2 were then adjusted (adj_-) for DCC, calving month,

Table 2. Numbers of weekly phenotypes and cows considered in the 4-trait analysis

Trait ¹	Lactation 1		Lactation 2		Total cows
	Weekly phenotypes	Cows	Weekly phenotypes	Cows	
wMY24	122,720	3,728	91,594	2,887	4,626
wBW	102,582	3,253	78,137	2,553	4,161
Total cows		3,728		2,888	4,627

¹wMY24 = weekly average of fat- and protein-corrected daily milk yield standardized for a 24-h production period, preadjusted for environmental effects; wBW: weekly average of daily BW corrected for feed intake variation compared with the first DIM, preadjusted for environmental effects.

and age at calving, as well as milkings per day (MN) for MY24, using the equations

$$\text{adj_MY24}_{iqlmntz} = \text{MY24}_{iqlmntz} - \widehat{\text{MN}}_{iq} - \sum_{d=1}^6 \hat{x}_{dmq} \theta_{dt} - \sum_{d=1}^6 \hat{u}_{dpq} \theta_{dt} - \sum_{f=1}^4 \hat{v}_{fq} \delta_{fz}$$

and

$$\text{adj_BW}_{iqlmntz} = \text{BW}_{iqlmntz} - \sum_{d=1}^6 \hat{x}_{dmq} \theta_{dt} - \sum_{d=1}^6 \hat{u}_{dpq} \theta_{dt} - \sum_{f=1}^4 \hat{v}_{fq} \delta_{fz}.$$

The averages of adj_MY24 and adj_BW per week in milk (WIM) were calculated for each cow from WIM 1 to WIM 44 (wMY24 and wBW). Cows with fewer than 9 weekly phenotypes, as well as phenotypes from herd-test week groups with fewer than 10 cows were discarded. The numbers of phenotypes and cows remaining after filtering are presented in Table 2.

Then, 4-trait random regression analyses were performed on the weekly averages with WOMBAT software. The models included the fixed effect of herd-test week (HTW), the random effects of permanent environment and additive genetic value as second-order Legendre polynomials, and a residual whose heterogeneous variance was presumed to be constant within each of 7 periods: WIM 1, 2–3, 4–7, 8–13, 14–21, 22–33, and 34–44. The model was structured as follows:

$$y_{iqlt} = \text{HTW}_{lq} + \sum_{r=1}^3 p_{irq} \varphi_{rt} + \sum_{r=1}^3 a_{irq} \varphi_{rt} + e_{iqlt},$$

where

- y_{iqlt} is the observation for the q th trait (1 to 4) of animal i recorded on WIM t , in the l th herd \times test week contemporary group;
- HTW_{lq} is the fixed effect of the l th level of the herd \times test week effect on the q th trait;

- a_{irq} and p_{irq} are the r th random regression coefficients that describe the trajectory of the additive genetic effect and permanent environmental effects, respectively, for the q th trait in the i th cow (second-order Legendre orthogonal polynomials were used to model the additive genetic and permanent environmental effects);
- φ_{rt} is the r th covariate at WIM t of Legendre orthogonal polynomials for additive genetic and permanent environment effects;
- e_{iqlt} is the residual random effect associated with y_{iqlt} .

Genetic Correlations Between Early BW Loss and Milk Production, Heritabilities

From the effect estimates in the single-trait analyses of daily data, we calculated least-squared means of BW that revealed that the maximum BW loss of cows was reached, on average, 29 d after calving in both L1 (28.0 kg) and L2 (29.5 kg); that is, in the fifth week of lactation. We therefore defined **BWL5** (the loss of BW from WIM 1 to WIM 5) as wBW at WIM 5 minus wBW at WIM 1, and we calculated the following:

- Genetic variance of BWL5 in L1 and L2 as

$$\sigma_g^2(\text{BWL5}_{Lj}) = (\varphi_5 - \varphi_1)' \mathbf{G}_{\text{wBW}_{Lj}} (\varphi_5 - \varphi_1);$$

- Genetic variance of wMY24 at WIM t in L1 and L2 as

$$\sigma_g^2[\text{wMY24}(t)_{Lj}] = (\varphi_t)' \mathbf{G}_{\text{wMY24}_{Lj}} (\varphi_t);$$

- Genetic covariance between BWL5 and wMY24 at WIM t in L1 and L2 as

$$\sigma_g[\text{BWL5}; \text{wMY24}(t)_{Lj}] = (\varphi_5 - \varphi_1)' \mathbf{C}_{\text{wBW}, \text{wMY24}_{Lj}} \varphi_t,$$

where φ_t is the vector containing the 3 covariates at WIM t of the Legendre orthogonal polynomials; $\mathbf{G}_{\text{wBW}_{Lj}}$ is the 3×3 matrix containing the genetic covariance estimates between the 3 additive genetic random regression coefficients for wBW in lactation j ; $\mathbf{G}_{\text{wMY24}_{Lj}}$ is the 3×3 matrix containing the genetic covariance estimates between the 3 additive genetic random regression coefficients for wMY24 in lactation j ; and $\mathbf{C}_{\text{wBW,wMY24}_{Lj}}$ is the 3×3 matrix containing the genetic covariance estimates between the 3 additive genetic random regression coefficients for wBW and the 3 additive genetic random regression coefficients for wMY24 in lactation j .

The permanent environmental variances $\left\{ \sigma_{\text{pe}}^2(\text{BWL5}_{Lj}), \sigma_{\text{pe}}^2[\text{wMY24}(t)_{Lj}] \right\}$ and covariances $\left\{ \sigma_{\text{pe}}[\text{BWL5,wMY24}(t)_{Lj}] \right\}$ were obtained with the same formulae, by replacing the \mathbf{G} submatrices with the corresponding \mathbf{P} submatrices, where \mathbf{P} is the 12×12 matrix containing the covariance estimates between the permanent environmental regression coefficients for wBW and wMY24 in lactations 1 and 2.

Then, the genetic correlation between BWL5 and wMY24 at WIM t in lactation j was calculated as follows:

$$r_{\text{gBWL5,wMY24a}}(t) = \sigma_{\text{g}}[\text{BWL5}; \text{wMY24a}(t)_{Lj}] / \sqrt{\sigma_{\text{g}}^2(\text{BWL5}_{Lj}) \sigma_{\text{g}}^2[\text{wMY24a}(t)_{Lj}]}.$$

Finally, the heritability of wBW and wMY24 at WIM t in L1 and L2 was calculated, respectively, as

$$h^2[\text{wBW}(t)_{Lj}] = \sigma_{\text{g}}^2[\text{wBW}(t)_{Lj}] / \left\{ \sigma_{\text{g}}^2[\text{wBW}(t)_{Lj}] + \sigma_{\text{pe}}^2[\text{wBW}(t)_{Lj}] \right\} + \sigma_{\text{e}}^2[\text{wBW}(t)_{Lj}]$$

and

$$h^2[\text{wMY24}(t)_{Lj}] = \sigma_{\text{g}}^2[\text{wMY24}(t)_{Lj}] / \left\{ \sigma_{\text{g}}^2[\text{wMY24}(t)_{Lj}] + \sigma_{\text{pe}}^2[\text{wMY24}(t)_{Lj}] \right\} + \sigma_{\text{e}}^2[\text{wMY24}(t)_{Lj}]$$

where $\sigma_{\text{e}}^2[\text{wBW}(t)_{Lj}]$ and $\sigma_{\text{e}}^2[\text{wMY24}(t)_{Lj}]$ are the estimated residual variances for wBW and wMY24 at WIM t for lactation j , respectively.

The heritability of BWL5 was calculated in 2 ways. First, we divided the genetic variance of BWL5 by the estimate of the phenotypic variance obtained from the variance components estimated from the random regression as described above:

$$h_{\text{a}}^2(\text{BWL5}_{Lj}) = \sigma_{\text{g}}^2(\text{BWL5}_{Lj}) / \left[\sigma_{\text{g}}^2(\text{BWL5}_{Lj}) + \sigma_{\text{pe}}^2(\text{BWL5}_{Lj}) + \sigma_{\text{e}}^2(\text{BWL5}_{Lj}) \right],$$

where $\sigma_{\text{e}}^2(\text{BWL5}_{Lj})$ is the estimated residual variance for BWL5 at lactation j , calculated as $\sigma_{\text{e}}^2[\text{wBW}(5)_{Lj}] + \sigma_{\text{e}}^2[\text{wBW}(5)_{Lj}]$, since the model applied in WOMBAT software assumes independent residuals (i.e., null residual covariances) for wBW at different WIM. This assumption, if not valid, could result in an overestimate of residual variance and therefore an underestimation of heritability for BWL5. Therefore, we also estimated the phenotypic variance of BWL5_{Lj} as $\text{var} \left[\left(y_{\text{ilm5}} - \widehat{\text{HTW}}_{\text{m}} \right) - \left(y_{\text{ilm1}} - \widehat{\text{HTW}}_{\text{n}} \right) \right]$, where y_{ilm5} and y_{ilm1} are the wBW values of animal i in lactation 1 at WIM 5 and 1, respectively, and $\widehat{\text{HTW}}_{\text{m}}$ and $\widehat{\text{HTW}}_{\text{n}}$ are the solutions for the corresponding m th and n th levels of the herd \times test week effect from the multivariate random regression analyses. The second estimates for the heritability of BWL5_{Lj} were therefore calculated as follows:

$$h_{\text{b}}^2(\text{BWL5}_{Lj}) = \sigma_{\text{g}}^2(\text{BWL5}_{Lj}) / \text{var} \left[\left(y_{\text{ilm5}} - \widehat{\text{HTW}}_{\text{m}} \right) - \left(y_{\text{ilm1}} - \widehat{\text{HTW}}_{\text{n}} \right) \right].$$

The same approach was used with the loss in BW from WIM 1 to WIM10 (BWL10), but the results were very similar and are not presented.

RESULTS

Body Weight Change Throughout the Lactation

The magnitude of the average BW loss at the beginning of lactation reached 28 kg in L1 and 29.5 kg in L2. The period of weight loss lasted 29 d on average, in both L1 and L2. The curves of raw and adjusted body weight with DIM are presented in Figure 1 for both first and second lactations.

Variance Components and Heritabilities

The genetic and permanent environmental covariance estimates between the random regression coefficients for BW and for milk production in lactations 1 and

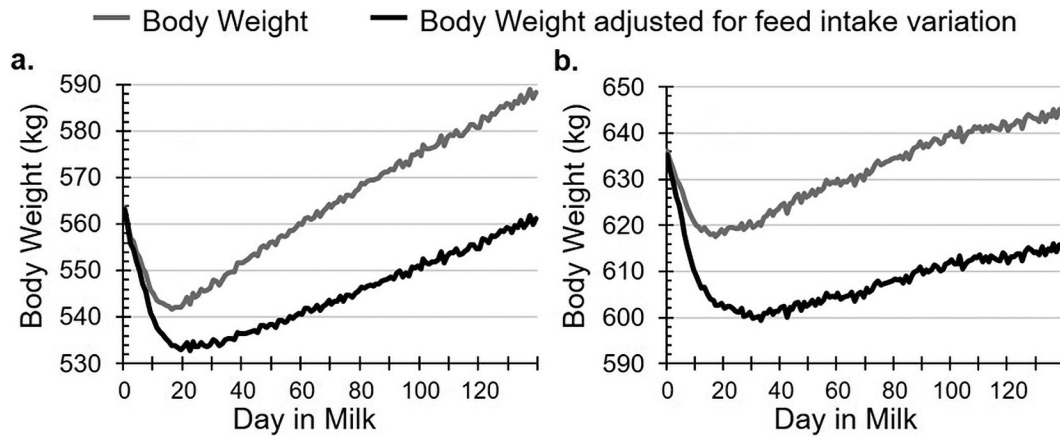


Figure 1. Evolution of the daily averages of body weight and of body weight adjusted for feed intake variation, from calving day to DIM 140 in lactation 1 (a) and lactation 2 (b).

2—constituting the **G** and **P** matrices, respectively—are presented in Table 3 and Table 4, and the residual variance estimates are presented in Table 5.

The values of estimated additive genetic, permanent environmental, and residual variances across lactations 1 and 2 for wMY24 and wBW are presented in Figure 2. For both traits, the variances for the 3 random components showed similar global evolutions across lactations 1 and 2. The residual variance dropped sharply during the first few weeks of lactation and then remained stable (wBW) or declined slowly until the end of the period of study (wMY24). The permanent environmental variances showed a large initial decrease until approximately WIM 10, followed by a slow constant increase up to WIM 35 and then a sharp increase. The variation in genetic variance across lactation was smaller than that of the 2 other components, and exhibited an initial decrease followed by a plateau and then an increase. An exception to this pattern was observed for wBW in the first lactation, for which the genetic variance was stable until approximately WIM 8 and then increased steadily until the end of the study period.

The resulting heritability values (h^2) are presented in Figure 3. Heritability for wMY24 followed a similar evolution in both lactations, increasing regularly from 0.08 in WIM 1 to 0.20 in WIM 15, after which it remained almost constant for primiparous cows and increased to 0.25 in WIM 35 in the second lactation. Heritability for wBW was markedly higher than for wMY24, rising from 0.31 to 0.53 in WIM 25 in the first lactation and then decreasing progressively to 0.40, and rising from 0.43 to 0.56 at WIM 10 in the second lactation and then declining regularly to 0.41.

The BWL5 genetic SD was equal to 5.1 kg in L1 and 3.6 kg in L2. With a mean loss of 29 kg, the corre-

sponding genetic coefficients of variation were 17.5 and 12.5% in L1 and L2, respectively. These values are high and show that large variations are possible due to direct or indirect selection. However, this variation is relatively limited compared with the measurement noise and the phenotypic variance. Accordingly, the heritability for BWL5, estimated using the random regression model, was low: 0.039 in L1 and 0.018 in L2. When we instead estimated the phenotypic variance of BWL5 directly from the variance of the adjusted phenotypes, we did not obtain markedly higher estimates: h_b^2 for BWL5 was equal to 0.042 and 0.020 in L1 and L2, respectively, confirming the low heritability of BW loss in early lactation.

Genetic Correlations Within Traits

The genetic correlations (r_g) between wMY24 at different stages of lactation are presented in Figure 4, and those for wBW are shown in Figure 5. The r_g correlations were very high between wMY24 at consecutive WIM (a consequence of random regression) and decreased as the interval between records increased. This decrease was faster for primiparous cows than for cows in their second lactation. To illustrate, the r_g between wMY24 at WIM 10 and WIM 40 was 0.70 in the second lactation but only 0.40 in the first lactation.

As observed for wMY24, r_g was very high between wBW values for adjacent WIM and decreased as the interval between records increased. However, the rate of r_g decline with increasing time intervals was much slower than for milk production; the minimum r_g values (0.76 and 0.92 in lactations 1 and 2, respectively) were observed between values of wBW at WIM1 and WIM 44. For example, r_g values between wBW at WIM 5 and wBW at other time points were higher than 0.90 up to

Table 3. Genetic covariance estimates between random regression coefficients for BW and milk production in lactations 1 and 2 (the **G** matrix)¹

Trait	wMY24 in lactation 1			wMY24 in lactation 2			wBW in lactation 1			wBW in lactation 2		
	c1	c2	c3	c1	c2	c3	c1	c2	c3	c1	c2	c3
wMY24 in lactation 1												
c1	6.372	0.3465	-0.4319	7.441	1.046	0.1785	26.10	-0.5858	0.4620	12.61	-2.837	1.304
c2	0.3465	1.470	0.1728	1.936	0.9027	0.0399	3.891	2.022	-0.8199	14.56	0.2975	-0.7798
c3	-0.4319	0.1728	0.6963	-0.4092	0.5613	0.3088	-14.68	-0.0046	1.016	-7.194	1.737	-0.4159
wMY24 in lactation 2												
c1	7.441	1.936	-0.4092	10.98	1.657	0.4843	58.98	5.496	-0.9378	61.79	-0.9850	0.0873
c2	1.936	0.9027	0.5613	1.657	1.509	0.2964	-26.75	-3.656	1.053	-22.57	0.1118	-0.3057
c3	0.1785	0.0399	0.3088	0.4843	0.2964	0.8206	2.696	-1.837	1.222	5.693	-0.6806	-1.297
wBW in lactation 1												
c1	26.10	3.891	-14.68	58.98	-26.75	2.696	2.125	149.5	-66.11	2,238	-42.09	42.52
c2	-0.5858	2.022	-0.0046	5.496	-3.656	-1.837	149.5	92.08	-21.82	224.0	40.35	-15.36
c3	0.4620	-0.8199	1.016	-0.9378	1.053	1.222	-66.11	-21.82	21.32	-73.72	-9.729	3.274
wBW in lactation 2												
c1	12.61	14.56	-7.194	61.79	-22.57	5.693	2,238	224.0	-73.72	2.612	21.08	31.33
c2	-2.837	0.2975	1.737	-0.9850	0.1118	-0.6806	-42.09	40.35	-9.729	21.08	39.86	-7.282
c3	1.304	-0.7798	-0.4159	0.0873	-0.3057	-1.297	42.52	-15.36	3.274	31.33	-7.282	13.21

¹wMY24 = weekly average of fat- and protein-corrected daily milk yield standardized for a 24-h production period, preadjusted for environmental effects; wBW = weekly average of daily body weight corrected for feed intake variation compared with the first DIM, preadjusted for environmental effects; c1, c2, and c3 are, respectively, the 3 random regression coefficients for the constant, first-, and second-order orthogonal Legendre polynomial for wMY24 or wBW in lactation 1 or 2. In bold type: variance estimates.

Table 4. Permanent environmental covariance estimates between the random regression coefficients for BW and milk production in lactations 1 and 2 (the **P** matrix)¹

Trait	wMY24 in lactation 1			wMY24 in lactation 2			wBW in lactation 1			wBW in lactation 2		
	c1	c2	c3	c1	c2	c3	c1	c2	c3	c1	c2	c3
wMY24 in lactation 1												
c1	21.92	0.8934	-0.5449	9.236	-0.7404	-0.7839	77.26	-4.626	6.302	66.66	4.484	-1.699
c2	0.8934	6.081	-1.230	1.551	1.420	-0.3583	0.4577	17.54	-3.838	3.464	1.634	-2.074
c3	-0.5449	-1.230	3.093	-1.074	-0.2951	0.4075	1.823	-5.289	5.101	-0.0509	-2.977	0.4763
wMY24 in lactation 2												
c1	9.236	1.551	-1.074	28.43	0.9835	1.166	31.19	4.265	2.326	28.00	-6.461	3.445
c2	-0.7404	1.420	-0.2952	0.9835	12.21	-1.028	-7.610	0.8236	-0.5553	-1.441	16.88	-6.616
c3	-0.7839	-0.3583	0.4075	1.166	-1.028	5.864	3.685	0.5655	0.0340	0.7024	-3.382	7.398
wBW in lactation 1												
c1	77.26	0.4577	1.823	31.19	-7.610	3.685	1,850	75.69	28.87	1,394	83.39	26.95
c2	-4.626	17.54	-5.289	4.265	0.8236	0.5655	75.69	246.8	-19.26	169.8	41.67	2.524
c3	6.302	-3.838	5.101	2.326	-0.5553	0.0340	28.87	-19.26	106.3	32.36	20.99	20.59
wBW in lactation 2												
c1	66.66	3.464	-0.0509	28.00	-1.441	0.7024	1,394	169.8	32.36	2,029	191.8	25.71
c2	4.484	1.634	-2.977	-6.461	16.88	-3.382	83.39	41.67	20.99	191.8	259.7	2.971
c3	-1.699	-2.074	0.4763	3.445	-6.616	7.398	26.95	2.524	20.59	25.71	2.971	109.0

¹wMY24 = weekly average of fat- and protein-corrected daily milk yield standardized for a 24-h production period, preadjusted for environmental effects; wBW = weekly average of daily body weight corrected for feed intake variation compared with the first DIM, preadjusted for environmental effects (kg); c1, c2, and c3 are, respectively, the 3 random regression coefficients for the constant, first-, and second-order orthogonal Legendre polynomial for wMY24 or wBW in lactation 1 or 2. In bold type: variance estimates.

Table 5. Residual variance estimates for BW and milk production throughout lactations 1 and 2¹

WIM	wMY24 in lactation 1	wMY24 in lactation 2	wBW in lactation 1	wBW in lactation 2
1	30.48	55.46	491.5	543.5
2 to 3	17.07	29.97	216.8	231.0
4 to 7	5.075	8.869	65.91	85.31
8 to 14	3.007	4.219	69.06	82.55
15 to 21	2.704	4.221	63.85	80.72
22 to 33	2.368	3.339	62.51	83.71
34 to 44	2.113	2.862	65.92	81.14

¹WIM = week in milk; wMY24 = weekly average of fat- and protein-corrected daily milk yield standardized for a 24-h production period, preadjusted for environmental effects; wBW = weekly average of daily body weight corrected for feed intake variation compared with the first DIM, preadjusted for environmental effects (kg).

WIM 24 in the first lactation and higher than 0.96 up to WIM 24 in the second lactation.

Genetic Correlations Between wMY24 and wBW

Estimates of genetic correlations between wMY24 and wBW at different stages of lactation are shown in Figure 6. Overall, the genetic relationships between the 2 traits were low to moderate, varying from -0.1 to 0.3 in the first lactation and from 0.1 to 0.6 in the second lactation. Moreover, r_g between wMY24 at a given lactation stage and wBW appeared to be relatively stable regardless of the WIM considered for wBW, which can be explained by the very high r_g between all wBW values throughout a lactation.

However, the temporal dynamic of r_g between daily milk production and BW differed between the 2 lactations. In primiparous cows, wMY24 appears to be almost genetically independent of wBW during the first 5 WIM. After that, r_g increases progressively up to 0.3 in the middle of lactation, and then decreases until the end of lactation. In contrast, in the second lactation, r_g is strongest in early lactation (0.60), with the heaviest cows producing the most milk; then the correlation decreases progressively to 0.10 at WIM 44.

Genetic Correlations Between BW Loss in Early Lactation and wMY24

Estimates of genetic correlations between BWL5 and wMY24 throughout lactations 1 and 2 are presented in Figure 7. In L1 cows, a moderate negative genetic correlation was found between BWL5 and wMY24 before WIM 17, starting from a minimum at WIM 1 (-0.26) and then becoming progressively closer to 0. After approximately WIM 17, however, BWL5 and wMY24 appear to be genetically independent. In L2 cows, the genetic correlations between BWL5 and wMY24 were

weaker, declining from 0.1 to -0.1 from WIM 1 to WIM 20, and then increasing up to 0.1 in the second half of lactation.

DISCUSSION

Design and Data

For the purposes of performing a genetic study of the evolution of body reserves, the ideal approach would be to obtain body condition scores recorded at several stages of lactation from a large number of cows. Unfortunately, such data are difficult to obtain on a large scale. To overcome this problem, we used the abundant daily data automatically recorded by milking robots on commercial farms to evaluate the genetic relationships between body mobilization in early lactation and milk production. These data are rather noisy due to random variation in digestive content and water intake, but this random noise can be accounted for thanks to the sheer abundance of data. The main issue with this approach is the lack of data on individual daily feed intake, which is not monitored in commercial herds. This generates a bias that cannot be corrected based on the number of records. Indeed, our approach is based on the assumption that weight loss in early lactation reflects a decrease in body reserves due to mobilization. However, we must not neglect the fact that the amount of feed ingested, which is at its minimum at parturition and increases sharply during lactation, partially hides the weight loss of cows in early lactation and could lead to underestimation of body mobilization (Faverdin et al., 2017). The magnitude of the increase in digestive content during the first month (approximately $+7$ kg DMI, corresponding to about $+30$ to 35 kg of digestive content, according to Lefebvre et al., 2022) is on the same order as that of body mobilization or possibly even higher. In addition, this increase in feed intake is not constant across animals but is positively correlated with milk production. Therefore, to account for this, we had to adjust daily BWR for each individual based on daily estimates of digestive content. To do this, we developed prediction equations for DMI in L1 and L2 based on individual values of MY24r and BWR, and calibrated the equations using another data set on Holstein cows for which DMI was available (Martin et al., 2021). We are well aware of the drawbacks of studying the relationship between milk production and values of BW adjusted based on these same weights and milk production, but it appeared to be the most pertinent approach available to us. Another major assumption is the value of 4.5 kg of digestive content per kilogram of DMI, which was determined experimentally from another set of animals (Faverdin et al., 2017). This

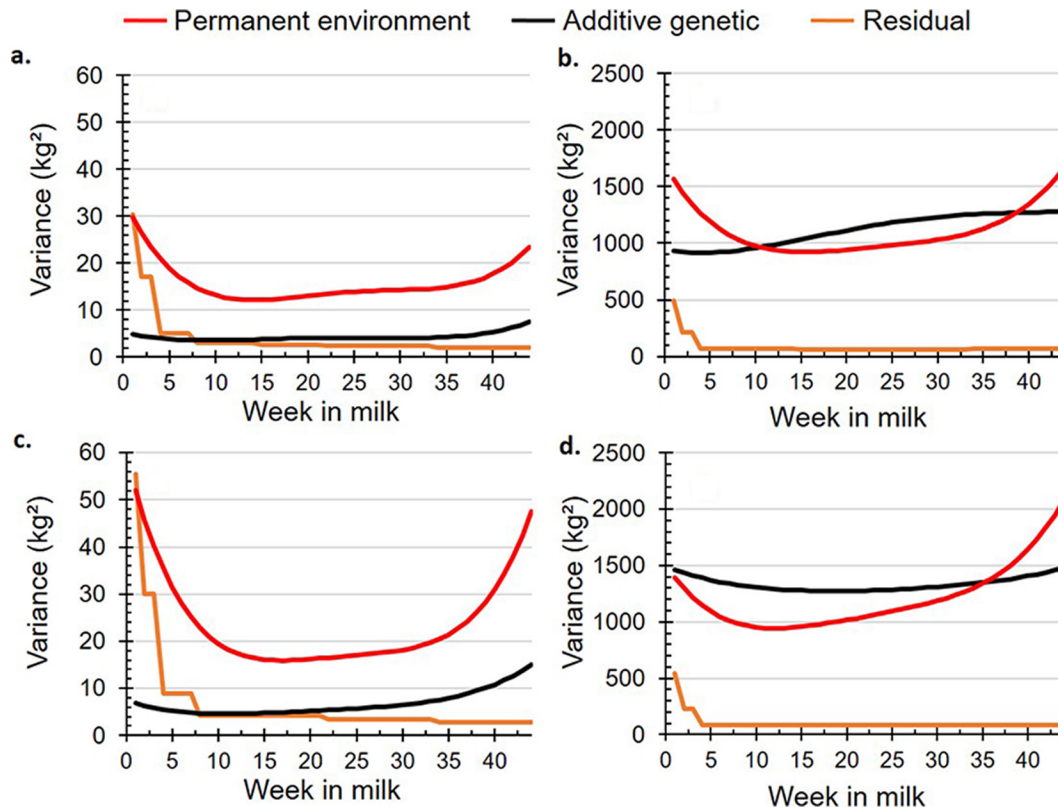


Figure 2. Estimates of variances for the genetic, permanent environmental, and residual effects throughout lactation for weekly average of fat- and protein-corrected daily milk yield standardized for a 24-h production period in lactation 1 (a) and lactation 2 (c), and for weekly average of daily body weight corrected for feed intake variation in lactation 1 (b) and lactation 2 (d).

coefficient varies based on the diet and the transit time in the rumen, and this particular value (4.5 kg/kg of DMI) corresponds to the rich diet based on corn silage and concentrate used in the population in our study. Although our approach is not perfect, we view it as much better than working with unadjusted body weights. Indeed, using raw weights would generate irrelevant results in which higher-producing cows lose less weight simply because they eat more. This adjustment for digestive content change increased from 0 kg at DIM 1 to 12 kg (SD = 3.9 kg) at DIM 29 and to a maximum of 29 kg (SD = 6.4 kg) at DIM 180 in first lactations and decreased thereafter. The corresponding figures were 19 kg (SD = 6.4 kg) at DIM = 29 and a maximum of 30 kg (SD = 7.4 kg) at DIM 147 in second lactations.

Extent of Weight Loss and Duration of the Mobilization Period

An initial result of our analysis is that the magnitude of the average BW loss at the beginning of lactation (−28 kg in L1 and −29.5 kg in L2) and the average length of the period of weight loss (29 d) were lower and

shorter, respectively, than what is typically assumed for high-yielding Holstein cows on commercial farms. Our results are consistent with the observations of Lefebvre et al. (2022) on French Holstein cows (parity ranging from 1 to 7) from experimental herds; in that study, an analysis of daily BWr and DMI measurements throughout lactation led to the estimation of a BW loss of about 37 kg after 1 month of lactation (after adjustment for variations in digestive content). Koenen and Veerkamp (1998) also present averages of unadjusted live weights measured during lactation on Holstein-Friesian heifers that seem to show very early nadirs and limited weight loss (532 kg, 520 kg, 523 kg, and 537 kg at wk 0, 3, 5, and 10, respectively). Toshniwal et al. (2008) report a maximum weight loss of 24 to 31 kg after 5 weeks in first lactation and 38 kg after 6 weeks in second lactation. In the latter 2 studies, the statistics presented were obtained on weights not adjusted for changes in feed intake during lactation, which tends to underestimate the duration and magnitude of weight loss. Nevertheless, these elements seem to corroborate our observations and results. It is important to note that primiparous cows have not yet finished growing, and their daily weight gain thus partially masks body

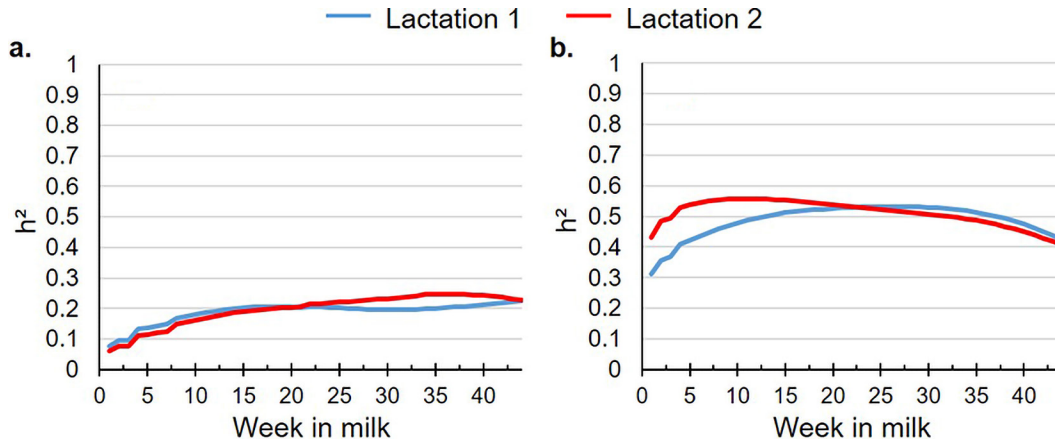


Figure 3. Estimates of heritability throughout lactation for weekly average of daily milk yield adjusted for protein and fat content (a) and for weekly average of daily body weight corrected for feed intake variation (b) in lactation 1 and lactation 2.

mobilization, leading to an underestimation of its amplitude and duration. However, the growth rate in the second lactation is more limited, making this effect less relevant. The explanation may simply be that body mobilization is less important than generally thought, even in high-yielding dairy cows, probably because their fat reserves are limited. The reductions in cow body fatness in the last decades, indirect consequence of selection, may explain why the duration and amplitude of weight loss is somewhat lower in our study than as observed by Toshniwal et al. (2008).

Estimated Variance Components, Heritabilities, and Genetic Correlations

The pattern we observed for the different variance components of wMY24 through the course of lacta-

tion (decrease at the beginning of lactation, minimum in the middle, increase at the end) is similar to those presented in other studies of genetic parameter estimates for test-day milk yield (Druet et al., 2003, 2005; Bignardi et al., 2011). Heritability values for wMY24 are minimal at the beginning of a lactation and tend to stabilize after 120 DIM. These changes in heritability coefficients were mainly due to residual and permanent environmental components. Indeed, genetic variances were nearly constant, whereas residual and permanent environmental variances were more variable, and higher at the beginning of the lactation. The values obtained here are somewhat lower than those estimated by Druet et al. (2005) in French Holstein cows in their first (0.15 to 0.41) or second (0.24 to 0.44) lactation, and by Muir et al. (2007) in Italian Holsteins in their first (0.27 to 0.34) or second lactation (0.22 to 0.37), but are close

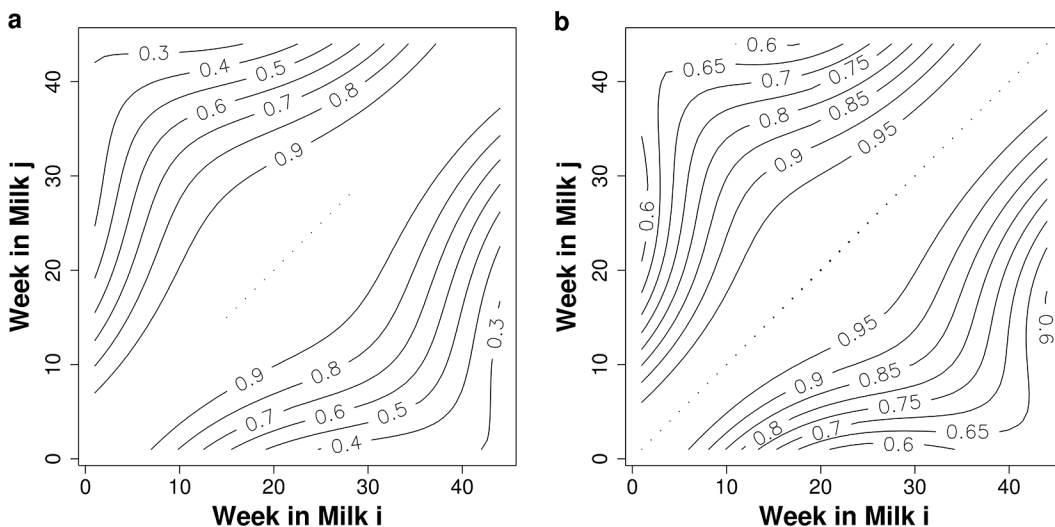


Figure 4. Genetic correlation estimates between weekly average of fat- and protein-corrected daily milk yield standardized for a 24-h production period, adjusted for protein and fat content at different stages of lactation 1 (a) or lactation 2 (b).

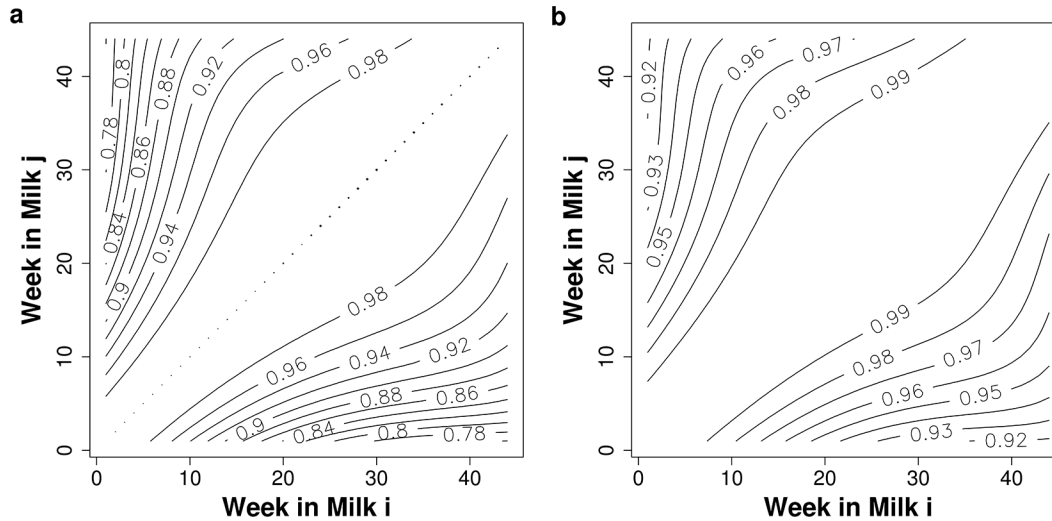


Figure 5. Genetic correlation estimates between weekly average of daily body weight adjusted for feed intake variation at different stages of lactation 1 (a) or lactation 2 (b).

to the estimates reported by Bignardi et al. (2011) in Brazilian Holsteins (up to 0.30). Several factors could explain our lower heritability values. First, daily or weekly measurements are more strongly correlated with each other than are the monthly measurements used in the studies indicated above, perhaps leading to higher permanent environmental variance and lower heritability for wMY24. Moreover, in our study, the cows were free to be milked as often as they wanted, whereas in other, older studies, the number of milkings per day was fixed, and the measurement conditions were probably more homogeneous across cows. The effect of the number of milkings per day is included in the model for

MY24, but this adjustment may be imperfect. Finally, the number of cows is relatively small, and the genetic variability in this population is limited.

Fewer references exist in the literature for genetic parameters for test-day body weight of lactating cows than for milk yield, probably because until recently it was difficult to repeatedly weigh a large number of heavy animals over a long period of time. Our estimates of heritability for wBW (0.31 to 0.53 in L1, 0.43 to 0.56 in L2) tended to be a bit lower than the values estimated by Berry et al. (2003) for multiparous Holstein-Friesian cows (0.48 to 0.61). However, our results are consistent, although somewhat lower in L1 in the

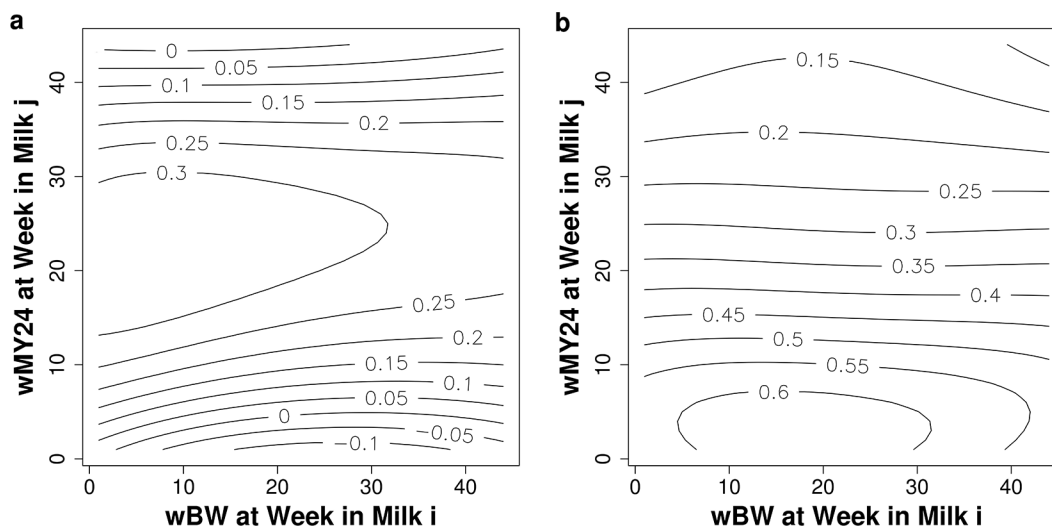


Figure 6. Genetic correlation estimates between weekly average of daily body weight adjusted for feed intake variation (wBW) and weekly average of daily milk yield adjusted for protein and fat content (wMY24) at different stages of lactation 1 (a) or lactation 2 (b).

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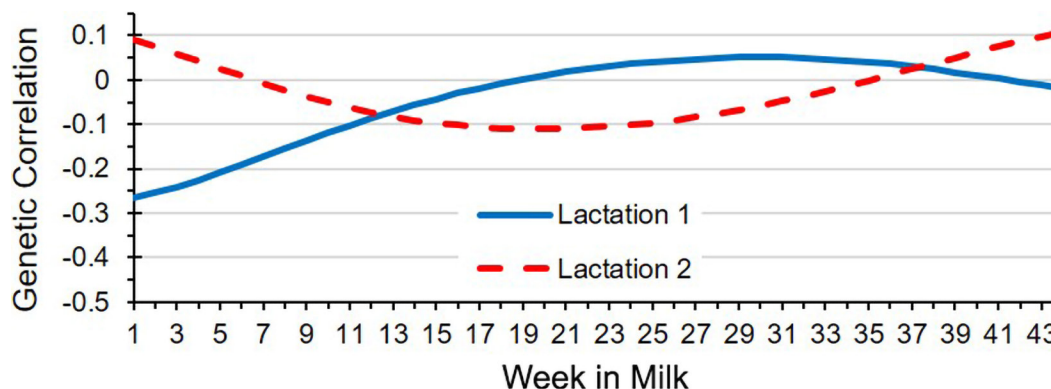


Figure 7. Genetic correlation estimates between BW loss during the first 5 wk after calving and daily fat- and protein-corrected milk yield throughout lactations 1 and 2.

first 5 wk of lactation, with the heritabilities estimated by Koenen and Veerkamp (1998) for Holstein-Friesian heifers (0.43 in wk 0 to 0.56 in wk 25), as well as with the estimates of Toshniwal et al. (2008) for Holstein cows (0.50 to 0.56).

The genetic correlations between values of wMY24 obtained several weeks apart were very high but different from 1, which suggests that measurements at different lactation stages represent different traits. The same was true for wBW, even though, as expected, across a given interval, r_g was higher for wBW than for wMY24, since a recording of BW is necessarily quite similar to those of the previous days. Instead, it is conceivable that milk production may be deeply dependent on various underlying phenomena that change during a lactation stage.

In primiparous cows, milk yield during the first 2 mo of lactation appeared to be genetically independent of BW at any point during lactation. After this, the genetic relationship with BW progressively strengthened until it reached 0.34 in the middle of lactation, and then decreased again until the 2 traits were again independent at WIM 44. This suggests that, once corrected for age differences, the heaviest cows tended to have the highest lactation peak, but the initial rate of increase in production and the persistence of milk yield were more or less independent of the size of the cow in L1. On the contrary, in L2, the heaviest cows tended to have higher milk yields in the first 3 mo of lactation, but the genetic relationship between BW and milk yield weakened after the third month of lactation.

All BW measurements taken during the first 5 wk of lactation (i.e., the period of weight loss due to mobilization) were highly correlated with each other ($r_g > 0.98$ in L1 and $r_g > 0.99$ in L2). Similarly, Koenen and Veerkamp (1998) also reported genetic correlations of 0.99 between body weight at wk 0 and wk 5 of lacta-

tion. This explains the very low genetic variance and therefore the very low heritability estimates (0.04 in L1 and 0.02 in L2) for BWL5. This heritability value is consistent with that obtained by Berry et al. (2003) for body weight changes from 5 to 60 DIM in multiparous Holstein cows (0.06) but is lower than the heritability estimated by Toshniwal et al. (2008) for body weight loss during the first 30 d of lactation (0.16) for first-, second-, and third-lactation Holstein cows. In the latter study, the estimated genetic correlation between body weight at DIM 0 and DIM 30 (about 0.93) was, however, lower than in our study, which could result in a higher genetic variance, and thus in a higher heritability, for weight loss.

The moderate negative genetic correlation found in L1 cows between BWL5 and wMY24 before WIM 17, which was the strongest at WIM 1 (-0.26), suggests that stronger body mobilization in early lactation is genetically associated with higher milk production. This is consistent with the results of Berry et al. (2003), who reported moderate unfavorable genetic correlations between milk yield and changes in both body weight and BCS during the first 2 mo of lactation. However, from approximately the fourth month of lactation, BWL5 and wMY24 appeared to be genetically independent in L1 cows. Furthermore, our estimates indicate that the genetic correlation between BWL5 and wMY24 was even weaker in L2 cows than in L1.

Certainly, the low heritability of weight loss in early lactation implies that selection to reduce body mobilization may be difficult. However, our results are encouraging. They suggest that, despite the slightly unfavorable correlation between body mobilization and milk production in early lactation in L1, and given the correlation of less than 1 between milk production in early and later lactation, selection to limit body mobilization while preserving milk production may be

possible. The increasing number of commercial farms equipped with milking robots, coupled with the growing availability of cow genotypes, will make it possible to consider the implementation of a large-scale program of genomic evaluation on weight loss to reduce body mobilization in early lactation. However, this will require the creation of systemic means of collecting information from these farms, and the development of tools for the automatic validation of BWR data from visits to robots.

CONCLUSIONS

Milking robots are a valuable source of data for monitoring weight changes and evaluating body mobilization in early lactation. It is unfortunate that we did not have data on the individual daily feed intake of the cows to adjust their BWR and were instead required to use predictions based on potentially debatable assumptions. Although they were only approximations, these predictions seemed consistent. Even with this in mind, though, we argue that our results demonstrate that it may be possible to select cows with high milk yield after the lactation peak while limiting body mobilization. If this kind of daily data become available on a large scale for selection, we may consider using this trait to limit BW loss and facilitate the transition period, instead of or in addition to selecting on functional traits to counterbalance the effects of the transition period.

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