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Genetic parameters and relevance for heat stress assessment in dairy cattle of 2 udder health traits: Somatic cell score and differential somatic cell count

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ABSTRACT

Somatic cell count is widely used for large-scale udder health monitoring and remains a proxy for mastitis incidence still used in many genetic evaluation systems. This trait and its log-transformation, SCS, are thus also available to study the effect of heat stress on mammary gland health. Currently, a new trait called differential somatic cell count (DSCC), which represents the percentage of neutrophils and lymphocytes in the total SCC, is increasingly phenotyped simultaneously with SCC. By combining information, SCS and DSCC could more closely reflect the direct trait than SCS alone, providing a better proxy for mastitis incidence including during heat stress events. On this basis, the first objective of this study was to evaluate the interest of DSCC for heat stress assessment with a focus on mammary gland health with SCS as comparison. Additionally, the interest of both traits for genetic evaluation of udder health thermotolerance was explored. Because studies providing basal genetic parameters for DSCC are still rare, they were also estimated in this study. To do so, a random regression model on DIM was performed considering each parity as a different trait. For both SCS and DSCC, similar averaged daily heritability (0.10 to 0.11 for SCS and 0.11 to 0.14 for DSCC) and repeatability (0.61 to 0.64 for SCS and 0.54 to 0.63 for DSCC) were obtained. Moderate averaged daily genetic correlations were also estimated between SCS and DSCC (0.43 to 0.55). From the residuals of the same model, average residual responses with temperature-humidity index (THI) were studied. The results showed that DSCC reaction in mean and in variance with high THI was stronger than SCS. In addition, the reaction with increasing THI seemed to be inconsistent between lactation numbers for SCS conversely to DSCC. In this way, DSCC presented more relevant characteristics than SCS to discriminate thermotolerant and thermosensitive cows for udder health. However, for general heat stress detection, udder health traits seemed not to be the most adapted biomarkers. Low heritability (0.02 to 0.03 for SCS and 0.03 to 0.04 for DSCC) and repeatability (0.12 to 0.18 for SCS and 0.20 to 0.26 for DSCC) values were also obtained for SCS and DSCC newly defined thermotolerance traits.
Key words: heat stress, somatic cell traits, genetic parameters, residuals

INTRODUCTION

Although more and more countries are incorporating direct clinical mastitis incidence into genetic selection programs, SCC continues to be a widely recognized indicator of udder health, also reflecting subclinical mastitis in dairy cows. It is therefore predominantly used in routine milk recording (ICAR, 2022) as it provides a reliable and controlled measurement. Indeed, during an udder infection, an increase of SCC is expected due to the recruitment of white blood cells, especially neutrophils (Alhussien and Dang, 2018). However, some pathogens only cause a modest increase of SCC and udder inflammation can occur even when SCC is low (Bradley and Green, 2005; Zecconi et al., 2019). In this way, analyzing the cellular populations composing SCC could help to detect udder issues. This information is now more and more often routinely available through the new indicator called differential somatic cell count (**DSCC**; Damm et al., 2017). The indicator DSCC is defined as the percentage of neutrophils and lymphocytes in total SCC and is thus expected to increase in the presence of udder inflammation (Damm et al., 2017). It has been suggested that the combination of SCC and DSCC information could improve the detection of mammary infection compared with SCC alone (Schwarz et al., 2019, 2020b), especially in animals presenting low SCC (Pilla et al., 2013). Currently, genetic parameters for SCS have been estimated with a variety of models (Martins et al., 2011; Alam et al., 2015; Soumri et al., 2020), whereas only repeatability models generally regrouping several parities have been used for DSCC (Bobbo et al., 2019, 2020; Pegolo et al., 2021; Ablondi et al., 2023), ignoring the longitudinal aspect of this novel trait across the lactation.

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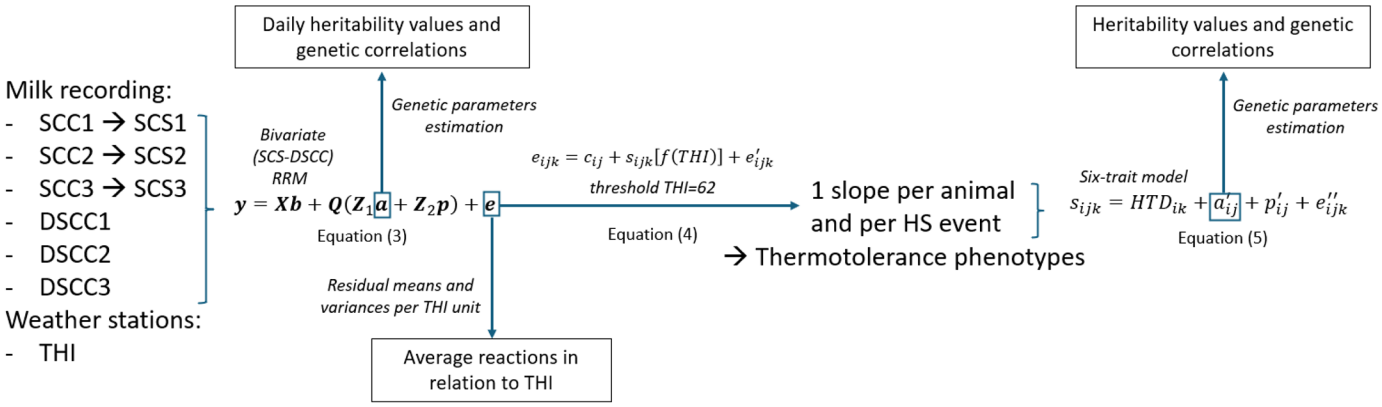

Figure 1. Overview of the methods used in this study. To estimate genetic parameters for SCS and DSCC as well as to generate residuals corrected for systematic effects, bivariate random regression models (RRM) were fitted (Equation 3). Those residuals were then used to evaluate SCS and DSCC relation with THI as well as to produce SCS and DSCC thermotolerance phenotypes by generating a residual slope per animal and event of heat stress (Equation 4). Finally, genetic parameters for those new thermotolerance phenotypes were estimated from a 6-trait model (Equation 5). SCC1 = somatic cell count for parity 1; SCC2 = somatic cell count for parity 2; SCC3 = somatic cell count for parity 3; SCS1 = somatic cell score for parity 1; SCS2 = somatic cell score for parity 2; SCS3 = somatic cell score for parity 3; DSCC1 = differential somatic cell count for parity 1; DSCC2 = differential somatic cell count for parity 2; DSCC3 = differential somatic cell count for parity 3; THI = temperature-humidity index.

In another context, heat stress is known to affect udder health (Vitali et al., 2016; Rakib et al., 2020) and numerous studies focused on the effect of heat stress on SCC and SCS due to their large-scale availability (Smith et al., 2013; Carabaño et al., 2014; Lambertz et al., 2014; Hammami et al., 2015; Tao et al., 2018; Hagiya et al., 2019; M'Hamdi et al., 2021; Negri et al., 2021; Moore et al., 2023; Vinet et al., 2023). However, the effect of heat stress on DSCC is still poorly studied while it could provide additional and routinely available information about heat stress effect on mammary gland health. In addition, no information is known about the genetic aspects of this new trait's response to temperature and humidity.

On this basis, the objective of this research was to determine the value of SCS and DSCC as routine indicators of mammary gland health in the context of heat stress by (1) studying their residuals response to the temperature-humidity index (**THI**) and (2) estimating direct genetic parameters for SCS and DSCC as well as genetic parameters for their reaction with THI.

MATERIALS AND METHODS

An overview of the methods used is represented in Figure 1. Briefly, 3 models were applied in this study. First, a random regression model (**RRM**) on DIM was fitted to estimate direct genetic parameters for SCS and DSCC and generate residuals. These residuals, obtained after correcting for systematic effects such as the lactation stage and the period of recording, were used to evaluate the impact of heat stress on SCS and DSCC. Then, to estimate the individual responses to heat stress, slopes of the reaction with THI for each animal at each event of heat stress were generated with a second model based on the residuals. Those slopes were considered as heat stress phenotypes. Finally, a third model was fitted on these newly defined thermotolerance phenotypes to estimate genetic parameters. Globally, those steps allowed to estimate genetic parameters for direct SCS and DSCC and for heat stress response of SCS and DSCC as well as to determine the interest of those traits to detect heat stress and evaluate heat tolerance.

Data

The SCC and DSCC data were collected over the period of 2019 to 2023 from routine milk recording analyses of Walloon Holstein cows in their first, second, or third parity and between 5 and 305 DIM. For SCC, records lower than 10,000 cells/mL and higher than the mean + 5 SD, which corresponds to 3,560,000 cells/mL, were deleted. For DSCC, no value is reported when SCC was found to be below 50,000 cells/mL. To avoid removing all records presenting low SCC, DSCC was considered as missing value when SCC <50,000 as well as when DSCC was lower than the mean − 5 SD, which corresponds to a DSCC value of 14%. Only lactations with at least 3 records and herd × test-day (**HTD**) with at least 5 records were considered. Records of cows in their second and third parity were retained even if there is no record for their first parity during the study period. A total of 719,270 and 390,390 records were kept respectively for SCC and DSCC including 307,127 and 148,556 records from first-lactation cows, 242,444 and 133,491 records from second lactation cows and 169,699 and 108,343 records from third lactation cows.

The SCC values were converted to SCS using the following equation (Wiggans and Shook, 1987):

$$\mathrm{SCS} = \left[\log_2\left(\frac{\mathrm{SCC}}{100,000}\right)\right] + 3. \quad [1]$$

Weather data from the same period were extracted from the Agromet platform (Dandrifosse et al., 2024). It includes hourly temperature (T) and relative humidity (RH) recorded by weather stations of the Pameseb network, which consists of 30 stations scattered across Wallonia and separated by approximately 30 km. Every herd of this study was associated with the weather data from the station closest to the farm by the Walloon breeder association before providing us the data to preserve anonymity of farms. Hourly THI were then calculated with the following formula (NRC, 1971; Bohmanova et al., 2007):

$$\mathrm{THI} = \left(1.8 \times \mathrm{T} + 32\right) - \left[\left(0.55 - 0.0055 \times \mathrm{RH}\right) \times \left(1.8 \times \mathrm{T} - 26\right)\right], \quad [2]$$

Daily THI was obtained by performing the mean of the 24 hourly THI values of a given day. Days without 24 records were not considered. To take into account the delay between the onset of heat stress and the consequences on dairy cows, classes of the mean of the THI of the test-day and the 3 previous days were used as in Lemal et al. (2025). Those THI classes were created by rounding mean THI values to the closest integer.

Statistical Model for Phenotypes

A bivariate RRM model was used to jointly estimate genetic parameters of SCC and DSCC within each parity separately and to generate residuals:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Q}\left(\mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{p}\right) + \mathbf{e}, \quad [3]$$

where $\mathbf{y}$ is the vector of test-day observations for 2 of the 6 traits studied (SCS-lactation 1 and DSCC-lactation 1 or SCS-lactation 2 and DSCC-lactation 2 or SCS-lactation 3 and DSCC-lactation 3); $\mathbf{b}$ is the vector of fixed effects for herd × year (HY) of recording, month of recording, minor classes of DIM (60 classes of 5 DIM), major classes of DIM (10 classes of 30 DIM) × season of calving, and age at calving (5 classes per lactation number); $\mathbf{a}$ is the vector of additive genetic random regression coefficients; $\mathbf{p}$ is the vector of permanent environment random regression coefficients; $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$ are the incidence matrices linking observations to the effects; $\mathbf{Q}$ is the covariate matrix of second-degree Legendre polynomials for standardized DIM [$x = 2(\mathrm{DIM} - \mathrm{DIM}_{\mathrm{minimum}})/(\mathrm{DIM}_{\mathrm{maximum}} - \mathrm{DIM}_{\mathrm{minimum}}) - 1$]; and $\mathbf{e}$ is the vector of residuals. Residual variances were considered independent and constant over the DIM.

This model includes a fixed HY effect instead of the classical HTD effect to allow the study of residual means in relation to THI. Indeed, for a given HTD, the THI is the same for all records and the residual means over THI are thus equal to 0 if the HTD effect is added in the model. For the study of variances, a HTD effect could be kept, but results were similar with the HY effect or the HTD effect (data not shown). In this way, the same model was chosen for studying both means and variances. A fixed month of recording effect was also included in the model to remove the seasonal effects that are not directly associated with the THI. The model is almost identical to the one in Lemal et al. (2025) where the same residual analysis method was used. However, a random effect for HY of calving was not included because preliminary studies did not show relevance of including this effect for traits related to somatic cells in contrast to traits related to milk yield and composition (Vanderick et al., 2022). A bivariate model was preferred to estimate genetic correlations between SCS and DSCC to mitigate the technical bias resulting from the availability of DSCC data only when SCC is equal to or above 50,000 cells/mL.

All models were fitted and (co)variance components estimated using the BLUPF90 family of programs (Misztal et al., 2014).

Average Residual Reactions in Relation to THI

The effect of THI on the studied traits was based on residual responses to THI instead of the solutions of a direct THI effect in the model as in Lemal et al. (2025). This residual approach allows to correct phenotypes for systematic effects while preventing interactions between those interfering effects and the heat stress effect generally represented by a THI effect in the model. To do so, residuals estimated from model [3] were associated with the mean THI of the test-day and the 3 previous days. Residuals were expressed as standardized residuals by dividing them by the SD of the residual values to allow comparison between traits. For every THI class with at least 500 records, standardized residual means and variances were calculated and represented as a function of THI. On this basis, 2 curves by trait and by parity were generated including one for the residual mean evolution with THI and one for the variance evolution with THI. Additionally, global curves containing residuals from all lactation numbers were created. Due to the higher number of records when residuals from all parities were grouped, means and variances for higher THI classes

were represented. Polynomials of degree 5 were fitted on the curves for a better appreciation of trends.

Residual Slopes with THI

To generate thermotolerance phenotypes, slopes of the reaction with THI for each animal at each event of heat stress were calculated based on residual values when the THI was higher than a threshold of 62 with the following model:

$$e_{ijk} = c_{ij} + s_{ijk}\left[f\left(\text{THI}\right)\right] + e'_{ijk}, \quad [4]$$

where e_{ijk} is the residual value estimated with model [3] for trait i (SCS-lactation 1, SCS-lactation 2, SCS-lactation 3, DSCC-lactation 1, DSCC-lactation 2, or DSCC-lactation 3); c_{ij} is the fixed effect for animal j; s_{ijk} is the slope of the regression on the THI (mean of the THI of the day and the 3 previous days) for animal j during recording k with $f(\text{THI}) = 0$ when $\text{THI}_{\text{test-day}} \leq 62$ and $f(\text{THI}) = \text{THI}_{\text{test-day}} - 62$ when $\text{THI}_{\text{test-day}} > 62$; and e'_{ijk} is the residual.

Similar methods are often used on phenotypes to determine the effect of THI on various traits (Carabaño et al., 2014; McWhorter et al., 2023; Lemal et al., 2024). Because model [3] was already used to correct phenotypes for systematic effects but also to avoid interactions between effects, residuals were used instead of phenotypes. Slopes for each animal and each event of heat stress were generated as thermotolerance phenotypes. An animal fixed effect was included in the model to ensure that the baseline level of each animal is comparable to generate slopes based on the same starting point. Indeed, residual averages per cow are not equal to 0 after model [3]. A slope for each animal and for each event of heat stress were generated to be able to consider that animals respond differently to heat stress and that a given animal response to heat stress can vary from one episode to another. It also allows to include, in the following model, episode-specific effects such as animal characteristics or an HTD effect. The threshold of 62 was chosen based on the residual reactions with THI represented in Figure 6, and Hammami et al. (2015) also used the same threshold for Walloon Holstein cows.

Statistical Model for Slopes

A 6-trait repeatability model was used to estimate genetic parameters of thermotolerance for SCS and DSCC based on the slopes calculated with model [4]:

$$s_{ijk} = HTD_{ik} + a'_{ij} + p'_{ij} + e''_{ijk}, \quad [5]$$

where s_{ijk} is the residual slope calculated with model [4] for trait i (SCS-lactation 1, SCS-lactation 2, SCS-lactation 3, DSCC-lactation 1, DSCC-lactation 2, and DSCC-lactation 3); HTD_{ik} is the fixed effect for HTD k; a'_{ij} is the random additive genetic effect for animal j; p'_{ij} is the permanent environment effect for animal j; and e''_{ijk} is the residual.

Herd × test-day was chosen as fixed effect due to the significance of that effect when fitting a simplified model using the Proc Mixed procedure in SAS (SAS version 9.4, SAS Institute Inc., Cary, NC). In the same way, no effects associated with the cow lactation characteristics were added due to the lack of significance of those effects.

Heritability and Repeatability Estimations

(Co)variance components estimated from model [3] were used to calculate daily heritability (h^2) and daily repeatability (ρ) values over the DIM scale using the following formulas computing these parameters for each DIM d:

$$h^2_{id} = \frac{\sigma^2_{a\text{-}id}}{\sigma^2_{a\text{-}id} + \sigma^2_{p\text{-}id} + \sigma^2_{e\text{-}i}}, \quad [6]$$

$$\rho_{id} = \frac{\sigma^2_{a\text{-}id} + \sigma^2_{p\text{-}id}}{\sigma^2_{a\text{-}id} + \sigma^2_{p\text{-}id} + \sigma^2_{e\text{-}i}}, \quad [7]$$

where h^2_{id} is the daily heritability of trait i (SCS-lactation 1, SCS-lactation 2, SCS-lactation 3, DSCC-lactation 1, DSCC-lactation 2, or DSCC-lactation 3) at DIM d (between 5 and 305); ρ_{id} is the daily repeatability of trait i at DIM d; $\sigma^2_{a\text{-}id}$ is the additive genetic variance for trait i at DIM d; $\sigma^2_{p\text{-}id}$ is the permanent environment variance for trait i at DIM d, and $\sigma^2_{e\text{-}i}$ is the residual variance for trait i. Additive genetic variances and permanent environment variances at DIM d were respectively calculated as the diagonals of $\mathbf{QG_0Q'}$ and $\mathbf{QP_0Q'}$ with $\mathbf{G_0}$ and $\mathbf{P_0}$ being the respective base covariance matrices among Legendre polynomial coefficients of the trait of interest and $\mathbf{Q}$ being the matrix containing Legendre polynomials for DIM d.

Heritability and repeatability of SCS and DSCC thermotolerance traits were calculated based on (co)variance components estimated from model [5] using classical formulas for heritability $\left[h^2 = \sigma^2_a \Big/ \left(\sigma^2_a + \sigma^2_p + \sigma^2_e\right)\right]$ and repeatability $\left[\rho = \left(\sigma^2_a + \sigma^2_p\right) \Big/ \left(\sigma^2_a + \sigma^2_p + \sigma^2_e\right)\right]$.

Genetic Correlation Estimations

(Co)variance components estimated from model [3] were used to calculate daily genetic correlation (r_g) and daily phenotypic correlation (r_P) values over the DIM scale using the following formulas:

$$r_{g\text{-}i_1i_2d} = \frac{cov_a\left(i_1i_2\right)_d}{\sqrt{\left(\sigma^2_{a\text{-}i_1d} \times \sigma^2_{a\text{-}i_2d}\right)}}, \quad [8]$$

$$r_{P\text{-}i_1i_2d} = \frac{cov_P\left(i_1i_2\right)_d}{\sqrt{\left(\sigma^2_{P\text{-}i_1d} \times \sigma^2_{P\text{-}i_2d}\right)}}, \quad [9]$$

where r_g and r_P are the daily genetic and phenotypic correlation between trait i_1 and trait i_2 (SCS-lactation 1 and DSCC-lactation 1 or SCS-lactation 2 and DSCC-lactation 2 or SCS-lactation 3 and DSCC-lactation 3) at DIM d (between 5 and 305), respectively; $\sigma^2_{P\text{-}i_1d}$ and $\sigma^2_{P\text{-}i_2d}$ are the phenotypic variances for trait i_1 and trait i_2 at DIM d calculated by summing the additive genetic $\left(\sigma^2_{a\text{-}i_1d}\right.$ or $\left.\sigma^2_{a\text{-}i_2d}\right)$, permanent environment, and residual variances for trait i_1 and trait i_2 at DIM d. $cov_P\left(i_1i_2\right)_d$ is the phenotypic covariance between trait i_1 and trait i_2 at DIM d calculated by summing the additive genetic $\left[cov_a\left(i_1i_2\right)_d\right]$ and permanent environment covariances between trait i_1 and trait i_2 at DIM d. Additive genetic variances and permanent environment variances at DIM d were estimated as described previously. Additive genetic covariances and permanent environment covariances at DIM d were respectively calculated as the diagonals of $\mathbf{QG_{0cov}Q'}$ and $\mathbf{QP_{0cov}Q'}$ with $\mathbf{G_{0cov}}$ and $\mathbf{P_{0cov}}$ the respective matrices containing base covariances among Legendre polynomial coefficients between the 2 traits of interest (i_1 and i_2) and $\mathbf{Q}$ the matrix containing Legendre polynomials for DIM d.

Genetic correlations between SCS and DSCC thermotolerance traits were calculated based on (co)variance components estimated from model [5] using the Pearson correlation formula $\left[r = cov\left(X,Y\right)\Big/\sqrt{\left(\sigma^2_X\sigma^2_Y\right)}\right]$.

RESULTS AND DISCUSSION

Data Distribution

Descriptive statistics for SCC, SCS, and DSCC are shown in Table 1. More records were obtained for lower parities compared with higher parities, but the proportion of records for DSCC compared with SCC and SCS increased with lactation number due to the lower amount of SCC records with less than 50,000 cells, which generated a missing value for DSCC. The average DSCC value obtained was 74.00%, which corresponds to the mean obtained by Damm et al. (2017) across several countries (74.53%) but was higher than the values reported in other studies (63.40%, Ablondi et al., 2023; 62.07%, Bobbo et al., 2019; 67.00%, Bobbo et al., 2020; 62.90%, Stocco et al., 2023).

As expected, SCC and SCS means as well as the SD were lower for lower parities compared with higher parities (Schutz et al., 1990; Schwarz et al., 2020a; Huang et al., 2023). Conversely, DSCC mean was the highest for the first lactation number and similar for the 2 other lactation numbers, whereas the SD was the lowest for the first lactation number and similar for the 2 others. In the literature, Huang et al. (2023) obtained the highest mean for the first parity similarly to our results, whereas Schwarz et al. (2020a) showed a constant increase of the average DSCC with the lactation number and Bobbo et al. (2019) reported the lowest value for parity 2 and the highest for parity 3+.

Based on the separation proposed by Zecconi et al. (2019) and used by Ablondi et al. (2023), 59.24% of records with SCC ≥50,000 cells/mL were associated with good udder health (SCC <200,000 cells/mL and DSCC

Table 1. Descriptive statistics for SCC, SCS, and differential somatic cell count (DSCC)

Trait	Parity	N records	N cows	Mean	SD	Minimum	Maximum
SCC (× 1,000 cells/mL)	All	719,270	81,085	168.14	358.63	20.00	3,560.00
	1	307,124	58,006	132.17	298.43		
	2	242,444	46,098	172.75	363.72		
	3	169,699	32,568	226.63	434.93		
SCS	All	719,270	81,085	2.51	1.63	0.68	8.15
	1	307,124	58,006	2.28	1.50		
	2	242,444	46,098	2.54	1.65		
	3	169,699	32,568	2.90	1.75		
DSCC (%)	All	390,390	73,414	74.00	11.73	14.10	97.70
	1	148,556	46,745	75.60	10.84		
	2	133,491	39,800	72.98	12.12		
	3	108,343	29,816	73.06	12.17		

<68.5%), 23.09% with a risk of mastitis (SCC <200,000 cells/mL and DSCC ≥68.5%), 16.49% with inflammatory mastitis (SCC ≥200,000 cells/mL and DSCC ≥68.5%), and 1.18% with chronic mastitis (SCC ≥200,000 cells/mL and DSCC <68.5%) (Figure 2). However, an important proportion of cows in the chronic mastitis group (9.45%) were cows with less than 10 DIM. In this way, the high SCC levels for those cows were more probably related to the natural transition from the dry period to lactation rather than an indication of chronic mastitis. The repartitions obtained were in line with Ablondi et al. (2023) but with a higher proportion of healthy cows in our dataset, which could be due to the limits chosen to consider outliers. By looking at the different parities separately, the first-lactation cows presented the highest proportion of records classified as healthy but also as risk of mastitis which was expected as first-lactation cows present in average less SCC than cows in higher lactation numbers. However, despite the higher average DSCC of first-lactation cows, they presented a similar proportion of records above the DSCC threshold of 68.5% compared with lactation 2 and smaller compared with lactation 3. The tendency of primiparous cows to have a lower proportion of chronic mastitis and higher DSCC values could be due to the absence of infections in previous parities that can affect the level of SCC in multiparous cows (Harmon, 1994; Green et al., 2002) and to a higher activity of their neutrophils compared with multiparous cows (Dang et al., 2014; Huang et al., 2023).

Raw Phenotypes

Effect of Lactation Stage Across and Within Lactation Number. Lactation curves for SCC and SCS presented high values in the beginning of lactations followed by a fast decrease and a slow re-increase until the end of lactation (Figure 3). The curve shapes were relatively similar for the 3 parities but with increasing values with increasing lactation number as reflected by the general means discussed previously. These shapes correspond to the results of other studies as reviewed by Alhussien and Dang (2018). Conversely, lactation curves for DSCC presented the lowest values at the beginning of lactations followed by a fast increase and a slow re-decrease until the end of lactations (Figure 3). Lactation curves for parities 2 and 3 were similar in both level and shape. The lactation curve for parity 1 started similarly to lactation 2 and 3, but the re-decrease after the peak was less important. Those results were consistent with the similar DSCC means obtained for parity 2 and parity 3 and the highest value for parity 1. In the literature, Kirkeby et al. (2020) showed that the evolution of DSCC with DIM followed the evolution of milk yield and is opposite to the SCC evolution with DIM, as we obtained. An opposite trend between SCC and DSCC was also obtained by Stocco et al. (2023). However, Schwarz et al. (2020a) obtained similar lactation curves for SCC and DSCC.

Effect of Month or Season of Recording Across and Within Lactation Number. It is relatively accepted that SCC and SCS tend to increase during summer months (Olde Riekerink et al., 2007; Vitali et al., 2016; Alhussien and Dang, 2018; Tao et al., 2018), which was also the case in this study with a similar increase and a peak in August for all parities (Figure 4). Concerning DSCC, the tendency was less clear with an increase during the summer but also a second peak in March. As for the lactation stage, parities 2 and 3 exhibited highly similar curves, whereas first-lactation cows had higher values but also seemed more stable over the year than cows in later parities. In the literature, a season effect is generally represented instead of a month effect. Magro et al. (2023) showed the highest values for DSCC during the summer season followed by the spring season, whereas the lowest values were obtained in autumn and winter. Stocco et al. (2023) also had the highest value during summer and a low value during winter, but spring and autumn were relatively similar. Only Schwarz et al. (2020a) separated each month with the highest value in August and the lowest in November, but their data did not cover a whole year. On this basis, as for SCC and SCS, the increase in DSCC during the summer seems consistent across studies. However, the second peak around March is difficult to detect in other studies.

Effect of THI Across and Within Lactation Number. Because the size of THI classes decreases with extreme THI, for graphical representation, the minimum THI class was set to 30 and only classes with at least 500 records were kept for high THI. Based on raw phenotypes, SCC and SCS increased with THI but reached their maximum just before a THI of 70 and then seemed to slightly decrease (Figure 5). By looking at the 3 lactation numbers separately, similar tendencies were observed but the lower number of records prevented to detect the potential decrease at the highest THI. Conversely, the reaction of DSCC with high THI showed a clear decrease around a THI of 65. Once again, the curves of parities 2 and 3 were highly similar while the curve of parity 1 exhibited higher values. The shape of the curve was also different with a relative stability and only a slight decrease at the highest THI for records from first-lactation cows, whereas later lactation cows presented an increase around a THI of 55 that reached its maximum around a THI of 65 before to decrease. As reviewed by Tao et al. (2018), numerous studies highlighted an increase in SCC or SCS during the summer when the THI was higher but, as they suggested, it could be due to other factors than hyperthermia. On this basis and knowing the effect of the DIM and the month of

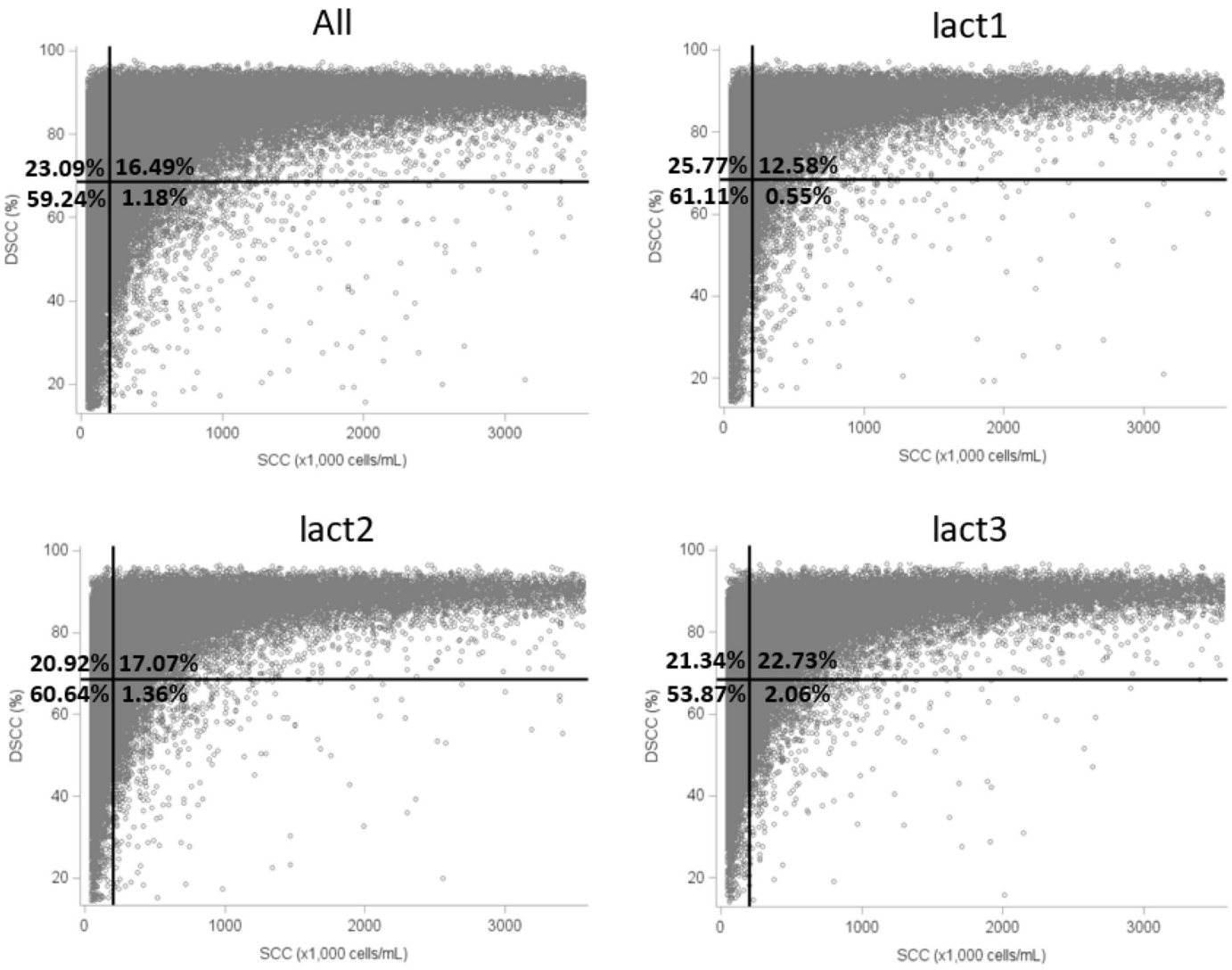

Figure 2. Distribution of records with SCC >50,000 cells/mL, based on the combination of SCC (× 1,000 cells/mL) and differential somatic cell count (DSCC, %) for all data and for each lactation number (lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3) separately. Lower left: good udder health (SCC <200,000 cells/mL and DSCC <68.5%); upper left: risk of mastitis (SCC <200,000 cells/mL and DSCC ≥68.5%); upper right: inflammatory mastitis (SCC ≥200,000 cells/mL and DSCC ≥68.5%); lower right: chronic mastitis (SCC ≥200,000 cells/mL and DSCC <68.5%).

recording on SCS and DSCC discussed previously, we applied an RRM on raw phenotypes to correct for those effects among others. Then, the reaction of the residuals to THI was studied, as performed in Lemal et al. (2025) to avoid a biased analysis due to interfering effects as discussed below.

Residual Analysis

To allow the interpretation of the effect of THI on SCS and DSCC without the interference of other known effects discussed previously, residuals from model [3] were studied instead of raw phenotypes or the least squares means of a THI effect.

Mean of Residuals. The first set of curves generated based on the residuals of model [3] are represented in Figure 6. Upper curves regrouped residual means from the 3 parities while residual means from each parity separately are shown by the lower curves. As for the raw residuals, the minimum THI class was set to 30 and only classes with at least 500 records were kept for high THI. Unexpectedly, the residual mean for SCS tended to decrease with the highest THI by looking at all residuals. However, this decrease started only at the highest THI and is relatively low compared with other traits studied in Lemal et al. (2025) with the same methodology and even compared with DSCC in this study. By focusing on each parity separately, an opposite trend is obtained for

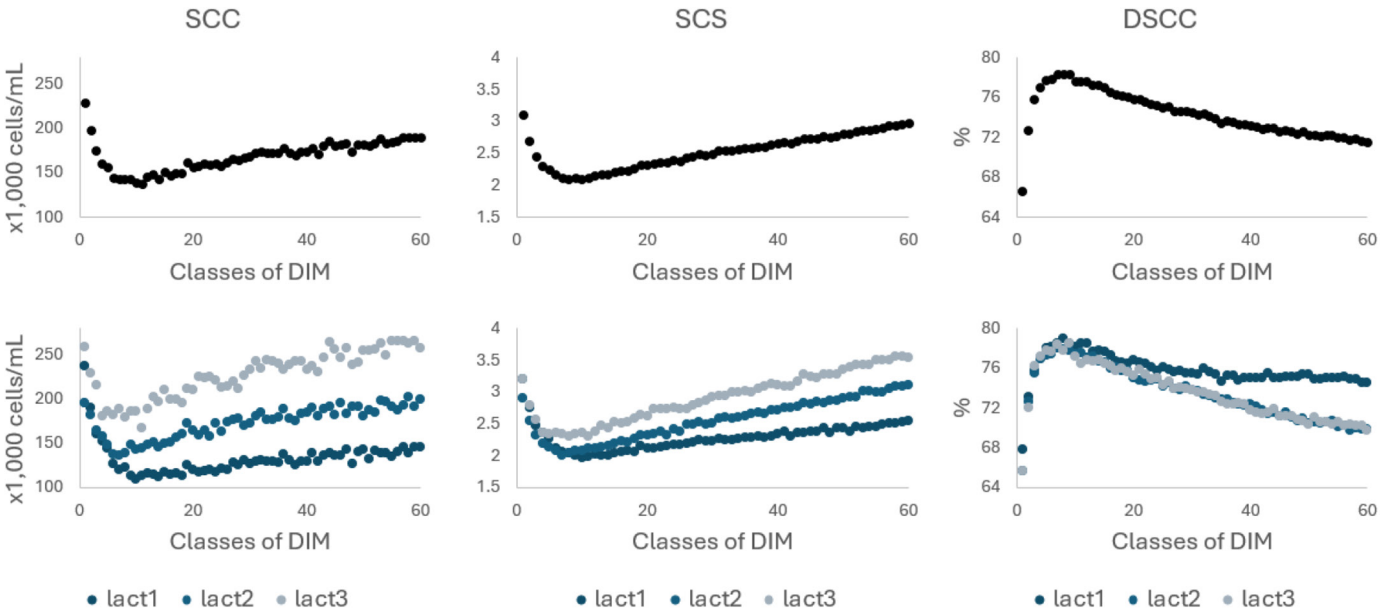

Figure 3. Phenotypic means of SCC (× 1,000 cells/mL), SCS, and differential somatic cell count (DSCC, %) by classes of DIM (classes of 5 DIM) for all of the dataset (upper line) and by lactation number (lower line; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3).

parity 1 compared with parities 2 and 3. Indeed, first-lactation cows had the tendency to have phenotypes with a higher value than expected for SCS when the THI is high which is represented by an increase of residual means, whereas cows in their second and third lactation presented slightly lower values than expected. This could be due to the higher basal level of SCC and SCS of cows in higher lactation numbers compared with first lactation. The selection applied to cows in their first lactation could also contribute to this difference in pattern.

As reviewed by Tao et al. (2018), SCC are known to increase during summer months when the THI is also higher than the rest of the year but studies in controlled environments generating hyperthermia did not show an effect on

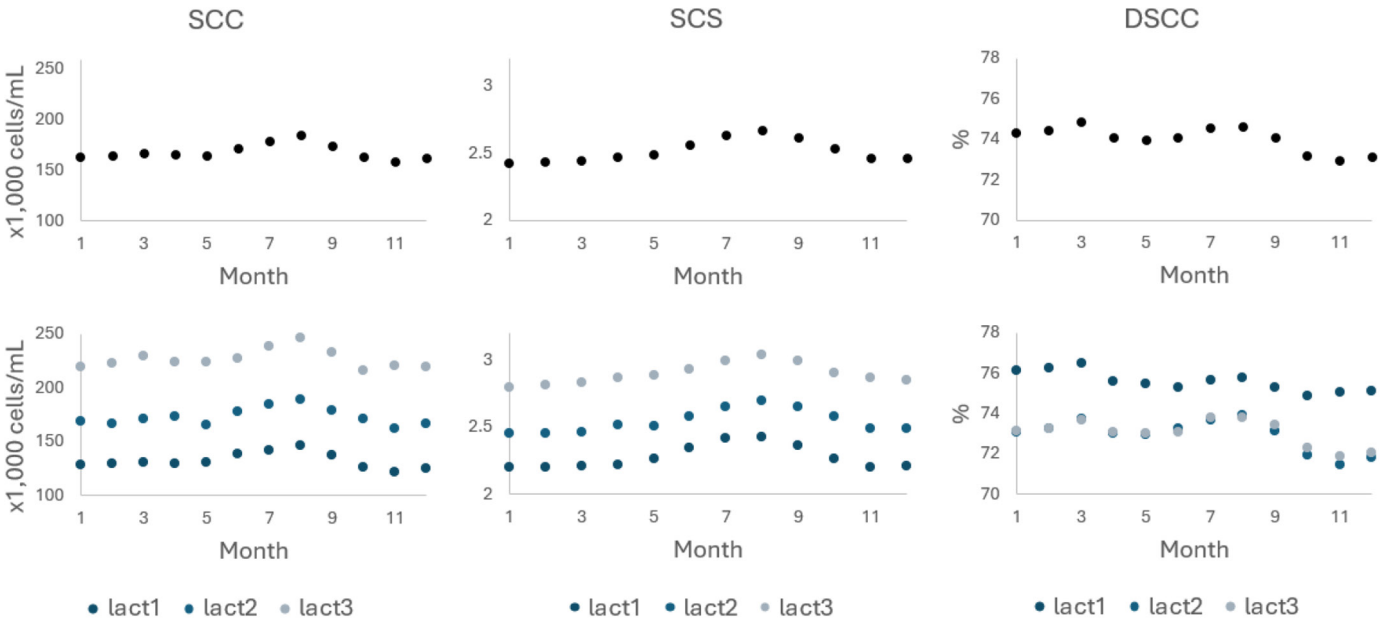

Figure 4. Phenotypic means of SCC (× 1,000 cells/mL), SCS, and differential somatic cell count (DSCC, %) by month of recording for all of the dataset (upper line) and by lactation number (lower line; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3).

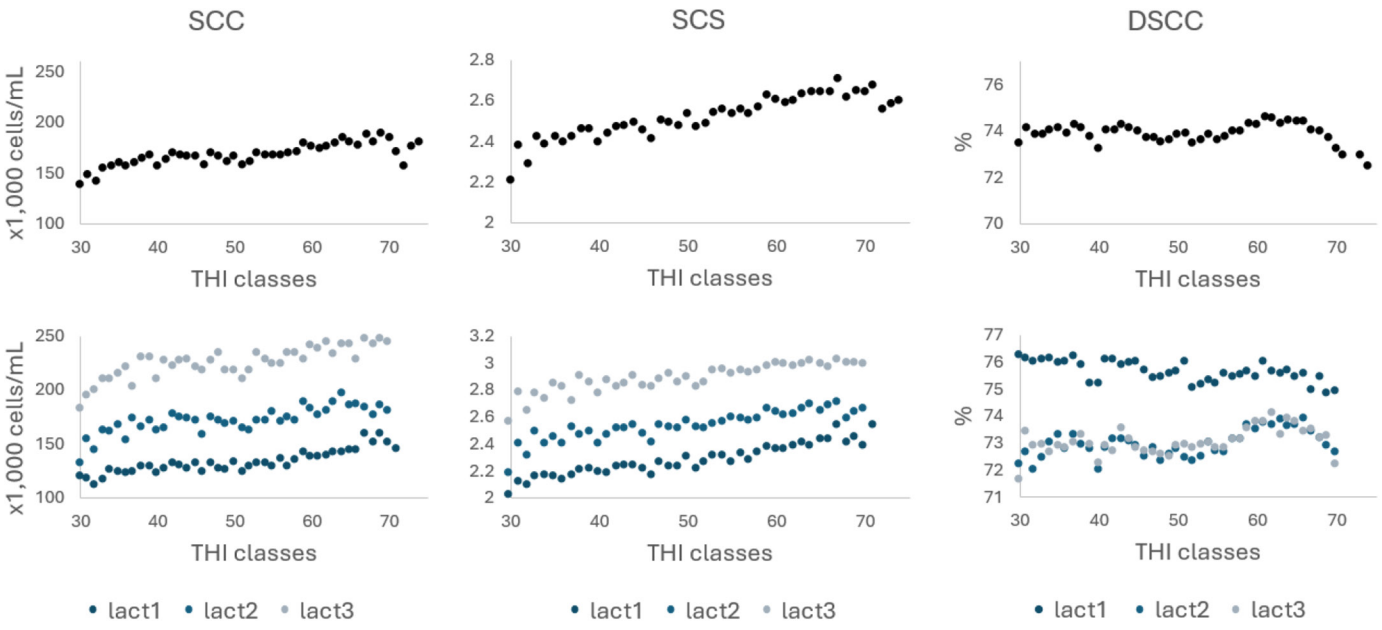

Figure 5. Phenotypic means of SCC (× 1,000 cells/mL), SCS, and differential somatic cell count (DSCC, %) by THI classes (classes of 1 THI unit; mean of the THI of the day of recording and the 3 previous days) for all of the dataset (upper line) and by lactation number (lower line; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3). Only THI classes with at least 500 records are represented. The maximum THI class reaching a minimum of 500 records is 71 for the first lactation number, 70 for the second and third lactation numbers, and 74 for the whole dataset combining records from first, second, and third lactations.

SCC. When models were used to correct for interfering effects, heat stress seemed often to increase SCS (Lambertz et al., 2014; Hagiya et al., 2019; M'Hamdi et al., 2021; Negri et al., 2021; Moore et al., 2023; Lemal et al., 2024), but Smith et al. (2013) obtained a decrease. Vinet et al. (2023) also showed an increase of the THI effect for SCS with THI, but it was followed by a decrease at the highest THI. This curve is similar to those we obtained for raw phenotypes. Finally, Carabaño et al. (2014) obtained erratic patterns and model-dependent interpretations for SCS in relation with THI. On this basis, the effect of heat stress on SCS is not fully clear and seems hard to differentiate from the seasonal increase of SCS. Based on our results, the effect of heat stress on SCS seems also highly dependent on the lactation number.

Conversely, results for DSCC presented similar curves for all 3 parities with a relatively clear threshold at a THI around 62. A threshold is already visible on raw phenotypes, especially for parities 2 and 3. In the literature, few studies have investigated the effect of THI on DSCC in dairy cows. To our knowledge, only Moore et al. (2023) showed a significant increase of DSCC between 3 increasing THI classes.

The decrease of DSCC with THI observed in our study could be due to several causes. Indeed, the observed decrease could be due to a decrease in the proportion of neutrophils and lymphocytes or an increase in the proportion of other cell types or a combination of both. Heat stress is already known to negatively affect the immune response of dairy cows by affecting white blood cell viability, activity, and recruitment (Bagath et al., 2019; Dahl et al., 2020; Lemal et al., 2023), which could lead to the lower average proportion of neutrophils and lymphocytes in SCC when THI is high. In addition, Lengi et al. (2022) highlighted an increase in the concentration of epithelial cells in the milk of heat-stressed cows, which could also participate in the reduction in DSCC percentage with high THI.

Variance of Residuals. The second set of curves generated based on the residuals of model [3] are represented in Figure 7. Similarly to the residual means, the upper curves regrouped residuals from all parities allowing to have more data for high THI classes, whereas they were kept separated in the lower curves. Concerning SCS, when all parities were grouped, the variance stayed relatively stable with increasing THI classes, whereas different patterns were observable for the different parities separately. However, the decrease observed for the first parity seemed to be an artifact because only the first parity reached the minimum number of 500 records, but this decrease was observed for all parities and was not persistent with higher THI classes. Conversely, DSCC presented smoother curves with a clear increase of variability when THI classes exceeded 65 with all parities grouped as well as when separated. Only parity 2 had a less clear increase but only THI classes until 70 reached

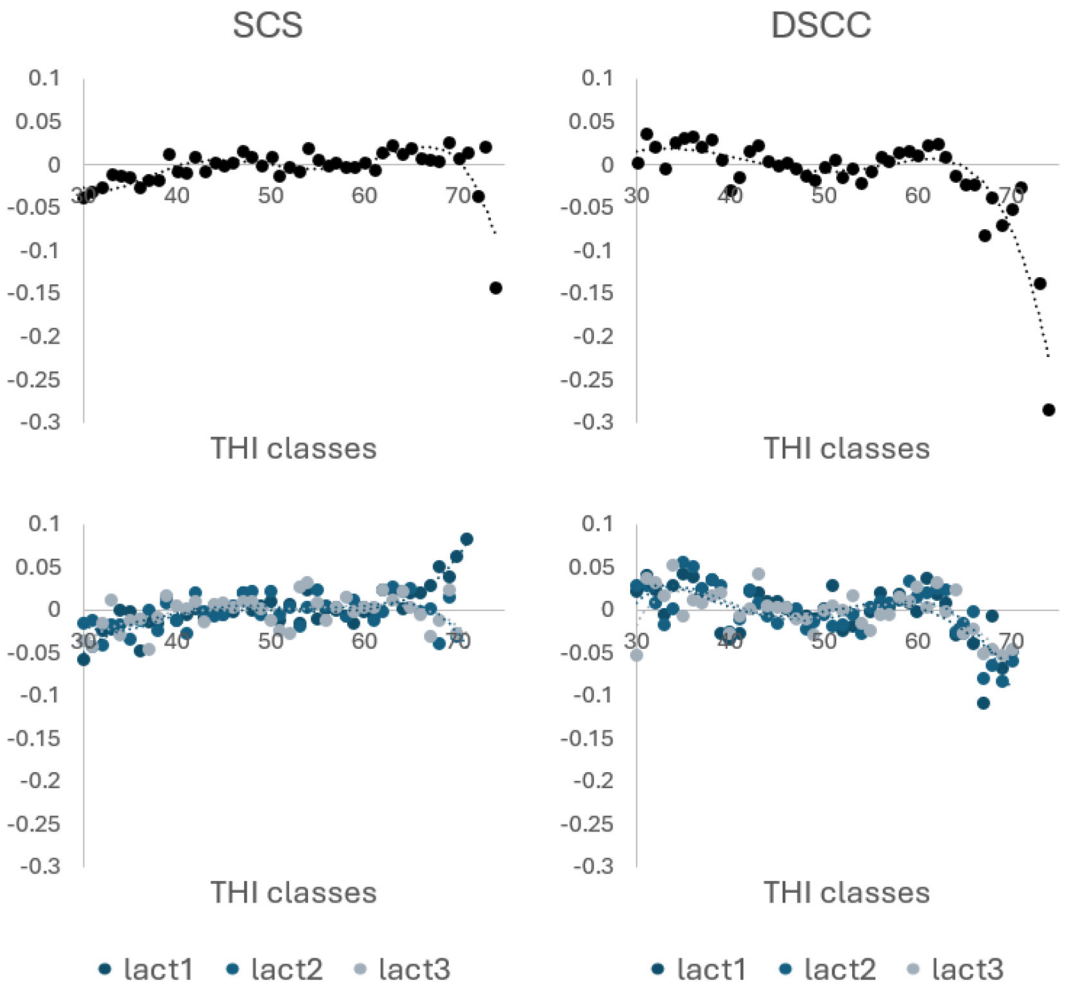

Figure 6. Means of standardized residuals estimated from model [3] for SCS and differential somatic cell count (DSCC, %) by THI classes (classes of 1 THI unit; mean of the THI of the day of recording and the 3 previous days) for all of the dataset (upper line) and by lactation number (lower line; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3). Only THI classes with at least 500 records are represented. The maximum THI class reaching a minimum of 500 records is 71 for the first lactation number, 70 for the second and third lactation numbers, and 74 for the whole dataset combining records from first, second, and third lactations.

the 500 records for that curve. The increase of variability for DSCC when THI was high suggested that the decrease of mean described previously could only apply to a portion of the cows recorded.

Genetic Parameters

Heritability and Repeatability of SCS and DSCC. Heritability and repeatability for direct SCS and DSCC for parities 1 to 3 over DIM were estimated based on model [3] and represented in Figure 8. The average heritability values for parities 1, 2, and 3 were 0.11, 0.11, 0.10 for SCS and 0.11, 0.14, 0.12 for DSCC, respectively. The average repeatability values for parities 1, 2 and 3 were 0.61, 0.62, 0.64 for SCS and 0.54, 0.60, 0.63 for DSCC, respectively. In general, heritability values for test-day SCS were in line with the literature (Kennedy et al., 1982; Costa et al., 2019; Tiezzi et al., 2020; Pegolo et al., 2021; Ablondi et al., 2023; Pérez-Cabal et al., 2024), but repeatability values were higher (Costa et al., 2019; Ablondi et al., 2023). Concerning DSCC, the available studies were more limited. Ablondi et al. (2023) obtained a heritability of 0.08 and a repeatability of 0.36, Bobbo et al. (2019) observed a heritability of 0.08, Bobbo et al. (2020) documented a heritability of 0.09, and Pegolo et al. (2021) found a heritability of 0.11. For both heritability and repeatability, the values in this study were slightly higher, especially for parity 2.

By looking at each parity separately, for SCS, average heritability values were very close with the highest for the first lactation and the lowest for the third lactation. Conversely, for DSCC, the average heritability value for parity 2 was higher than that for parity 1 and 3. Concerning repeatability for SCS, the 3 parities presented similar

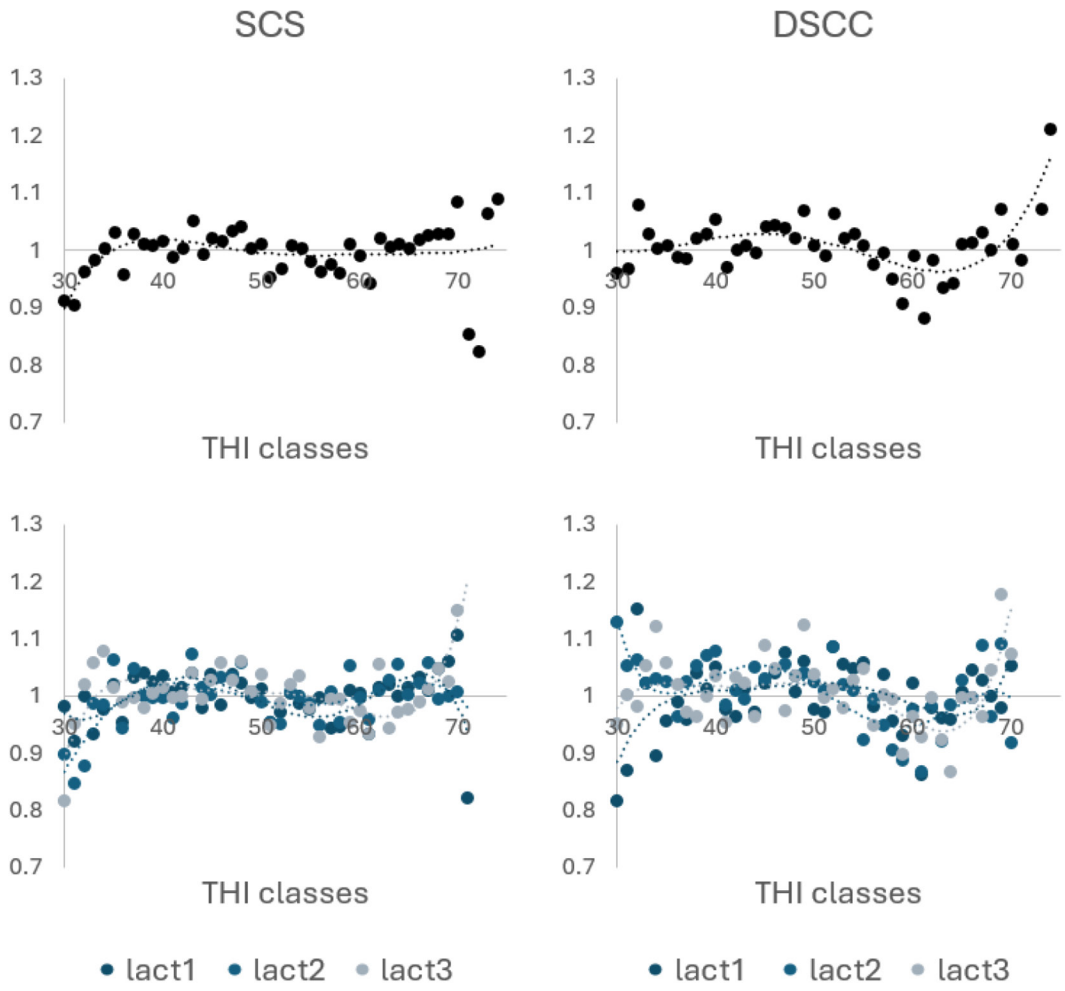

Figure 7. Variances of standardized residuals estimated from model [3] for SCS and differential somatic cell count (DSCC, %) by THI classes (classes of 1 THI unit; mean of the THI of the day of recording and the 3 previous days) for all of the dataset (upper line) and by lactation number (lower line; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3). Only THI classes with at least 500 records are represented. The maximum THI class reaching a minimum of 500 records is 71 for the first lactation number, 70 for the second and third lactation numbers, and 74 for the whole dataset combining records from first, second, and third lactations.

results with only a slight increase with lactation number. For DSCC, parities 2 and 3 showed relatively similar values but lactation 1 was lower. Those results suggest an increased stability of records for cows with increasing lactation number for SCS and DSCC. For DSCC especially, first lactation was clearly distinct from lactation 2 and 3 suggesting that cows could exhibit more variability in first lactation and reach consistent records in higher lactation numbers. This observation was in line with the clear phenotype difference between records from cows in first parity and those in later parities.

In the literature, several studies on SCS obtained a higher heritability for first lactation compared with later lactation numbers (Negussie et al., 2006; Alam et al., 2015; Atashi and Hostens, 2021), but other studies obtained opposite results with an increase in heritability with lactation number (Da et al., 1992; Miglior et al., 2009). For DSCC, no other study in our knowledge presented heritability and repeatability values for different parities separately.

Heritability and Repeatability of Residual Slopes of SCS and DSCC. Heritability and repeatability for newly defined udder health thermotolerance traits based on residual slopes estimated with model [5] are shown in Table 2. Heritability and repeatability values showed a slight increase with increasing lactation numbers and were marginally higher for DSCC than for SCS, but were globally low for both SCS (heritability from 0.02 to 0.03 and repeatability from 0.12 to 0.18) and DSCC (heritability from 0.03 to 0.04 and repeatability from 0.20 to 0.26). Those low values could be due to the inconsistency of slopes for a given animal. Indeed, an increase of SCS and DSCC is often due to mastitis that is not necessarily linked to heat stress but can drastically modify the result-

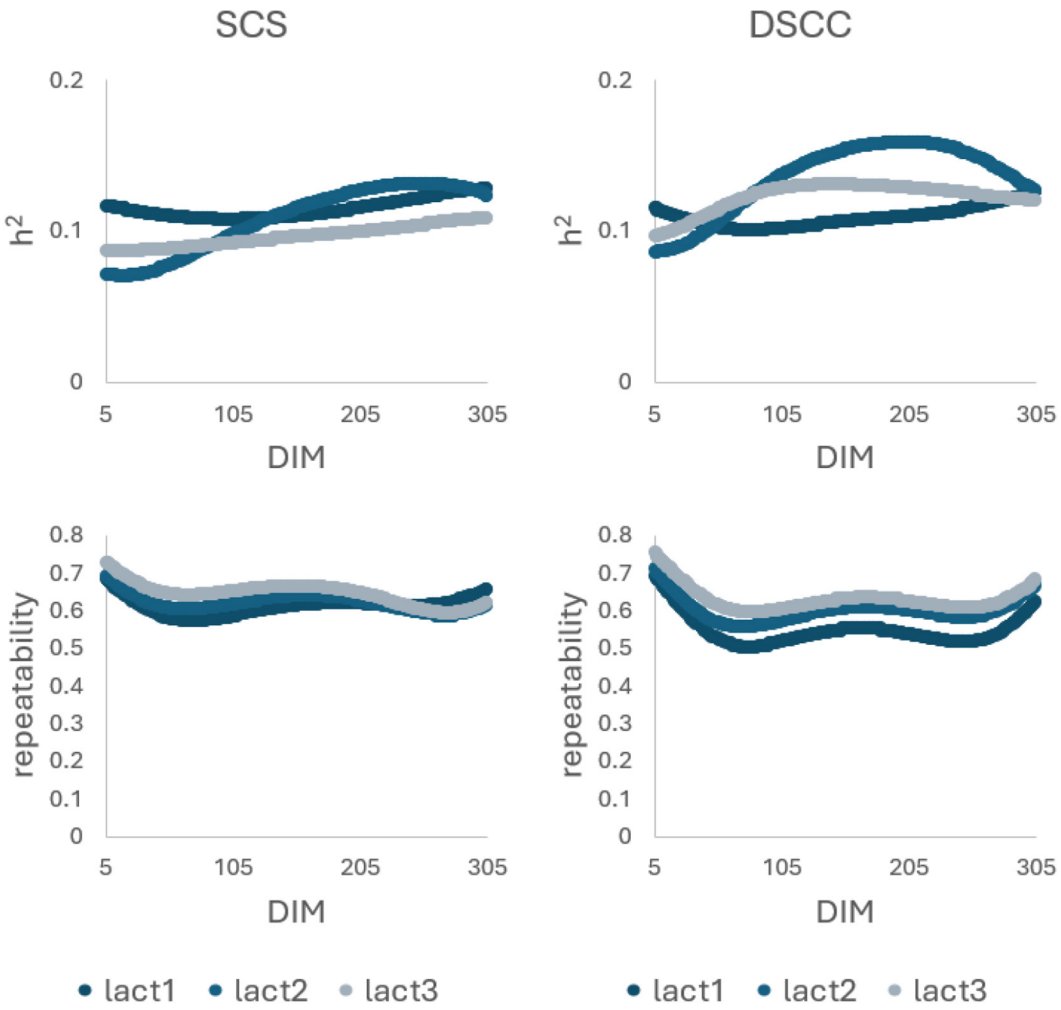

Figure 8. Heritability (h^2) and repeatability for SCS and differential somatic cell count (DSCC, %) along the DIM scale for first, second, and third parity, based on variances estimated with model [3]; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3.

ing slopes. In the literature, heritability for thermotolerance of SCS is based on variations of SCS along the THI scale and not on thermotolerance phenotypes (residual slopes in this case), making comparisons difficult.

Genetic Correlations Between SCS and DSCC. Daily genetic and phenotypic correlations between direct SCS and DSCC from the corresponding parity calculated based on variance components from model [3] are represented in Figure 9. All correlations were positive which is in line with the increase of both traits in case of mastitis. The average phenotypic correlations between SCS and DSCC were increasing with lactation number (0.42, 0.44, 0.50). Concerning genetic correlation, the highest average correlation was obtained for parity 3 (0.55), the lowest for parity 2 (0.43), and parity 1 was intermediate (0.53). In all cases, the highest correlations were obtained at the beginning and at the end of lactation. In the literature, Bobbo et al. (2019), Pegolo et al. (2021), and Ablondi et al. (2023) obtained higher genetic correlations (between 0.60 and 0.66), but those studies were all working on herds from the same region, which could explain their similarity and the difference with our results.

Table 2. Heritability and repeatability for newly defined SCS and DSCC thermotolerance traits (residual slopes with THI) from parity 1 to 3, based on (co)variances estimated with model [5]

Trait[1]	h^2	Repeatability
SCS1	0.02	0.12
SCS2	0.02	0.18
SCS3	0.03	0.18
DSCC1	0.03	0.20
DSCC2	0.04	0.26
DSCC3	0.04	0.26

[1]SCS1 = somatic cell score for parity 1; SCS2 = somatic cell score for parity 2; SCS3 = somatic cell score for parity 3; DSCC1 = differential somatic cell count for parity 1; DSCC2 = differential somatic cell count for parity 2; DSCC3 = differential somatic cell count for parity 3.

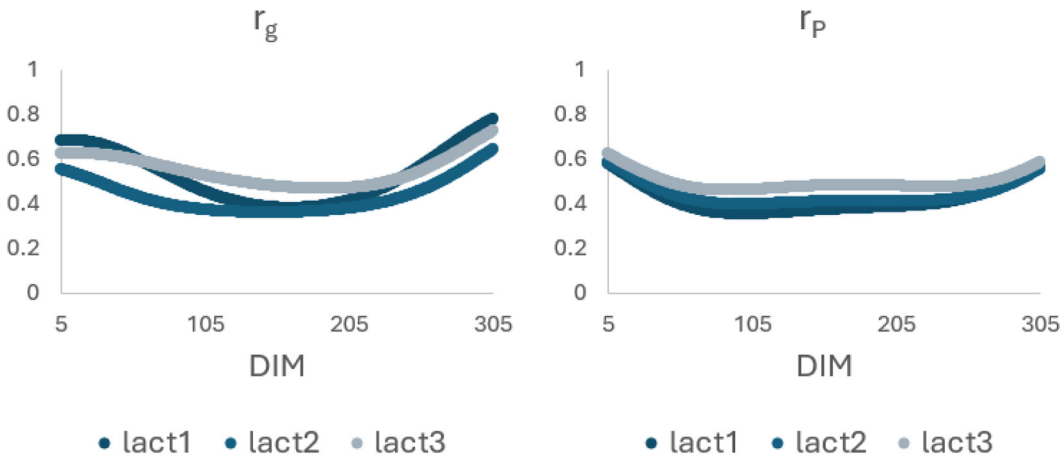

Figure 9. Genetic (r_g) and phenotypic (r_P) correlations between SCS and differential somatic cell count (DSCC, %) along the DIM scale for first, second, and third parity, based on (co)variances estimated with model [3]; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3.

Genetic Correlations Between Residual Slopes of SCS and DSCC. Genetic correlations between newly defined thermotolerance traits (residual slopes) for SCS and DSCC for parity 1 to 3 are shown in Table 3. Relatively high genetic correlations were obtained between SCS and DSCC slopes for the corresponding parities (0.48 to 0.67). However, genetic correlations between SCS slopes from different parities and DSCC slopes from different parities were generally low (0.00 to 0.19). As discussed for heritability and repeatability, those results could be highly influenced by mastitis events, not necessarily resulting from heat stress events. Indeed, a cow with mastitis is expected to have an increase of both SCS and DSCC, whereas a cow recovering from mastitis is expected to present a decrease of both SCS and DSCC. However, a given cow affected by mastitis for one summer but not during another can present totally different slopes, which could result in low consistency between lactation numbers.

Relevance of SCS and DSCC for the Assessment of Udder Health Thermotolerance

Routine milk recording provides large-scale information about milk yield, milk composition, and SCC (ICAR, 2022). For routine and large-scale assessment of heat stress, those parameters are of great interest. By focusing on the effect of heat stress on udder health, SCC (generally log-transformed in SCS) is thus one of the first-choice traits. However, DSCC information is more and more often available simultaneously with SCC providing a new and similarly available trait associated with udder health (Damm et al., 2017). A limitation concerning DSCC availability, however, is the absence of records when SCC is lower than 50,000 cells/mL.

In the literature, the effect of heat stress on DSCC is still little studied, in contrast to SCS that is often considered as increasing during heat stress, as discussed previously. However, this increase in SCS is observed during the whole summer period, which can create confusion with the specific effect of heat stress. Those interfering effects were removed as much as possible by studying residuals instead of raw phenotypes. On this basis, the residual mean reaction with THI obtained for DSCC was stronger than for SCS even if both traits reacted weakly compared with some milk component traits (Lemal et al., 2025). Moreover, the direction of variation was variable with the lactation number for SCS, whereas DSCC presented similar responses for all parities. However, in general, the results obtained were relatively unexpected. Indeed, only SCS average residuals of first-lactation cows were increasing with high THI, whereas heat stress is often associated with a higher risk of mastitis that increases both SCS and DSCC (Dahl, 2018; Vitali et al., 2020;

Table 3. Genetic correlations between SCS and DSCC from parity 1 to 3 based on (co)variances estimated with model [3] (upper off-diagonal elements) genetic correlations for SCS and DSCC newly defined thermotolerance traits (residual slopes with THI) from parity 1 to 3 based on (co)variances estimated with model [5] (lower off-diagonal elements)

Trait[1]	SCS1	SCS2	SCS3	DSCC1	DSCC2	DSCC3
SCS1		—	—	0.53	—	—
SCS2	0.03		—	—	0.43	—
SCS3	0.19	0.00		—	—	0.55
DSCC1	0.48	0.02	0.08		—	—
DSCC2	−0.02	0.64	−0.01	0.09		—
DSCC3	0.12	−0.02	0.67	0.10	0.01	

[1]SCS1 = somatic cell score for parity 1; SCS2 = somatic cell score for parity 2; SCS3 = somatic cell score for parity 3; DSCC1 = differential somatic cell count for parity 1; DSCC2 = differential somatic cell count for parity 2; DSCC3 = differential somatic cell count for parity 3.

Lemal et al., 2023). This could be due to the delay between the heat stress event and the recording; heat stress could contribute to an increase of mastitis occurrence in the longer term. The average decrease in DSCC could be a sign of an average weaker capability of immune response against future mastitis pathogens or a weaker immune response against current infections or both. In another way, a decrease of DSCC could also be the result of a higher desquamation of mammary epithelial cells. By looking at residual variability, SCS stayed relatively stable, whereas DSCC residual variance increased with high THI. Those results suggest that SCS and DSCC are not very specific biomarkers for heat stress due to the weak response in mean of SCS and the high variability of reactions during heat stress for DSCC. However, DSCC could potentially help to identify cows with a weakened immune capability after an event of heat stress.

Concerning selection against heat stress, the heritability values were low for both SCS and DSCC, making selection possible but difficult. The relatively low repeatability values and genetic correlations between parities also suggest a low consistency of SCS and DSCC responses during different heat stress events for a given cow, which can partially explain the low heritability values obtained. Indeed, a cow presenting mastitis during a hot period will present a high level of both SCS and DSCC even if heat stress is not linked to the disease. This lack of consistency led us to choose to generate thermotolerance phenotypes consisting of a slope per cow and per event of heat stress instead of only one slope per cow. This type of approach seems relevant with SCS and DSCC which can vary greatly over time, depending on the infectious status, but could potentially be extended to other phenotypes.

CONCLUSIONS

This study presented the effect of various systematic effects including lactation parameters and period of recording on the well-known SCS as well as on the novel trait DSCC. After correction of those effects with an RRM model, moderate daily genetic correlations between SCS and DSCC were obtained and both traits presented similar average daily heritability and high repeatability. Based on residuals from the same model, DSCC presented globally more interesting parameters to assess heat stress than SCS. Indeed, the DSCC reaction with THI was stronger, similar for all lactation numbers, and the increasing variability when THI was high could help to discriminate thermotolerant and thermosensitive animals for udder health. However, those traits seem not to be the most adapted for global detection of heat stress and selection against it, especially due to the lack of consistency in their responses.

NOTES

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Nonstandard abbreviations used: SCC1 = somatic cell count for parity 1; SCC2 = somatic cell count for parity 2; SCC3 = somatic cell count for parity 3; SCS1 = somatic cell score for parity 1; SCS2 = somatic cell score for parity 2; SCS3 = somatic cell score for parity 3; DSCC = differential somatic cell count; DSCC1 = differential somatic cell count for parity 1; DSCC2 = differential somatic cell count for parity 2; DSCC3 = differential somatic cell count for parity 3; HTD = herd × test-day; HY = herd × year; ; lact1 = lactation 1; lact2 = lactation 2; lact3 = lactation 3; RRM = random regression model; THI = temperature-humidity index.

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