Genetic Parameters for a Multiple-Trait Multiple-Lactation Random Regression Test-Day Model in Italian Holsteins

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ABSTRACT

The objectives of this study were to estimate variance components for test-day milk, fat, and protein yields and average daily SCS in 3 subsets of Italian Holsteins using a multiple-trait, multiple-lactation random regression test-day animal model and to determine whether a genetic heterogeneous variance adjustment was necessary. Data were test-day yields of milk, fat, and protein and SCS (on a $\log_2$ scale) from the first 3 lactations of Italian Holsteins collected from 1992 to 2002. The 3 subsets of data included 1) a random sample of Holsteins from all herds in Italy, 2) a random sample of Holsteins from herds using a minimum of 75% foreign sires, and 3) a random sample of Holsteins from herds using a maximum of 25% foreign sires. Estimations of variances and covariances for this model were achieved by Bayesian methods using the Gibbs sampler. Estimated 305-d genetic, permanent environmental, and residual variance was higher in herds using a minimum of 75% foreign sires compared with herds using a maximum of 25% foreign sires. Estimated average daily heritability of milk, fat, and protein yields did not differ among subsets. Heritability of SCS in the first lactation differed slightly among subsets and was estimated to be the highest in herds with a maximum of 25% foreign sire use (0.19 ± 0.01). Genetic correlations across lactations for milk, fat, and protein yields were similar among subsets. Genetic correlations across lactations for SCS were 0.03 to 0.08 higher in herds using a minimum of 75% or a maximum of 25% foreign sires, compared with herds randomly sampled from the entire population. Results indicate that adjustment for heterogeneous variance at the genetic level based on the percentage of foreign sire use should not be necessary with a multiple-trait random regression test-day animal model in Italy.

Key words: random regression, test-day model, genetic parameter

INTRODUCTION

The test-day model used in Canada is a multiple-trait (milk, fat, and protein yields and SCS), multiple-lactation (first 3 lactations) random regression (fourth-order Legendre polynomials) test-day animal model (Schaeffer et al., 2000). The model used in this study has been improved from the model of Schaeffer et al. (2000) with the use of Legendre polynomials, and used the Wilmlink function. A similar random regression test-day model was recently implemented in Italy (Canavesi et al., 2004), replacing a lactation model for yield traits and repeatability test-day model for SCS (Samoré et al., 2001a,b). To implement a test-day model in Italy, genetic parameters needed to be estimated in the Italian Holstein population. Numerous studies have reported genetic parameters for test-day milk production traits using various random regression models (Jamrozik et al., 1997; Liu et al., 2000; Pool et al., 2000; Jakobsen et al., 2002; Samoré et al., 2002), and results varied with the kind of genetic model used.

Adoption of a random regression test-day model as the official genetic evaluation model for production traits and SCS in Italy was required to improve the efficiency of the selection program for the Holstein breed. Previous to the adoption of the random regression test-day model in Italy, a lactation model was used to calculate genetic evaluations for production traits with a preadjustment for heterogeneity of genetic variance across herds by applying similar methodology as described by Wiggans and Van Raden (1991).

Problems with heterogeneity of variance across herds and the subsequent impact on selection and estimation of breeding values have been largely investigated. Animal models usually assume that variances across herds are homogeneous. As the level of production increases, the within-herd phenotypic standard deviation tends to increase, and subsequently higher heritabilities may result. Different ways to account for heterogeneity have

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been suggested (Hill et al., 1983; Hill, 1984; Mirande and Van Vleck, 1985; Short et al., 1990; Meuwissen and van der Werf, 1991; Visscher et al., 1991; Wiggans and Van Raden, 1991; Kachman and Everett, 1992). Most methods adjust production data before applying genetic evaluation procedures, assuming homogeneous variances. In other studies, techniques have been developed to include heterogeneous variances across herds directly in the model used for genetic evaluation (De Veer and Van Vleck, 1987; Foulley et al., 1991; Meuwissen et al., 1996). The method proposed by Meuwissen et al. (1996) to describe heterogeneity of variance accounts for covariances among observations while jointly modeling the mean and phenotypic variance of the input data. Adjustments for heterogeneity of variances across herds are applied to official genetic evaluations in all test-day models and in lactation animal model official evaluations in France, Spain, and the United States.

Studies on heterogeneity of variance have been conducted in Italy since the early 1990s. A specific problem in Italy has been related to the distribution of daughters in different herds classified according to within-herd milk yield variances. Studies have shown a different dissemination of AI sire semen across levels of production. Italian Holstein breeders widely use imported sires, mostly from the United States and Canada. Those imported sires have been used disproportionately across herd levels of production (Rozzi and Civati, 1988), where the best sires were mostly used in high-producing herds. Variances were found to be heterogeneous across herds, and several methods to account for that variation were investigated (Canavesi et al., 1994, 1995a,b). Since 1993, a preadjustment for heterogeneity of variance has been used in the official genetic evaluation model in Italy. Genetic variance across herds stratified by use of foreign semen was found to be heterogeneous because of very different herd size and herd production levels (Cassandro, 2000). To use test-day methodology for the genetic evaluation of production traits, it was important to assess whether adjustment for heterogeneity of genetic variance was still necessary. In addition, it was important to be consistent with previous research (Cassandro, 2000) and to classify herds according to foreign sire use to compare results between the 2 models.

Very little research has been done in an attempt to compare the efficiency of the different approaches in adjusting for heterogeneity of variances. In general terms, the methodology most often applied to official lactation genetic evaluations is preadjustment of the data. In fact, a phenotypic preadjustment has been the official method for Italy, Canada, and the United States. France still applies a linear mixed model assuming het-

erogeneous variances (Robert-Granié et al., 1999), and in the Netherlands, a multiplicative model developed by Meuwissen et al. (1996) for the lactation model is still used in the test-day evaluation. A comparison of methods of adjustment was presented by Robert-Granié et al. (1999), and both approaches led to the same results. In Italy, Canavesi et al. (1998) compared the preadjustment approach with the adjustment within the model. The preadjustment applied in Canada and Italy and the multiplicative model applied in the Netherlands were compared by using a lactation repeatability animal model. Results showed that all methods of adjustment equally reduced the overestimation of bull dam EBV attributable to heterogeneity (Canavesi et al., 1998). Thus, the choice of approach can be based on practical considerations, accounting for technicalities such as the time required to run the evaluation and difficulties in applying the methodology and explaining the results. In Italy, the choice of a phenotypic adjustment was preferred over the multiplicative approach because it was less time demanding.

Application of adjustment for heterogeneity of variance in random regression test-day models has a very recent history. The Nordic joint random regression test-day evaluation model in Finland, Denmark, and Sweden adjusts for heterogeneity of variance (Lidauer and Mäntysaari, 2001; Lidauer et al., 2006; Mäntysaari et al., 2006). To date, no studies have compared the effect of different methods of adjustment on EBV applied to multiple-trait random regression test-day models. Because of the complexity of the multiple-trait, multiple-lactation test-day model for genetic evaluation, the preadjustment approach to accounting for heterogeneity of variance was chosen over the adjustment in the genetic model.

Advantages of a test-day model in comparison with a lactation model include 1) more efficient use of data as it is collected in the field, 2) a genetic model that more closely defines the true biology of a dairy cow, 3) better estimation of environmental effects, especially at the herd level, and 4) more accurate cow indexes, which can improve the precision of EBV for bulls (Schaeffer et al., 2000). A random regression test-day model allows for estimation of genetic effects throughout lactation and produces persistency of lactation as a by-product, which provides an additional tool to select cows that are easier to manage, have fewer fertility problems, and have less production stress.

The objectives of this study were to 1) estimate variance components for production traits and SCS using a multiple-trait, multiple-lactation random regression test-day model on a random sample of Holsteins from all herds in Italy, 2) estimate variance components using the same model on 2 subsets of data randomly se-

lected based on herds with high or low use of foreign sire semen, and 3) compare variance components for these 3 data subsets to determine whether a genetic heterogeneous variance adjustment would be necessary based on the percentage of foreign sire use.

MATERIALS AND METHODS

Data

Data were test-day yields of milk, fat, and protein and SCS (on a $\log_2$ scale) from the first 3 lactations of Italian Holsteins collected from 1992 to 2002. Days in milk ranged from 5 to 305. Cows were not required to have first-lactation data to be included in the study. All 4 traits were required on each test day. Herds were randomly sampled after requiring a minimum of 50 cows with records over the entire data collection period (All). Two additional random samples were extracted from 2 subsets of the entire data set. One data set contained a random sample of test-day records from herds using a minimum of 75% foreign sire semen (High), and a second data set contained a random sample of test-day records from herds using a maximum of 25% foreign sire semen (Low). Data for these 2 subsets were sampled similarly to the subset described for the entire population. This type of herd classification based on use of foreign sire semen was derived from a previous study on Italian Holsteins that investigated the presence of heterogeneity of variance across herds at a phenotypic and genetic level (Cassandro, 2000). Table 1 shows the number of test-day records, herds, and cows randomly sampled for all 3 data subsets and the number of records discarded for each edit.

Nineteen parity-age classes were created: 8 in first lactation, 6 in second lactation, and 5 in third lactation. Two seasons of calving were defined: March to August and September to February. Four regions were created by grouping 96 provinces into similar geographic areas. Contemporary groups were defined by herd-testday-parity. The number of fixed-effect classes for each lactation for each subset of data is shown in Table 1.

Model

The model for trait r (milk, fat, protein or SCS) in lactation p (first, second, or third) was

$$y_{ijkprt} = HTDP_{ipr} + \sum_{m=0}^4 \beta_{kmpr} z_{tm} + \sum_{m=0}^4 \alpha_{jmpr} z_{tm} + \sum_{m=0}^4 \rho_{jmpr} z_{tm} + e_{ijkprt},$$

where y_{ijkprt} was the record on trait r of cow j in lactation p on DIM t , within-herd test-day effect i , and in the subclass k for season-age of calving; $HTDP_{ipr}$ was the fixed herd-testday-parity effect; β_{kmpr} were fixed regression coefficients specific to subclass k of age-season of calving; α_{jmpr} were random additive genetic coefficients specific to cow j ; ρ_{jmpr} were random permanent environmental (PE) coefficients specific to cow j ; e_{ijkprt} was the residual effect for each observation; and z_{tm} were covariates. The same function (Legendre polynomial of order 4, but with $z_0 = 1$) was used for all fixed and random regressions.

In matrix notation, the model can be written as

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wp} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations (ordered as traits within cow within lactation); $\mathbf{b}$ includes fixed effects; $\mathbf{a}$ includes random genetic regression coefficients; $\mathbf{p}$ includes random PE regression coefficients; $\mathbf{e}$ is the vector of residual effects; and $\mathbf{X}$, $\mathbf{Z}$, and $\mathbf{W}$ are the incidence matrices. Assume that

$$\mathbf{y} | \mathbf{b}, \mathbf{a}, \mathbf{p}, \mathbf{R} \sim N(\mathbf{Xb} + \mathbf{Za} + \mathbf{Wp}, \mathbf{R}),$$

and

$$\text{Var}[\mathbf{a}'\mathbf{p}'\mathbf{e}'] = \begin{pmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{I} \otimes \mathbf{P} & 0 \\ 0 & 0 & \mathbf{R} \end{pmatrix}$$

where $\mathbf{G}$ is the 60×60 covariance matrix of the additive genetic regression coefficients, $\mathbf{A}$ is the additive genetic covariance matrix among all animals, and $\mathbf{P}$ is the 60×60 covariance matrix of the permanent environmental regression coefficients. Blocks within $\mathbf{R} = \sum^+ \mathbf{R}^{p,s}$ contain diagonal matrices (4×4) of residual covariances among traits with elements that depend on lactation (p) and the interval of DIM (s). Four intervals of DIM were defined: 1) When DIM were between 5 and 45 d, then $s = 1$; 2) $s = 2$ when DIM were between 46 and 115 d; 3) $s = 3$ when DIM were between 116 and 265 d; and 4) $s = 4$ when DIM were between 266 and 305 d. Residual covariances among traits on the same test day were therefore allowed to be different from zero, and residual covariances were the same within a given interval within parity. Covariances among residuals for records made on different DIM were assumed to be zero in this model.

Genetic Parameter Estimation

Estimations of variances and covariances for this model were achieved by Bayesian methods with Gibbs

Table 1. Description of data and effects in the model

Item	All	Foreign sire use within herd	
		High	Low
Test-day (TD) records, total	45,408,413	3,647,960	11,990,171
TD records ¹	34,128,260	1,883,231	7,001,843
TD records, ¹ random sample	141,696	145,285	144,081
Herds, total	21,459	515	3,280
Herds ¹	18,751	509	3,268
Herds >50 cows, no missing traits	9,872	400	2,139
Herds, ¹ random sample	41	30	44
Average daily within-herd phenotypic SD of milk yield, kg	7.01	7.54	6.91
Average daily milk production, kg	29.2	30.2	28.2
Lactation 1	27.5	28.5	26.4
Lactation 2	30.3	31.2	29.4
Lactation 3	31.0	32.0	30.2
Cows, total	3,072,449	226,096	753,458
Cows ¹	2,482,183	135,040	505,815
Cows, ¹ random sample	10,275	10,106	10,093
Number of animals in relationship matrix	22,802	20,008	21,316
HTDP classes, random sample			
Lactation 1	3,240	2,855	3,836
Lactation 2	3,184	2,821	3,801
Lactation 3	3,081	2,759	3,794
PARS classes, random sample			
Lactation 1	48	64	64
Lactation 2	36	48	48
Lactation 3	30	40	40

¹Records with no missing traits: All = Italian Holstein population; High = Italian Holstein herds using a minimum of 75% foreign sires; HTDP = herd-testday-parity classes; Low = Italian Holstein herds using a maximum of 25% foreign sires; PARS = parity-age-region-season classes.

sampling to generate samples from marginal posterior distributions (Jamrozik and Schaeffer, 1997). Flat priors were assumed for the fixed effects and multivariate normal for the random effects, and proper inverted Wishart with a minimal number of degrees of belief was taken for covariance components. Canadian Holstein (co)variance components (Muir et al., 2004) estimated with an identical model were used as starting and prior values. A single chain length of 100,000 was generated for each data set. The first 5,000 samples were discarded as the burn-in period. The remaining 95,000 samples were used to estimate the variance and covariance components. Convergence of Gibbs sampling was determined based on inspection of plots of realizations of selected components. Using properties of orthogonal polynomials, we calculated variances for 305-d milk, fat, and protein yields as $301^2 \times \text{var}(a_{i0})$, where a_{i0} was an intercept for the respective trait (Jamrozik and Schaeffer, 2003). Somatic cell score was expressed as an average daily value of this trait from 5 to 305 DIM with variances equal to $\text{var}(a_{i0})$. Covariances among 305-d yield traits were then estimated as $301^2 \times \text{cov}(a_{i0}, a_{j0})$. Daily heritability was defined as a ratio of additive genetic variance to the sum of additive genetic, PE, and residual variance for each DIM from 5 to 305 d.

RESULTS AND DISCUSSION

Descriptive Statistics

Although each data set was initially different in size, the number of test-day records and cows with records randomly sampled for each data set was held approximately constant (Table 1). Fewer High herds were randomly selected (30) compared with Low and All herds because High herds tended to milk more cows. In general, High herds tended to have a larger number of cows per herd and a higher phenotypic standard deviation of daily milk yield (7.54 kg/d) compared with Low (6.91 kg/d) and All (7.01 kg/d) herds. The number of herd-testday-parity classes in High herds was lower than that in All or Low herds, which was indicative of a large herd size in High herds.

Variances

Table 2 shows the genetic, PE, and residual variances (posterior means) for cumulative 305-d milk, fat, and protein yields and average daily SCS for all 3 data sets. The genetic, PE, and residual variance of 305-d milk, fat, and protein yields was higher in High herds, compared with Low herds, and increased with lactation.

Table 2. Genetic, permanent environmental (PE), and residual variance (posterior SD) for cumulative 305-d milk, fat, and protein yields and average daily SCS

Lactation no.	Trait	All			High			Low		
		Genetic	PE	Residual	Genetic	PE	Residual	Genetic	PE	Residual
1	Milk ¹	5,307.23 (372.58)	10,189.28 (332.17)	1,546.21 (13.33)	5,384.10 (379.49)	10,102.22 (326.97)	1,711.87 (14.86)	4,673.57 (314.65)	9,487.08 (297.43)	1,358.66 (12.44)
	Fat	893.00 (59.83)	1,141.32 (48.11)	553.56 (4.31)	888.01 (60.66)	1,202.97 (47.32)	580.22 (4.61)	693.55 (47.00)	1,066.29 (39.89)	404.25 (3.40)
	Protein	477.29 (34.53)	903.73 (30.89)	197.73 (1.76)	455.49 (33.93)	865.14 (29.01)	210.37 (1.85)	405.47 (28.99)	839.70 (27.31)	167.39 (1.58)
	SCS	0.36 (0.03)	0.97 (0.03)	1.39 (0.01)	0.41 (0.03)	0.84 (0.03)	1.35 (0.01)	0.41 (0.03)	0.92 (0.03)	1.19 (0.01)
2	Milk ¹	8085.57 (572.21)	15,488.78 (556.21)	2,227.79 (24.41)	8,678.92 (651.00)	16,789.24 (581.55)	2,396.34 (25.15)	7,188.79 (457.16)	13,062.45 (440.95)	1,945.96 (20.95)
	Fat	1,492.77 (91.02)	1,801.08 (77.17)	831.67 (7.80)	1,675.42 (102.17)	2,003.17 (80.43)	865.41 (8.16)	1,251.86 (77.66)	1,443.79 (61.54)	631.97 (6.04)
	Protein	791.22 (57.17)	1,399.06 (54.11)	263.84 (2.79)	813.83 (59.04)	1,442.42 (52.78)	275.46 (2.83)	662.44 (46.87)	1,161.49 (42.04)	217.60 (2.34)
	SCS	0.41 (0.03)	0.99 (0.03)	1.36 (0.01)	0.43 (0.03)	0.95 (0.03)	1.34 (0.01)	0.40 (0.03)	1.05 (0.03)	1.26 (0.01)
3	Milk ¹	9,593.90 (739.11)	16,873.78 (758.53)	2,451.72 (34.92)	10,722.22 (867.34)	16,954.47 (755.74)	2,827.29 (37.10)	8,777.26 (577.71)	14,240.46 (545.83)	2,204.95 (29.34)
	Fat	1,685.61 (124.46)	1,948.06 (107.55)	908.89 (11.19)	1,812.53 (134.34)	2,329.03 (114.98)	992.21 (11.47)	1,275.02 (82.34)	1,706.61 (77.48)	718.09 (8.37)
	Protein	939.22 (76.61)	1,522.96 (74.26)	283.18 (3.95)	964.00 (78.04)	1,566.06 (70.62)	313.79 (3.99)	756.09 (54.05)	1,273.57 (54.22)	235.78 (3.09)
	SCS	0.60 (0.05)	1.00 (0.05)	1.38 (0.02)	0.60 (0.05)	0.98 (0.04)	1.40 (0.02)	0.61 (0.05)	1.10 (0.05)	1.22 (0.01)

¹Milk (kg²)/100; All = random sample of test-day records from all Italian Holstein herds, High = random sample of test-day records from herds using a minimum of 75% foreign sires, Low = random sample of test-day records from herds using a maximum of 25% foreign sires.

With a few exceptions, the genetic, PE, and residual variance of 305-d yield in All herds tended to fall somewhere between the respective variance in the High and Low herds, which is intuitive because All herds should represent the amalgamation of herds with high, average, and low foreign sire use. Zavadilova et al. (2005) reported genetic, PE, and residual variances for 305-d milk yield in Czech Holsteins that were even lower than those estimated in Low herds in this study.

No differences were detected in estimated genetic variance of average daily SCS among data sets. Average daily PE variance of SCS tended to be higher in Low herds compared with that in High herds, and average daily residual variance tended to be higher in High herds compared with Low herds. Samoré et al. (2001a) reported that genetic variance of SCS did not differ among regions in Italy that differed in the milk products produced, and therefore areas where milk quality was of greater importance than others. That result and the current result could potentially be extended to conclude that no difference existed in genetic variance of SCS among areas or herds with different sire use.

Table 3 has the sum of squares (Euclidean matrix norm squared) for genetic, permanent environmental (PE), and residual (averaged over intervals in DIM), by lactation, of covariance components for the All, Low, and High data sets. The ratios of (All-Low):All and (All-

High):All indicated the degree of similarity between the variance components of the Low and High data sets compared with the All data sets, respectively. No ratio was greater than 2.3%; therefore, the variance components of the Low and High data sets were not significantly different from the All data sets.

Heritability

Table 4 has average daily heritability for milk, fat, and protein yields and average daily SCS estimated in all 3 data sets. In general, average daily heritability for yield traits was very similar across data sets and the posterior standard deviation of heritability was small (ranged from 0.012 to 0.018). Heritability of SCS in first lactation was estimated to be 0.165 in All herds, 0.188 in High herds, and 0.191 in Low herds. The differences among data sets in heritability of SCS in second and third lactations was minimal.

Although no practical differences were noted among average daily heritability estimated in the 3 subsets, daily heritability differed from the beginning to end of lactation among subsets. Estimated daily heritabilities for each data subset and trait throughout the first 3 lactations are shown graphically in Figure 1. Heritability of daily milk yield tended to be more stable over DIM in the first lactation compared with daily heritability in

Table 3. Sum of squares (Euclidean matrix norm squared) for genetic (G), permanent environmental (PE), and residual (E) effects (averaged over intervals in DIM), by lactation, of covariance components for All, Low, and High data sets

Effect	All	Low	All-Low	(All-Low):All	High	All-High	(All-High):All
	————— (%) —————						
G	551.2	441.6	8.5	1.5	634.7	7.6	1.4
PE	1,075.7	806.8	25.0	2.3	1,115.0	14.5	1.3
E ₁	32.3	26.3	0.6	1.8	40.3	0.7	2.0
E ₂	82.3	66.6	1.2	1.5	93.8	0.4	0.6
E ₃	106.1	87.4	1.1	1.0	133.2	2.0	1.9

the second and third lactations. Daily heritability of milk yield in the first lactation estimated in High and Low herds tended to be lower in early lactation and higher in late lactation (Figure 1C) compared with heritability estimated in All herds, which was more stable over the lactation. Daily heritability of milk yield in the first lactation in High herds ranged from a low of 0.24 in early lactation to a high of 0.34 at the end of lactation. Daily heritability of milk yield estimated in High herds ranged from 0.19 to 0.40 in the second lactation and ranged from 0.27 to 0.39 in the third lactation. Large drops or increases in daily heritability were noted at 45, 115, and 265 DIM when the residual variance

changed. Heritability of daily protein yield was lowest in early lactation (45 DIM) for High herds, and was equally as high in later lactation as in the Low and All herds (Figure 1A) for all lactations. Heritability of SCS was highest in early and late lactation but was fairly stable throughout the remainder of lactation for all lactations. Daily heritability of SCS in the first lactation estimated in All herds tended to be lower than that estimated in High and Low herds. No differences among daily heritability of SCS in different subsets were noted in the second or third lactation. Slight differences were observed among the posterior distribution of heritability of protein yield across subsets within each lactation

Table 4. Average daily heritability and genetic correlations (posterior SD) among lactations for daily milk, fat, and protein yields and average daily SCS estimated in all herds (All), high foreign sire use herds (High), and low foreign sire use herds (Low)

Trait	Lactation no.	Heritability			Lactation	Genetic Correlation		
		All	High	Low		All	High	Low
Milk	1	0.299 (0.015)	0.296 (0.014)	0.296 (0.014)	1, 2	0.788 (0.023)	0.767 (0.027)	0.762 (0.024)
	2	0.302 (0.015)	0.304 (0.015)	0.311 (0.013)	1, 3	0.698 (0.033)	0.695 (0.034)	0.711 (0.031)
	3	0.329 (0.017)	0.333 (0.018)	0.334 (0.015)	2, 3	0.857 (0.016)	0.853 (0.017)	0.854 (0.015)
	Cassandro (2000) ¹		0.364	0.358				
	1	0.274 (0.014)	0.264 (0.013)	0.276 (0.013)	1, 2	0.824 (0.018)	0.828 (0.018)	0.808 (0.020)
	2	0.291 (0.013)	0.307 (0.012)	0.312 (0.013)	1, 3	0.745 (0.026)	0.719 (0.029)	0.714 (0.027)
Fat	3	0.311 (0.015)	0.302 (0.015)	0.297 (0.013)	2, 3	0.838 (0.018)	0.834 (0.018)	0.823 (0.019)
	Cassandro (2000)		0.382	0.346				
	1	0.283 (0.014)	0.272 (0.014)	0.277 (0.013)	1, 2	0.788 (0.023)	0.773 (0.026)	0.759 (0.025)
	2	0.299 (0.015)	0.298 (0.014)	0.304 (0.014)	1, 3	0.694 (0.033)	0.667 (0.035)	0.687 (0.032)
	3	0.326 (0.017)	0.314 (0.017)	0.317 (0.015)	2, 3	0.849 (0.017)	0.840 (0.017)	0.837 (0.017)
	Cassandro (2000)		0.326	0.315				
Protein	1	0.165 (0.009)	0.188 (0.010)	0.191 (0.010)	1, 2	0.485 (0.044)	0.537 (0.039)	0.549 (0.042)
	2	0.211 (0.010)	0.212 (0.010)	0.205 (0.010)	1, 3	0.426 (0.047)	0.461 (0.047)	0.491 (0.043)
	3	0.252 (0.013)	0.248 (0.012)	0.255 (0.012)	2, 3	0.517 (0.041)	0.600 (0.034)	0.564 (0.037)
	Cassandro (2000)							
	1	0.165 (0.009)	0.188 (0.010)	0.191 (0.010)	1, 2	0.485 (0.044)	0.537 (0.039)	0.549 (0.042)
	2	0.211 (0.010)	0.212 (0.010)	0.205 (0.010)	1, 3	0.426 (0.047)	0.461 (0.047)	0.491 (0.043)
SCS	3	0.252 (0.013)	0.248 (0.012)	0.255 (0.012)	2, 3	0.517 (0.041)	0.600 (0.034)	0.564 (0.037)
	Cassandro (2000)							
	1	0.165 (0.009)	0.188 (0.010)	0.191 (0.010)	1, 2	0.485 (0.044)	0.537 (0.039)	0.549 (0.042)
	2	0.211 (0.010)	0.212 (0.010)	0.205 (0.010)	1, 3	0.426 (0.047)	0.461 (0.047)	0.491 (0.043)
	3	0.252 (0.013)	0.248 (0.012)	0.255 (0.012)	2, 3	0.517 (0.041)	0.600 (0.034)	0.564 (0.037)
	Cassandro (2000)							

¹305-d heritability from the repeatability lactation model.

Figure 1. Daily heritability of protein yield (A), fat yield (B), milk yield (C), and average daily SCS (D) estimated in high foreign sire use herds (High), all herds (All), and low foreign sire use herds (Low) across the first 3 lactations.

Figure 2. Posterior distribution of average daily heritability of protein yield estimated in high foreign sire use herds (High), all herds (All), and low foreign sire use herds (Low) in first lactation (A), second lactation (B), and third lactation (C).

(Figure 2). The 3 distributions were not clearly different and were more similar in the second lactation than in the first or third lactation.

Results from a similar analysis (Cassandro, 2000) using a repeatability lactation animal model showed a difference in heritability between High and Low herds (Table 4) for all yield traits, based on 10 samples for each herd class. The largest difference was reported between heritability of fat yield estimated in Low herds (0.346) and that estimated in High herds (0.382). More significant heterogeneity of genetic variance, specifically with fat yield, in the previous study compared with the present study may have resulted from the old lactation repeatability model lacking the ability to explain all genetic differences among animals. Heritability of yield calculated with a random regression model tends to increase as parity increases (Schaeffer et al., 2000). Thus, differences in the distribution of first- vs. later-parity cows in the different data sets may have created a difference in heritability with a lactation repeatability model that was removed when lactations were considered as different traits in the test-day model.

Average daily heritability for yield traits estimated in All herds ranged from 0.274 to 0.329 and increased with lactation (Table 4). Heritability of average daily SCS was generally lower than those for yield traits (0.165 to 0.252) and also increased with lactation. Estimated heritabilities for yield traits were lower in this study compared with estimates reported by Samoré et al. (2002) in Italy using a random regression test-day model with the Wilmink function as coefficients, and were much lower than estimates reported by Muir et al. (2004) in Canada using an identical model. Previous estimates of heritability of SCS in Italy were 0.06 to 0.09 in first lactation (varying by region) with a test-day repeatability model (Samoré et al., 2001a) and 0.15 to 0.25 with a multiple-trait random regression test-day model with the Wilmink function (Samoré et al., 2002). Estimates of heritability of SCS in this study tended to be only slightly lower than estimates in Canada. Several countries reported even higher heritabilities of yield traits than those in Canada, calculated with different random regression test-day models (the Netherlands, de Roos et al., 2001; Germany, Liu et al., 2000) and some reported lower heritabilities, similar to those in Italy (e.g., Finland, Lidauer et al., 2000), with the exception of first-lactation milk yield, which was higher.

With an identical model, heritability of yield traits and SCS in Canada were higher than those in Italy; however, within-trait genetic correlations across lactations were similar (Muir et al., 2004). Jamrozik et al. (2002), using a multiple-country first-lactation test-day model, showed that phenotypic and genetic parameters of milk yield differed between Canada and Italy. Heritability of 305-d milk yield in Finland was higher in first

Table 5. Genetic correlations among milk, fat, and protein yields and average daily SCS (posterior SD) within each lactation estimated in all herds (All), high foreign sire use herds (High), and low foreign sire use herds (Low)

Lactation no.	Trait	Genetic correlation		
		All	High	Low
1	Milk, fat	0.513 (0.035)	0.521 (0.033)	0.486 (0.034)
	Milk, protein	0.877 (0.010)	0.870 (0.010)	0.857 (0.011)
	Milk, SCS	0.116 (0.055)	0.127 (0.058)	0.157 (0.050)
	Fat, protein	0.622 (0.029)	0.605 (0.028)	0.579 (0.033)
	Fat, SCS	-0.040 (0.052)	-0.006 (0.052)	0.056 (0.049)
	Protein, SCS	0.120 (0.054)	0.099 (0.059)	0.149 (0.050)
2	Milk, fat	0.628 (0.027)	0.617 (0.026)	0.576 (0.029)
	Milk, protein	0.896 (0.009)	0.894 (0.009)	0.883 (0.009)
	Milk, SCS	-0.033 (0.055)	-0.087 (0.053)	-0.058 (0.047)
	Fat, protein	0.730 (0.021)	0.707 (0.022)	0.668 (0.025)
	Fat, SCS	-0.094 (0.052)	-0.154 (0.050)	-0.104 (0.049)
	Protein, SCS	-0.007 (0.057)	-0.065 (0.054)	-0.039 (0.048)
3	Milk, fat	0.657 (0.027)	0.638 (0.028)	0.592 (0.026)
	Milk, protein	0.900 (0.009)	0.897 (0.009)	0.888 (0.008)
	Milk, SCS	-0.212 (0.053)	-0.175 (0.054)	-0.142 (0.050)
	Fat, protein	0.751 (0.021)	0.723 (0.023)	0.683 (0.023)
	Fat, SCS	-0.184 (0.052)	-0.223 (0.051)	-0.157 (0.050)
	Protein, SCS	-0.173 (0.055)	-0.157 (0.056)	-0.115 (0.051)

and later lactations (0.42 and 0.34, respectively), and heritability of fat and protein yields in first and later lactations was similar to the results found here (0.28 and 0.27; 0.29 and 0.30, respectively; Lidauer et al., 2000). Heritability and genetic correlations among 305-d yields in the first 3 lactations were all higher in the Netherlands compared with any other country when a random regression test-day model was used to evaluate production traits (De Roos et al., 2001).

Genetic Correlations

Estimated genetic correlations among lactations for 305-d milk, fat, and protein yields were also very similar across subsets; however, estimated genetic correlations among lactations for SCS differed across subsets (Table 4). Genetic correlations among lactations for SCS esti-

Table 6. Average daily heritability (on the diagonal, in bold), genetic (above the diagonal), and permanent environmental (below the diagonal) correlations (posterior SD) for 305-d milk, fat, and protein yields, and average daily SCS in the first 3 lactations estimated in all herds

Lactation no.	Item	First lactation				Second lactation				Third lactation			
		Milk	Fat	Protein	SCS	Milk	Fat	Protein	SCS	Milk	Fat	Protein	SCS
1	Milk	0.30 (0.01)	0.51 (0.04)	0.88 (0.01)	0.12 (0.05)	0.79 (0.02)	0.40 (0.04)	0.67 (0.03)	0.13 (0.06)	0.70 (0.03)	0.37 (0.05)	0.57 (0.04)	-0.01 (0.05)
	Fat	0.86 (0.01)	0.27 (0.01)	0.62 (0.03)	-0.04 (0.05)	0.42 (0.04)	0.82 (0.02)	0.54 (0.03)	0.00 (0.05)	0.35 (0.05)	0.75 (0.03)	0.45 (0.04)	-0.04 (0.05)
	Protein	0.97 (0.00)	0.88 (0.01)	0.28 (0.01)	0.12 (0.05)	0.70 (0.03)	0.49 (0.04)	0.79 (0.02)	0.13 (0.06)	0.63 (0.04)	0.47 (0.04)	0.69 (0.03)	-0.01 (0.05)
	SCS	-0.18 (0.02)	-0.15 (0.02)	-0.15 (0.02)	0.16 (0.01)	0.01 (0.05)	-0.09 (0.05)	0.03 (0.05)	0.49 (0.04)	0.05 (0.05)	-0.02 (0.05)	0.07 (0.06)	0.43 (0.05)
2	Milk	0.48 (0.02)	0.40 (0.02)	0.47 (0.02)	-0.08 (0.02)	0.30 (0.01)	0.63 (0.03)	0.90 (0.01)	-0.03 (0.05)	0.86 (0.02)	0.51 (0.04)	0.74 (0.03)	-0.17 (0.05)
	Fat	0.37 (0.03)	0.50 (0.02)	0.41 (0.03)	-0.08 (0.03)	0.88 (0.01)	0.29 (0.01)	0.73 (0.02)	-0.09 (0.05)	0.51 (0.04)	0.84 (0.02)	0.60 (0.03)	-0.14 (0.05)
	Protein	0.47 (0.02)	0.44 (0.02)	0.50 (0.02)	-0.09 (0.02)	0.97 (0.00)	0.90 (0.01)	0.30 (0.01)	-0.01 (0.06)	0.78 (0.02)	0.63 (0.03)	0.85 (0.02)	-0.16 (0.05)
	SCS	-0.01 (0.03)	-0.02 (0.03)	-0.01 (0.03)	0.36 (0.02)	-0.24 (0.02)	-0.27 (0.03)	-0.22 (0.03)	0.21 (0.01)	-0.02 (0.06)	-0.06 (0.06)	0.00 (0.06)	0.52 (0.04)
3	Milk	0.36 (0.03)	0.27 (0.03)	0.34 (0.03)	-0.07 (0.03)	0.42 (0.02)	0.33 (0.03)	0.43 (0.03)	-0.14 (0.03)	0.33 (0.02)	0.66 (0.03)	0.90 (0.01)	-0.21 (0.05)
	Fat	0.30 (0.03)	0.39 (0.03)	0.33 (0.03)	-0.05 (0.03)	0.39 (0.03)	0.48 (0.03)	0.44 (0.03)	-0.16 (0.03)	0.88 (0.01)	0.31 (0.02)	0.75 (0.02)	-0.18 (0.05)
	Protein	0.36 (0.03)	0.33 (0.03)	0.39 (0.03)	-0.05 (0.03)	0.45 (0.03)	0.40 (0.03)	0.49 (0.02)	-0.15 (0.03)	0.97 (0.00)	0.91 (0.01)	0.33 (0.02)	-0.17 (0.05)
	SCS	0.05 (0.03)	0.02 (0.04)	0.06 (0.04)	0.26 (0.03)	0.02 (0.03)	-0.01 (0.04)	0.03 (0.03)	0.44 (0.03)	-0.23 (0.03)	-0.25 (0.03)	-0.21 (0.03)	0.25 (0.01)

mated in High and Low herds tended to be 0.03 to 0.08 higher than those estimated in All herds.

Genetic correlations among lactations for yield traits estimated in All herds ranged from 0.79 to 0.82 between the first and second lactations, from 0.84 to 0.86 between the second and third lactations, and 0.70 to 0.75 between the first and third lactations (Table 5). Genetic correlations among lactations tended to be similar for milk and protein yields and slightly higher for fat yield, compared with milk and protein yields. Genetic correlations among lactations for SCS were lower (0.43 to 0.49) than those for yield traits but, similarly, were highest between the second and third lactation. Estimates of genetic correlations among lactations for all traits were significantly higher (0.12 to 0.38) than previous estimates (Samoré et al., 2002) and estimates in Czech Holsteins (Zavadilova et al., 2005) but were similar to those estimated in Canada (Muir et al., 2004).

Genetic correlations among production traits within lactation estimated in All herds were moderate to high, ranging from 0.51 to 0.66 between fat yield and milk yield, from 0.88 to 0.90 between protein yield and milk yield, and from 0.62 to 0.75 between fat yield and protein yield (Table 6).

Genetic correlations among production traits tended to increase with lactation. Milk yield and SCS were positively correlated in first lactation (0.12), uncorrelated in second lactation (-0.03), and negatively corre-

lated in third lactation (-0.21). Because second- and third-lactation records were included without the requirement of a first-lactation record, this may have influenced results, specifically for SCS. For this trait, data collection did not begin on a national basis until 1994. Fewer than 5% of the animals included in the analysis had second- and third-lactation records but did not have first-lactation information. An additional 5% of the animals had only third-lactation information. Further studies may estimate parameters requiring first-lactation records to verify possible effects of selection.

Heterogeneous Variance

Several studies have investigated the heterogeneity of variances in different herds stratified by 4 within-herd average production and standard deviation classes of lactation records. Differences in heritability estimates varied from 0.15 to 0.31 for within-average milk production and from 0.12 to 0.30 for within-herd standard deviation classes (Canavesi et al., 1994). Research by Cassandro (2000) showed strong relationships between origin of semen used in the herd and number of cows, average production, and standard deviation per herd. Herds with a percentage of foreign semen use higher than 75% tended to have the highest within-herd production average and standard deviation. Because heterogeneity of variances affect bulls' EBV and bulls

are unevenly distributed across herds in Italy, the approach of stratifying herds by use of foreign semen was adopted as the preferred methodology to investigate the heterogeneity of genetic parameters that would strongly influence the accuracy of EBV of bulls.

This study of the relationship between the percentage of foreign or national bull semen on daily within-herd averages and standard deviations of production traits showed a positive correlation of around 0.20 with foreign semen and a correlation very close to 0 or slightly negative for national bull semen. Average daily production was consistently 10 to 15% higher in herds with more than 75% use of foreign semen compared with herds using more than 75% national bull semen.

CONCLUSIONS

Genetic parameters were estimated for a multiple-trait random regression test-day animal model with Legendre polynomials in Italian Holsteins on 3 subsets of data: a random sample of test-day records from all herds and 2 subsets of test-day records from herds differing in sire use (>75% foreign sire use herds and <25% foreign sire use herds). Heritability of yields (milk, fat, and protein) was lower and heritability of SCS was higher than in previous estimates (Samoré et al., 2002) with a similar model. Genetic correlations among lactations were significantly increased (0.12 to 0.38) compared with previous estimates and now coincide with parameters estimated in Canadian Holsteins using an identical model. Differences among parameters estimated in the 3 subsets were very small and do not warrant heterogeneous variance adjustments at the genetic level. Not accounting for heterogeneous variance attributable to the use of foreign sires in the Italian Holstein population should have only a negligible effect on EBV.

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