Genetic Analysis of Milk Urea Nitrogen and Lactose and Their Relationships with Other Production Traits in Canadian Holstein Cattle

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ABSTRACT

The objective of this research was to estimate heritabilities of milk urea nitrogen (MUN) and lactose in the first 3 parities and their genetic relationships with milk, fat, protein, and SCS in Canadian Holsteins. Data were a random sample of complete herds (60,645 test day records of 5,022 cows from 91 herds) extracted from the edited data set, which included 892,039 test-day records of 144,622 Holstein cows from 4,570 herds. A test-day animal model with multiple-trait random regression and the Gibbs sampling method were used for parameter estimation. Regression curves were modeled using Legendre polynomials of order 4. A total of 6 separate 4-trait analyses, which included MUN, lactose, or both (yield or percentage) with different combinations of production traits (milk, fat and protein yield, fat and protein percentages, and somatic cell score) were performed. Average daily heritabilities were moderately high for MUN (from 0.384 to 0.414), lactose kilograms (from 0.466 to 0.539), and lactose percentage (from 0.478 to 0.508). Lactose yield was highly correlated with milk yield (0.979). Lactose percentage and MUN were not genetically correlated with milk yield. However, lactose percentage was significantly correlated with somatic cell score (−0.202). The MUN was correlated with fat (0.425) and protein percentages (0.20). Genetic correlations among parities were high for MUN, lactose percentage, and yield. Estimated breeding values (EBV) of bulls for MUN were correlated with fat percentage EBV (0.287) and EBV of lactose percentage were correlated with lactation persistency EBV (0.329). Correlations between lactose percentage and MUN with fertility traits were close to zero, thus diminishing the potential of using those traits as possible indicators of fertility.

Key words: lactose, milk urea nitrogen, genetic parameter

INTRODUCTION

Valacta, the DHI organization responsible for milk recording in the province of Quebec, has been collecting data for MUN since 1997 in approximately two-thirds of herds enrolled in traditional milk recording. In 2001, Valacta also started collecting data for lactose in approximately one-third of milk-recorded farms. Phenotypic information of MUN and lactose is sent back to farmers for management purposes. The MUN is generally used as a noninvasive approach to monitor the animal's protein status and the efficiency of nitrogen utilization (Moore and Varga, 1986; Broderick and Clayton, 1997; Jonker et al., 1998; Eicher et al., 1999). Analysis of lactose was introduced by Valacta to include this trait in the calculation of the energy value of milk for the purpose of establishing energy requirements for feeding recommendations.

Literature regarding genetic parameters for MUN and lactose, and their relationships with other production traits in dairy cattle, is scarce. Concentration of MUN in Ontario herds has been shown to be heritable with low genetic correlations with production traits (Wood et al., 2003). In the study by Wood et al. (2003), heritabilities of MUN for the first 3 parities ranged between 0.44 to 0.59, and genetic correlations with production traits were close to zero in parities 1 and 3 and slightly positive in parity 2. Lower heritabilities for MUN have been found in 2 US studies (Vallimont et al., 2003; Mitchell et al., 2005). Both studies found greater heritabilities when MUN was analyzed by midinfrared spectroscopy than with wet chemistry. Wet chemistry methods directly measure urea nitrogen in milk, whereas infrared MUN values are calculated with prediction equations that use spectrum analyses. Mitchell et al. (2005) found a low positive genetic correlation between wet chemistry and midinfrared MUN (0.38

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and 0.23, in first and second parity, respectively). Two recent investigations from the Netherlands found heritability values for midinfrared MUN of 0.14 (Stoop et al., 2006) and of 0.22 (de Roos and de Jong, 2006). Stoop et al. (2006) used a fixed regression test-day model on a relatively small data set of first parity cows, whereas de Roos and de Jong (2006) used a random regression test-day model on a much larger data set of multiparous cows. Heritability of 0.23 was found for MUN by Gredler et al. (2006), using a multiple-trait animal model for MUN, BCS, days to first service, and fat:protein ratio.

Lactose percent has been reported to be highly heritable (0.53), according to a study in Holstein cows from Michigan (Welper and Freeman, 1992). The Michigan study included a relative large number of first-lactation cows (>5,000), and a lactation sire model was implemented to estimate variance components. Welper and Freeman (1992) found that lactose yield was less heritable (0.26) than, but highly correlated with, milk yield traits, and negatively correlated with milk content traits, whereas lactose percentage followed the opposite pattern. Stoop et al. (2006) found a higher heritability for lactose yield (0.47). They also estimated genetic correlations among various production traits. Lactose yield was highly correlated with fat and protein yield (0.58 and 0.86, respectively) and less correlated with MUN (0.22).

Miglior et al. (2006) found a statistically significant association between lactose percentage and MUN in first lactation with functional survival in Canadian Ayrshire and Holstein cows. In particular, Holstein cows were at a decreasing relative risk of being culled with increasing levels of MUN or lactose percentage. Miglior et al. (2006) concluded that the significant association between longevity with MUN and lactose was likely indirect because both traits have been found to be statistically associated with health and fertility status of cows, both of which are associated with longevity.

The underlying motivation for the study was the desire to assess the feasibility of routine estimation EBV for lactose and MUN and to explore their potential as indicator traits for female fertility by estimating their relationship with EBV of other economically important traits. In addition, we wanted to confirm previous findings on MUN by Wood et al. (2003) by using a larger data set and an improved model, as well as to estimate genetic parameters for lactose (yield and percentage), a trait for which literature is scarce. Therefore, the specific objectives of this research were to estimate a) heritabilities of MUN and lactose (yield and percentage) in the first 3 parities, b) their genetic relationships with milk, fat, protein, and SCS, c) breeding values for MUN and lactose percentage in Canadian Holsteins, and d)

correlations between bull EBV for MUN and lactose with other traits of interest.

MATERIALS AND METHODS

Test-day records collected from 2001 to 2004 were provided by Valacta for Holstein cows from Quebec farms. The data included animal registration number, herd, calving date, test date, milk yield, fat, protein and lactose percentages, SCC, MUN concentration, number of milkings per day, and a flag indicating supervised/unsupervised control. Full pedigree records were provided by Canadian Dairy Network (Guelph, Canada). All samples were analyzed by midinfrared spectroscopy using Fossomatic 4000 milk analysers (Foss Electric, Hillerød, Denmark) calibrated (wavelength = 9.6 μm) weekly. Calibration samples were analyzed for anhydrous lactose by HPLC (IDF Standard 198/ISO 22662) and for MUN by pH difference (IDF Standard 195/ISO 14637; International Committee for Animal Recording, 2006).

Records from DIM <5 and >305 d were eliminated. The SCC were log-transformed to SCS. Only records from the first 3 parities that had data for all production traits on a given test day, including lactose and MUN, were kept. Within cow, if parity 3 was present, parities 1 and 2 were also present, and if parity 2 was present, parity 1 was also present. Herds were required to have a minimum of 20 cows in the data set to be included in the analysis (~5 cows per year). The final edited data set included 892,039 test day records from 144,622 cows from 4,570 herds. To estimate variance components, a random sample of complete herds was extracted from the edited data set. A total of 5,022 cows from 91 herds (average 55 cows/herd) with 60,645 test-day records were randomly selected. The total number of animals (cows with own records + pedigree) included 15,532 animals.

Covariance components were estimated by Bayesian methods with Gibbs sampling using 6 separate 4-trait random regression test-day models. Custom-written software was used for the analysis. Analyzing all 9 traits in one model was computationally very demanding, and the option of several analyses using smaller number of traits was therefore chosen. The six 4-trait analyses were performed for the following group of traits: 1) Milk, lactose percentage, MUN, SCS; 2) Milk, lactose (kg), MUN, SCS; 3) Fat percentage, lactose percentage, MUN, SCS; 4) Protein percentage, lactose percentage, MUN, SCS; 5) Milk, fat (kg), protein (kg), SCS; and 6) Milk, fat percentage, protein percentage, SCS.

The model for a single trait (milk, fat, protein, SCS, MUN, or lactose) can be expressed in matrix notation by the equation

Table 1. Descriptive statistics of test-day records in complete edited data set

Parity	Test-day records	Cows	Milk (kg)		Fat %		Protein %		SCC ($\times 1,000/\text{mL}$)		MUN (mg/dL)		Lactose (%)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	507,761	144,622	27.0	6.4	3.83	0.68	3.30	0.32	184	574	10.73	3.34	4.69	0.18
2	273,452	75,924	31.7	9.1	3.79	0.72	3.30	0.35	244	655	11.22	3.38	4.57	0.22
3	110,826	31,900	33.5	9.7	3.79	0.73	3.26	0.35	309	782	11.16	3.31	4.52	0.24
Total	892,039	144,622	29.2	8.2	3.81	0.70	3.29	0.33	218	630	10.93	3.36	4.63	0.21

$$\mathbf{y}_m = \mathbf{H}_m \mathbf{h}_m + \mathbf{X}_m \mathbf{b}_m + \mathbf{W}_m \mathbf{p}_m + \mathbf{Z}_m \mathbf{a}_m + \mathbf{e}_m,$$

where $\mathbf{y}_m$ is a vector of observations from lactations 1, 2, and 3, for trait m ($m = 1, \dots, 4$), $\mathbf{h}_m$ is a vector of fixed herd – test-day effects; $\mathbf{b}_m$ is a vector of fixed regression coefficients for age/parity/season of calving effects (2 seasons and 19 age classes); $\mathbf{p}_m$ is a vector of random regression coefficients for permanent environmental effects; $\mathbf{a}_m$ is a vector of random regression coefficients for animal genetic effects; $\mathbf{e}_m$ is a vector of residuals; and $\mathbf{H}_m$, $\mathbf{X}_m$, $\mathbf{W}_m$, and $\mathbf{Z}_m$ are incidence matrices assigning observations to effects.

Regression curves were modeled using Legendre polynomials of order 4 as defined by Jamrozik et al. (2002).

The multiple trait model (4 traits at a time) was

$$\mathbf{y} = \mathbf{H}\mathbf{h} + \mathbf{X}\mathbf{b} + \mathbf{W}\mathbf{p} + \mathbf{Z}\mathbf{a} + \mathbf{e},$$

where $\mathbf{y} = [y_1', \dots, y_4']'$, $\mathbf{h} = [h_1', \dots, h_4']'$, $\mathbf{b} = [b_1', \dots, b_4']'$, $\mathbf{p} = [p_1', \dots, p_4']'$, $\mathbf{a} = [a_1', \dots, a_4']'$ and $\mathbf{e} = [e_1', \dots, e_4']'$; $\mathbf{H} = \Sigma^+ \mathbf{H}_m$, $\mathbf{X} = \Sigma^+ \mathbf{X}_m$, $\mathbf{W} = \Sigma^+ \mathbf{W}_m$, and $\mathbf{Z} = \Sigma^+ \mathbf{Z}_m$ (direct sum of matrices).

Expectations and covariance structure for random effects can be described in matrix notation as

$$\mathbf{E}(\mathbf{y}) = \mathbf{H}\mathbf{h} + \mathbf{X}\mathbf{b}, \mathbf{E}(\mathbf{p}) = \mathbf{0}, \mathbf{E}(\mathbf{a}) = \mathbf{0}, \mathbf{E}(\mathbf{e}) = \mathbf{0}$$

and

$$\mathbf{V}(\mathbf{p}) = \mathbf{I} \otimes \mathbf{P}_0, \mathbf{V}(\mathbf{a}) = \mathbf{A} \otimes \mathbf{G}_0, \mathbf{V}(\mathbf{e}) = \sum^+ \mathbf{R}^{p,s},$$

where $\mathbf{A}$ is the additive relationship matrix, and $\mathbf{P}_0$ and $\mathbf{G}_0$ are 60×60 covariance matrices for environmental

and genetic regression coefficients, respectively. Finally $\mathbf{R}^{p,s}$ are 4×4 matrices of residual covariances among traits with elements that depend on parity (p) and the interval of DIM (s). These intervals were defined as 5 to 45, 46 to 115, 116 to 205, and 206 to 305 DIM. Random effects of the model were assumed to be normally distributed, and the conditional distribution of the data was also normal. In addition, residual effects were assumed to be independent between cows and different DIM. Flat prior distributions were assumed for all fixed effects, and inverted Wishart distributions were used as priors for covariance matrices. Prior values for covariances were as estimated previously from Holstein data (Muir et al., 2004), and they were used with minimal number of degrees of freedom. Posterior means of (co)variance components were estimated using 90,000 samples after a burn-in of 10,000 samples for each 4-trait model. Daily heritability was defined as a ratio of genetic variance to the sum of genetic, permanent environmental ($\mathbf{PE}$), and residual variances for each DIM from 5 to 305 d, and averaged across the entire lactation for each of the first 3 lactations. Genetic correlations were calculated using (co)variances of the first regression coefficients as described by Wood et al. (2003).

Data for estimation of breeding values included an additional year of calving (2005) and had lower editing restrictions in comparison with criteria used to edit the data set for variance component estimation, as missing traits, parities, or both, were allowed. The data set for breeding value estimation included 1,317,798 test day records from 245,283 cows from 4,691 herds. Breeding values for milk yield, lactose percentage, MUN, and SCS were estimated using a 4-trait multiple-lactation

Table 2. Descriptive statistics of test-day records in random sample used for variance component estimation

Parity	Test-day records	Cows	Milk (kg)		Fat (%)		Protein (%)		SCC ($\times 1,000/\text{mL}$)		MUN (mg/dL)		Lactose (%)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	30,432	5,022	27.2	6.3	3.81	0.64	3.31	0.31	169	496	10.63	3.39	4.71	0.17
2	20,599	4,658	31.9	8.9	3.78	0.67	3.31	0.34	229	593	11.19	3.41	4.58	0.20
3	9,614	3,479	33.9	9.6	3.79	0.67	3.27	0.35	286	724	11.26	3.40	4.53	0.23
Total	60,645	5,022	29.9	8.3	3.80	0.66	3.31	0.33	170	499	10.92	3.41	4.63	0.21

Table 3. Phenotypic correlations among production traits

Item	Fat (kg)	Protein (kg)	Fat (%)	Protein (%)	SCS	MUN	Lactose (kg)	Lactose (%)
Milk	0.787	0.936	-0.362	-0.520	-0.083	-0.031	0.989	0.252
Fat (kg)		0.805	0.260	-0.250	-0.058	0.083	0.771	0.161
Protein (kg)			-0.238	-0.205	-0.062	-0.011	0.921	0.208
Fat (%)				0.470	0.045	0.182	-0.370	-0.168
Protein (%)					0.093	0.082	-0.529	-0.248
SCS						-0.100	-0.110	-0.227
MUN							-0.042	-0.072
Lactose (kg)								0.382

random regression test-day animal model. Variance components estimated with model 1 were used. The model for breeding value estimation was the same as the model used for parameter estimation with the addition of genetic groups, defined by country, sex, and year of birth. Pearson correlations between EBV of all traits evaluated in Canada with lactose percentage and MUN EBV were then estimated for a group of bulls that a) were born after 1990, b) had at least 20 daughters with lactose and MUN records, and c) had an official EBV for all other traits evaluated. It should be noted that EBV for lactose percentage and MUN were obtained using data from Quebec herds only (42% of milk recorded cows), whereas EBV for all other traits originated from national evaluations.

RESULTS AND DISCUSSION

Descriptive statistics of the complete edited data set ($n = 144,622$) and of the random sample data set used for parameter estimation ($n = 5,022$) for all production traits by parity are shown in Tables 1 and 2, respectively. Means and variances for all traits were practically the same between data sets. The sample for parameter estimation can therefore be considered a representative sample of the data. Table 3 shows raw phenotypic correlations among all traits in the original edited data set. Phenotypically, MUN had a low correlation with all traits, whereas lactose percentage was

positively correlated with yield traits and negatively correlated with fat and protein percentages as well as with SCS. Lactose yield followed the same pattern as lactose percentage but with much higher phenotypic correlations with yield traits. Phenotypic correlation between lactose yield and percentage was moderate and positive (0.382).

Heritabilities and correlations for the same trait-pair combinations were averaged across separate 4-trait analyses. Original heritabilities and correlations (genetic and permanent environment) that resulted from the 6 separate 4-trait analyses are in the Appendix. Average heritabilities for all traits and for each parity are presented in Table 4. Heritabilities for lactose yield and percentage were high (0.466 to 0.539). Welper and Freeman (1992), using a lactation model, estimated heritability to be 0.26 for lactose yield and 0.53 for lactose percent in Michigan Holstein cows.

Heritabilities for MUN (0.384 to 0.414) were lower than heritabilities for lactose. Wood et al. (2003) estimated heritabilities for MUN in Ontario herds and obtained larger values, ranging from 0.44 to 0.59. They used the same model as was used in the current study. However, because of the short period of data collection (<2 yr), lactations 1 to 3 were analyzed separately. The effect of using a shorter time period and only one parity per analysis is that very few (if any) cows with a record also had a dam with a record in the same analysis. In an animal model setting, it is then difficult to disentangle genetic and permanent environmental effects. As a result, the genetic variance and heritability might have been overestimated in Wood et al. (2003), and it may explain the difference in results with the current study.

In the current study, heritability for SCS tended to increase significantly over parities (0.189 to 0.338). No clear pattern was observed across lactations for MUN and lactose (yield and percentage). As expected, heritabilities for fat (0.533 to 0.555) and protein (0.561 to 0.586) percentages were markedly higher than heritabilities for fat (0.350 to 0.369) and protein (0.392 to 0.423) yield. Overall heritabilities for protein tended

Table 4. Average heritabilities by parity

Item	Parity		
	First	Second	Third
Milk	0.518	0.431	0.468
Fat (kg)	0.369	0.350	0.362
Protein (kg)	0.423	0.392	0.410
Fat (%)	0.555	0.533	0.543
Protein (%)	0.576	0.561	0.586
SCS	0.189	0.272	0.338
MUN	0.394	0.384	0.414
Lactose (kg)	0.539	0.466	0.490
Lactose (%)	0.478	0.506	0.508

Table 5. Average correlations among traits (averaged across analyses and lactations), with genetic correlations below diagonal and permanent environmental correlation above diagonal

Item	Milk	Fat (kg)	Protein (kg)	Fat (%)	Protein (%)	SCS	MUN	Lactose (kg)	Lactose (%)
Milk		0.857	0.960	-0.273	-0.392	-0.233	0.222	0.979	0.176
Fat (kg)	0.566		0.893	—	—	-0.244	—	—	—
Protein (kg)	0.894	0.684		—	—	-0.216	—	—	—
Fat (%)	-0.494	—	—		0.585	-0.005	0.286	—	0.013
Protein (%)	-0.538	—	—	0.659		0.165	0.037	—	0.080
SCS	0.001	-0.045	0.014	-0.109	0.009		-0.293	-0.024	-0.308
MUN	-0.094	—	—	0.425	0.200	-0.190		-0.092	0.299
Lactose (kg)	0.979	—	—	—	—	-0.024	-0.092		—
Lactose (%)	0.096	—	—	0.058	0.017	-0.202	-0.041	—	

to be higher than corresponding heritabilities for fat. Heritabilities for milk yield were very close to heritabilities of lactose (kg).

Table 5 shows genetic and permanent environmental correlations among production traits. Correlations were averaged across lactations and separate 4-trait analyses. Correlations for some trait pairs are missing, as they were not covered by the 6 separate 4-trait analyses. The MUN had a moderate and positive genetic correlation with fat percentage (0.425) and lower with protein percentage (0.200). The MUN had a negative genetic correlation with SCS (-0.190). Wood et al. (2003) found low genetic correlations of MUN with production traits (-0.05 to 0.32). All genetic correlations between lactose percentage and other traits were close to zero, with one exception: a genetic correlation of -0.202 with SCS. Lactose yield seemed to be the same trait genetically as milk yield, as their genetic correlation was very close to 1 (0.979). In a study by Welper and Freeman (1992), lactose percentage was negatively correlated with yield of milk, fat and protein (-0.16 to -0.30), and SCS (-0.11), and positively correlated with fat and protein percentages (0.16 to 0.29). The same investigation found a small genetic correlation between lactose yield and percentage (0.10); high correlations between lactose yield with milk (0.92), fat (0.68) and protein yield (0.89); and negative correlations with fat (-0.35) and

protein percentages (-0.37). As expected, negative genetic correlations were found in the current study between milk yield and fat and protein percentages, -0.494 and -0.538, respectively. No prior estimates from a test-day model are available in the literature for these traits. Using a lactation sire model on Holsteins, Cue et al. (1987) found negative genetic correlations between milk and fat percentage (-0.285) and protein percentage (-0.560).

Average genetic correlations among parities within traits are shown in Table 6. Correlations among parities for MUN, lactose percentage, and yield were quite high like for milk yield. Genetic correlations among parities for SCS were again quite low, confirming previous studies carried out in Canada (Jamrozik et al., 1998; Muir et al., 2004). Genetic correlations among parities for fat and protein percentages were much higher than corresponding values for fat and protein yield. Posterior standard deviations of all estimates (heritability, genetic, and permanent environmental correlations) ranged from 0.015 to 0.116.

Figures 1 to 3 show the genetic correlations among traits within DIM for parity 1 to 3, respectively. In first parity, genetic correlations among traits at same DIM tended to be between -0.2 and 0.2 during the full lactation. Genetic correlations between lactose percentage and MUN were close to zero in the first and last part of lactation, and close to -0.2 in the mid part of lactation. In second and third parity, genetic correlations were larger than in first parity, ranging from -0.5 to 0.5, with higher correlations in the last part of the lactation. Genetic correlations between lactose percentage and MUN in second and third parity were close to -0.2 in the first half of lactation and close to -0.4 in the second half of lactation. Table 7 shows residual correlations, within parity and DIM period, among milk, lactose percentage, MUN, and SCS. Residual correlations were generally small. Correlations were moderate and positive between milk and lactose percentage, with the largest being in the first period of second parity. Corre-

Table 6. Average genetic correlations among parities within trait

Item	Parity			Average across parities
	1 vs. 2	1 vs. 3	2 vs. 3	
Milk	0.786	0.737	0.897	0.807
Fat (kg)	0.741	0.603	0.791	0.712
Protein (kg)	0.739	0.585	0.793	0.706
Fat (%)	0.961	0.887	0.951	0.933
Protein (%)	0.887	0.863	0.838	0.863
SCS	0.543	0.395	0.562	0.500
MUN	0.846	0.744	0.870	0.820
Lactose (kg)	0.807	0.714	0.892	0.804
Lactose (%)	0.831	0.760	0.845	0.812

Table 7. Residual correlations among traits, within parity and DIM period (milk, lactose percentage, MUN, and SCS)

Item	First period (5 to 45 DIM)			Second period (46 to 115 DIM)			Third period (116 to 265 DIM)			Fourth period (366 to 305 DIM)		
	Lactose	MUN	SCS	Lactose	MUN	SCS	Lactose	MUN	SCS	Lactose	MUN	SCS
First parity												
Milk	0.377	-0.004	-0.163	0.145	-0.060	-0.105	0.109	-0.119	-0.109	0.130	-0.217	-0.111
Lactose		-0.044	-0.362		-0.033	-0.201		0.006	-0.234		-0.066	-0.272
MUN			-0.072			-0.072			-0.087			-0.024
Second parity												
Milk	0.386	-0.010	-0.159	0.077	-0.035	-0.156	0.113	-0.089	-0.142	0.237	-0.159	-0.214
Lactose		0.000	-0.327		0.006	-0.271		0.061	-0.273		0.004	-0.287
MUN			-0.111			-0.124			-0.131			-0.003
Third parity												
Milk	0.310	0.014	-0.128	0.107	-0.016	-0.079	0.095	-0.014	-0.184	0.174	-0.234	-0.063
Lactose		0.008	-0.248		0.039	-0.208		0.118	-0.283		0.229	-0.355
MUN			-0.171			-0.096			-0.188			-0.126

lations were consistently negative across parities and periods between lactose percentage and SCS. Residual correlations were also negative but smaller between MUN and SCS, and between milk and SCS. All other residual correlations were close to zero, including those between MUN and lactose percentage.

Figures 4 and 5 show the test-day genetic and PE variances by parity over DIM for lactose percentage and MUN, respectively. Variances were higher in the first month of lactation for both traits in all parities. After the first month of lactation, variances for MUN in all 3 parities tended to be quite similar over the

entire lactation period, until the last month when variances were again higher. The same pattern was observed for lactose percentage in first parity, whereas variances for lactose percentage in second and third parities tended to increase linearly in the second half of the lactation. Genetic variances were higher than PE variance across traits and parities. Table 8 includes residual variances by parity and stage of lactation for lactose percentage and MUN. Residual variances in the first period of lactation were higher than the second and third period across parities and traits. Values of residual variances did not change between the second

Figure 1. Genetic correlations among milk yield, lactose percentage, MUN, and SCS within DIM for parity 1.

Figure 2. Genetic correlations among milk yield, lactose percentage, MUN, and SCS within DIM for parity 2.

and third period of lactations. Residual variances in the fourth period were similar to the second and third period for lactose percentage in first and second parity,

whereas it increased in third parity. Residual variances in the fourth period were lower than the second and third period for MUN in second and third parity,

Figure 3. Genetic correlations among milk yield, lactose percentage, MUN, and SCS within DIM for parity 3.

Figure 4. Test-day genetic (G) and permanent environmental (PE) variances for lactose percentage by parity (1 to 3) over DIM.

whereas it increased in first parity. Overall, residual variances were lower than genetic variances for both traits, lower than PE variances for lactose percentage, and greater than PE variances for MUN.

Table 9 shows bull EBV correlations higher than 0.100 or lower than -0.100 between the trait of interest and MUN and lactose percentage. All production EBV, including lactose percentage and MUN, were expressed on a 305-d basis, with equal weights on the 3 parities.

The highest correlation for MUN was with fat percentage (0.287), whereas for lactose percentage the highest correlation was with lactation persistency (0.329), where persistency is defined as expected milk yield on d 280 as a percentage of yield on d 60 in lactation (Schaeffer et al., 2000). Correlations between lactose percentage and MUN with fertility traits were close to zero, thus decreasing the potential of using those traits as possible indicators of fertility.

Figure 5. Test-day genetic (G) and permanent environmental (PE) variances for MUN by parity (1 to 3) over DIM.

Table 8. Residual variances by parity and stage of lactation for lactose percentage and MUN

Item	First period (5 to 45 DIM)	Second period (46 to 115 DIM)	Third period (116 to 265 DIM)	Fourth period (366 to 305 DIM)
First parity				
Lactose (%)	0.011	0.004	0.004	0.004
MUN (mg/dL)	0.025	0.020	0.020	0.023
Second parity				
Lactose (%)	0.008	0.005	0.005	0.006
MUN (mg/dL)	0.024	0.021	0.019	0.017
Third parity				
Lactose (%)	0.013	0.006	0.006	0.011
MUN (mg/dL)	0.022	0.019	0.017	0.016

CONCLUSIONS

Previous findings of high heritability for MUN in Canadian herds were confirmed by this study. Average daily heritabilities were also moderately high for lactose yield (0.466 to 0.539) and lactose percentage (0.478 to 0.508). Lactose yield was highly correlated with milk yield, whereas lactose percentage and MUN were not genetically correlated with milk yield. However, lactose percentage was genetically correlated to SCS (−0.202), whereas MUN was genetically correlated with percentages of fat and protein. Although only data from a single province were included, genetic evaluations of MUN and lactose percentage were feasible using a multitrait random regression test-day model together with milk yield and SCS. Bull EBV of MUN were correlated with fat percentage EBV, whereas lactose percentage EBV were correlated with lactation persistency EBV. Lactose and MUN EBV were not correlated to any EBV of female fertility traits.

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Table 9. Correlations of bull EBV of MUN and lactose percentage with traits for which the absolute value of the correlation exceeded 0.10

Item	MUN	Lactose (%)
Milk	−0.106	−0.164
Protein (%)	0.144	0.100
Fat (kg)	0.208	0.101
Fat (%)	0.287	0.112
		0.128
		0.139
		0.329

¹Lifetime Profit Index, Canadian selection index.

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APPENDIX

Table A1. Parameters for analysis 1 [milk (kg), lactose percentage, MUN, and SCS]¹

Item	First parity				Second parity				Third parity			
	Milk (kg)	Lactose (%)	MUN	SCS	Milk (kg)	Lactose (%)	MUN	SCS	Milk (kg)	Lactose (%)	MUN	SCS
First parity												
Milk (kg)	0.536	0.061	0.250	−0.266	0.449	0.049	0.003	−0.007	0.281	0.033	−0.140	0.157
Lactose (%)	−0.048	0.478	0.210	−0.306	0.027	0.634	0.145	−0.113	−0.062	0.547	0.120	−0.030
MUN	−0.104	−0.215	0.405	−0.195	0.092	0.175	0.632	−0.117	0.079	0.128	0.514	−0.101
SCS	0.248	−0.070	−0.174	0.196	−0.168	−0.121	−0.050	0.334	−0.139	−0.090	−0.016	0.238
Second parity												
Milk (kg)	0.757	0.001	−0.109	0.192	0.396	0.257	0.231	−0.294	0.394	0.028	−0.034	0.079
Lactose (%)	−0.033	0.827	−0.110	−0.042	0.139	0.502	0.312	−0.349	0.083	0.617	0.213	−0.056
MUN	−0.170	−0.146	0.852	−0.177	−0.092	0.013	0.389	−0.334	0.116	0.139	0.659	−0.177
SCS	0.150	−0.071	−0.098	0.520	0.005	−0.255	−0.205	0.262	−0.154	−0.140	−0.193	0.379
Third parity												
Milk (kg)	0.780	−0.001	−0.127	0.165	0.954	0.114	−0.126	0.022	0.467	0.209	0.195	−0.096
Lactose (%)	0.013	0.746	−0.128	−0.010	0.197	0.855	−0.046	−0.183	0.197	0.515	0.380	−0.242
MUN	−0.192	−0.112	0.754	−0.152	−0.094	0.047	0.829	−0.197	−0.082	0.085	0.405	−0.362
SCS	0.011	−0.081	−0.028	0.347	−0.272	−0.255	−0.089	0.559	−0.279	−0.330	−0.192	0.339

¹Average daily heritabilities on diagonal, genetic correlations below diagonal, and permanent environment correlations above diagonal.

Table A2. Parameters for analysis 2 [milk (kg), lactose (kg), MUN, and SCS]¹

Item	First parity				Second parity				Third parity			
	Milk (kg)	Lactose (kg)	MUN	SCS	Milk (kg)	Lactose (kg)	MUN	SCS	Milk (kg)	Lactose (kg)	MUN	SCS
First parity												
Milk (kg)	0.544	0.980	0.255	−0.260	0.321	0.295	0.025	−0.039	0.310	0.284	−0.039	0.118
Lactose (kg)	0.983	0.539	0.246	−0.314	0.316	0.313	0.028	−0.062	0.285	0.277	−0.035	0.104
MUN	−0.137	−0.154	0.361	−0.214	0.068	0.069	0.659	−0.125	0.040	0.044	0.532	−0.072
SCS	0.239	0.226	−0.114	0.188	−0.184	−0.201	−0.087	0.332	−0.118	−0.129	−0.025	0.217
Second parity												
Milk (kg)	0.828	0.818	−0.099	0.193	0.463	0.986	0.217	−0.304	0.407	0.374	0.020	0.002
Lactose (kg)	0.785	0.807	−0.099	0.176	0.979	0.466	0.228	−0.353	0.381	0.375	0.039	−0.018
MUN	−0.182	−0.186	0.832	−0.105	−0.075	−0.060	0.374	−0.321	0.064	0.071	0.645	−0.149
SCS	0.168	0.155	−0.068	0.532	−0.025	−0.076	−0.200	0.280	−0.105	−0.135	−0.179	0.357
Third parity												
Milk (kg)	0.727	0.718	−0.112	0.109	0.888	0.866	−0.084	−0.085	0.478	0.976	0.181	−0.161
Lactose (kg)	0.693	0.714	−0.112	0.093	0.873	0.892	−0.077	−0.114	0.974	0.490	0.209	−0.221
MUN	−0.267	−0.265	0.723	−0.125	−0.154	−0.131	0.810	−0.196	−0.076	−0.061	0.404	−0.328
SCS	0.055	0.040	−0.050	0.399	−0.146	−0.170	−0.118	0.582	−0.208	−0.223	−0.229	0.339

¹Average daily heritabilities on diagonal, genetic correlations below diagonal, and permanent environment correlations above diagonal.

Table A3. Parameters for analysis 3 (fat and lactose percentages, MUN, and SCS)¹

Item	First parity				Second parity				Third parity			
	Fat (%)	Lactose (%)	MUN	SCS	Fat (%)	Lactose (%)	MUN	SCS	Fat (%)	Lactose (%)	MUN	SCS
First parity												
Fat (%)	0.579	-0.015	0.120	0.105	0.682	0.049	0.232	-0.135	0.533	0.018	0.270	-0.135
Lactose (%)	0.032	0.480	0.189	-0.319	-0.017	0.630	0.138	-0.119	-0.009	0.528	0.106	0.007
MUN	0.366	-0.201	0.405	-0.186	0.131	0.165	0.638	-0.098	0.220	0.125	0.524	-0.096
SCS	-0.161	-0.040	-0.197	0.170	0.109	-0.124	-0.037	0.324	0.098	-0.094	0.000	0.211
Second parity												
Fat (%)	0.972	0.037	0.355	-0.211	0.547	0.022	0.298	-0.032	0.645	-0.031	0.298	-0.075
Lactose (%)	0.024	0.832	-0.100	-0.036	0.035	0.510	0.306	-0.352	0.048	0.639	0.221	-0.082
MUN	0.383	-0.127	0.853	-0.206	0.402	0.022	0.395	-0.315	0.306	0.149	0.681	-0.192
SCS	-0.021	-0.067	-0.126	0.586	-0.065	-0.243	-0.232	0.267	-0.078	-0.174	-0.205	0.399
Third parity												
Fat (%)	0.955	0.064	0.306	-0.150	0.966	0.061	0.350	0.006	0.578	0.031	0.439	-0.089
Lactose (%)	0.055	0.766	-0.115	-0.014	0.058	0.841	-0.033	-0.153	0.107	0.507	0.368	-0.262
MUN	0.509	-0.084	0.769	-0.209	0.530	0.057	0.831	-0.200	0.506	0.109	0.426	-0.357
SCS	-0.084	-0.116	-0.041	0.433	-0.119	-0.222	-0.090	0.550	-0.101	-0.310	-0.212	0.333

¹Average daily heritabilities on diagonal, genetic correlations below diagonal, and permanent environment correlations above diagonal.**Table A4.** Parameters for analysis 4 (protein and lactose percentages, MUN, and SCS)¹

Item	First parity				Second parity				Third parity			
	Protein (%)	Lactose (%)	MUN	SCS	Protein (%)	Lactose (%)	MUN	SCS	Protein (%)	Lactose (%)	MUN	SCS
First parity												
Protein (%)	0.621	0.150	-0.036	0.165	0.500	0.064	0.125	-0.027	0.591	0.076	0.154	-0.040
Lactose (%)	0.060	0.475	0.218	-0.327	0.110	0.633	0.147	-0.125	0.129	0.524	0.110	0.010
MUN	0.081	-0.227	0.404	-0.203	0.034	0.196	0.654	-0.144	0.041	0.151	0.558	-0.149
SCS	-0.042	-0.029	-0.163	0.168	0.011	-0.130	-0.069	0.329	0.032	-0.070	-0.020	0.216
Second parity												
Protein (%)	0.896	0.012	0.161	-0.006	0.595	0.052	-0.006	0.151	0.479	0.042	0.093	0.057
Lactose (%)	-0.011	0.835	-0.136	-0.030	-0.038	0.504	0.319	-0.364	0.069	0.648	0.234	-0.099
MUN	0.147	-0.156	0.845	-0.144	0.189	-0.015	0.378	-0.349	0.110	0.168	0.695	-0.225
SCS	-0.019	-0.061	-0.060	0.577	0.085	-0.226	-0.161	0.259	0.052	-0.170	-0.221	0.407
Third parity												
Protein (%)	0.876	0.021	0.149	0.011	0.944	-0.004	0.193	0.003	0.620	0.037	0.154	0.179
Lactose (%)	0.010	0.767	-0.152	-0.042	-0.007	0.838	-0.077	-0.157	0.030	0.503	0.389	-0.248
MUN	0.300	-0.125	0.728	-0.137	0.324	0.007	0.804	-0.152	0.330	0.061	0.419	-0.348
SCS	-0.087	-0.105	0.033	0.423	-0.021	-0.192	-0.027	0.538	-0.016	-0.311	-0.206	0.342

¹Average daily heritabilities on diagonal, genetic correlations below diagonal, and permanent environment correlations above diagonal.

Table A5. Parameters for analysis 5 [milk (kg), fat (kg), protein (kg), and SCS]¹

Item	First parity				Second parity				Third parity			
	Milk (kg)	Fat (kg)	Protein (kg)	SCS	Milk (kg)	Fat (kg)	Protein (kg)	SCS	Milk (kg)	Fat (kg)	Protein (kg)	SCS
First parity												
Milk (kg)	0.489	0.819	0.949	-0.240	0.419	0.336	0.425	-0.027	0.381	0.281	0.356	0.054
Fat (kg)	0.556	0.369	0.872	-0.181	0.343	0.476	0.407	-0.098	0.358	0.456	0.405	-0.052
Protein (kg)	0.905	0.648	0.423	-0.198	0.386	0.373	0.435	-0.045	0.343	0.307	0.370	0.041
SCS	0.236	0.125	0.226	0.214	-0.172	-0.121	-0.170	0.332	-0.136	-0.077	-0.121	0.215
Second parity												
Milk (kg)	0.781	0.339	0.683	0.172	0.433	0.873	0.965	-0.308	0.481	0.368	0.477	-0.022
Fat (kg)	0.330	0.741	0.415	0.011	0.547	0.350	0.896	-0.313	0.432	0.497	0.486	-0.063
Protein (kg)	0.651	0.445	0.739	0.173	0.887	0.681	0.392	-0.285	0.488	0.415	0.523	0.010
SCS	0.175	0.167	0.202	0.518	0.000	-0.057	0.005	0.283	-0.129	-0.143	-0.122	0.384
Third parity												
Milk (kg)	0.672	0.199	0.569	0.167	0.827	0.354	0.716	-0.050	0.456	0.880	0.965	-0.201
Fat (kg)	0.306	0.603	0.380	0.032	0.460	0.791	0.579	-0.057	0.594	0.362	0.912	-0.238
Protein (kg)	0.518	0.275	0.585	0.171	0.698	0.468	0.793	-0.079	0.890	0.724	0.410	-0.166
SCS	0.107	0.099	0.114	0.388	-0.110	-0.156	-0.151	0.542	-0.153	-0.204	-0.188	0.327

¹Average daily heritabilities on diagonal, genetic correlations below diagonal, and permanent environment correlations above diagonal.**Table A6.** Parameters for analysis 6 [milk (kg), fat and protein percentages, and SCS]¹

Item	First parity				Second parity				Third parity			
	Milk (kg)	Fat (%)	Protein (%)	SCS	Milk (kg)	Fat (%)	Protein (%)	SCS	Milk (kg)	Fat (%)	Protein (%)	SCS
First parity												
Milk (kg)	0.502	-0.336	-0.413	-0.212	0.420	-0.188	-0.194	-0.013	0.281	-0.129	-0.197	0.099
Fat (%)	-0.533	0.532	0.596	0.064	-0.163	0.766	0.455	-0.106	-0.094	0.710	0.479	-0.167
Protein (%)	-0.576	0.643	0.532	0.153	-0.197	0.474	0.631	-0.029	-0.170	0.395	0.653	-0.103
SCS	0.193	-0.117	-0.073	0.196	-0.161	0.064	0.041	0.333	-0.118	0.059	0.059	0.224
Second parity												
Milk (kg)	0.776	-0.507	-0.518	0.163	0.432	-0.278	-0.466	-0.297	0.398	-0.187	-0.122	0.022
Fat (%)	-0.491	0.949	0.611	-0.152	-0.490	0.520	0.592	-0.030	-0.142	0.749	0.477	-0.149
Protein (%)	-0.468	0.633	0.878	-0.054	-0.521	0.662	0.528	0.151	-0.151	0.414	0.613	-0.024
SCS	0.153	-0.034	-0.021	0.524	-0.031	-0.047	0.050	0.281	-0.130	-0.042	0.015	0.359
Third parity												
Milk (kg)	0.768	-0.507	-0.510	0.128	0.917	-0.494	-0.495	-0.034	0.469	-0.206	-0.298	-0.156
Fat (%)	-0.475	0.914	0.607	-0.118	-0.447	0.935	0.621	-0.009	-0.459	0.509	0.566	-0.139
Protein (%)	-0.496	0.645	0.849	-0.056	-0.512	0.656	0.897	-0.004	-0.517	0.673	0.552	0.066
SCS	0.066	-0.036	0.010	0.382	-0.190	-0.028	0.066	0.598	-0.215	-0.038	0.065	0.347

¹Average daily heritabilities on diagonal, genetic correlations below diagonal, and permanent environment correlations above diagonal.