

GENETICS AND BREEDING

Genetic Variation in Lactation Means of Somatic Cell Scores for Six Breeds of Dairy Cattle

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ABSTRACT

Lactation means of somatic cell scores from sample days were used to estimate the components of variation for additive genetic, permanent environmental, and herd-sire interaction effects. Data included records of 4314 Ayrshire, 7845 Brown Swiss, 18,115 Guernsey, 1,135,752 Holstein, 67,862 Jersey, and 787 Milking Shorthorn cows from across the US. Records were preadjusted for length of lactation. Fixed effects of herd-year, calving age, and calving month were included in animal models for estimation of variance components. Additive genetic estimates from REML relative to a phenotypic variance of 1.00 were .07 for Ayrshires, .07 for Brown Swiss, .11 for Guerneys, .09 for Holsteins, .09 for Jerseys, and .08 for Milking Shorthorns; permanent environmental estimates were .25, .26, .22, .21, .20, and .35; and herd-sire interaction estimates were .04, .02, .00, .02, .02, and .01. Effects of calving age were similar for all regions of the US but differed for Jerseys and Holsteins. Effects of calving month were similar for all breeds. Cows calving during summer had the highest lactation means for somatic cell score from sample days. Impact of calving month was greatest in the Southeast.

(Key words: somatic cell, mastitis, breed, variance component, breed)

Abbreviation key: LSCS = arithmetic mean of sample day, log₂-transformed SCC for a lactation, SCS = sample day, log₂-transformed SCC.

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INTRODUCTION

Genetic evaluations for somatic cells in milk of US dairy cattle are being developed by USDA (H. D. Norman, 1993, personal communication). These evaluations will parallel current genetic evaluations for yield traits. However, much less is known about the genetics of somatic cells than about milk, fat, and protein yields; genetic information about somatic cells for US dairy breeds other than Holstein is especially scant.

One indicator of mastitis is SCC. Sample day, log₂-transformed SCC, often called linear somatic cell score (SCS), is the preferred trait for selection for mastitis resistance (1, 13, 14, 16). The use of SCS has been accepted by the National Cooperative DHI Program (12), and the arithmetic mean of SCS for a lactation (LSCS) often has been used as the lactation measure of somatic cells in milk (2, 3, 4, 9, 10, 11, 19, 22). Indeed, using SCS as an indicator trait for selection against mastitis has several advantages over direct selection to reduce clinical mastitis. Measurement of SCS is less expensive and more consistent than is assessment of clinical mastitis, which may explain higher estimates of heritability for SCS than for clinical mastitis (6, 16, 18). Also, SCS has a high correlation with bacteriological status of milk and, thus, to subclinical mastitis (18), which accounts for a major portion of economic loss from this disease. Recent REML estimates of heritability for LSCS have ranged from .05 to .27 (2, 3, 5, 6, 10, 18, 19). Earlier studies (4, 15) used sire models or relatively small numbers of records because of limited availability of somatic cell information and computational constraints. Boettcher et al. (3) estimated the heritability of LSCS from first lactation for Holsteins in five regions of the US and also combined data for a national analysis. Heritability estimates ranged from .08 to .16 for the five regions; the national estimate was .10.

Advances in computer resources and programming techniques have made variance

component estimation with animal models more feasible (7). Da et al. (5) found heritability of LSCS to be .12 by using an animal model with 13,017 records of 5278 cows. They included up to 4 records per cow and found that the component of variation from permanent environment was .27. Herd-sire interaction is used in current USDA genetic evaluations for yield traits to account for genotype-environment interaction (21). Da et al. (5) estimated herd-sire variance to be extremely small (.002) for a weighted LSCS. Banos and Shook (2) also found herd-sire interaction explained little variation in LSCS. Their estimates ranged from .011 to .017, depending on parity, compared with .018 to .030 for 305-d milk yield.

The objective of this study was to estimate variance components of LSCS for additive genetic, permanent environmental, and herd-sire interaction effects for US dairy cattle for use in genetic evaluations with a BLUP animal model and to compare estimates among six US dairy breeds. Another objective was to examine the effects of age and month of calving on LSCS.

MATERIALS AND METHODS

Data included LSCS records received by USDA for research purposes prior to December 1991. Records had been contributed since 1987 by Agri-Tech Analytics, Tulare, CA; Pennsylvania DHIA Service Center, University Park; Dairy Records Processing Center at Raleigh, NC; and Wisconsin DHI Cooperative, Madison; from 1987 to 1988 by Cornell Dairy Records Processing Laboratory, Ithaca, NY; since 1990 by Minnesota Dairy Records Processing Center, St. Paul; and since 1991 by DHI Computing Service, Inc., Provo, UT. Seven of nine US dairy records processing centers contributed data.

Initial data requirements were sire identification for cows with records, LSCS from 0 to 9.99, and reported number of sample days >0. Only a single sample day per lactation was required so that short records of cows culled for mastitis early in lactation would not be eliminated. The LSCS records were compared with records of milk yield currently used in genetic evaluations to ensure the integrity of identification, parentage, and birth and calving date information and the usability of yield

information. Following these initial edits, data included 24,646 Ayrshire, 43,135 Brown Swiss, 71,656 Guernsey, 4,147,017 Holstein, 302,211 Jersey, and 3557 Milking Shorthorn records of LSCS.

Adjustment of data for stage of lactation was not possible because reported information included only means of sample day SCS and number of days in milk at last sample day. Instead, the method of Boettcher et al. (3) was used to adjust for length of lactation at last sample day. Adjustments estimated for this study were similar to theirs and are not reported. Although only 1 sample d per lactation was required, further edits were made to ensure that number of sample days was representative of the corresponding length of lactation reported by requiring ≤ 60 , ≤ 100 , ≤ 140 , ≤ 180 , ≤ 220 , or ≤ 260 DIM for 1, 2, 3, 4, 5, or 6 sample d, respectively (3).

Cows were assigned to regions according to state code (Figure 1). No records were received from some states in the Midwest and West. Classes for age and month of calving were defined within region. Age classes (Table 1) were defined as by Boettcher et al. (3). Records were assigned to 1 of 12 monthly calving classes in each of the four regions for a total of 48 classes. Because of small numbers of records per age-region class for the Ayrshire, Brown Swiss, and Milking Shorthorn breeds, regions were combined so that age effects were national for these three breeds. For all breeds, records were deleted if there were <5 records per herd-year of calving or <10 records per age-region or calving month-region. Requiring a minimum number of records for each herd-year, age-region, or calving month-region had the greatest impact if total available records were few. Thus, a higher percentage of records was eliminated for Ayrshires, Brown Swiss, and Milking Shorthorns.

To reduce the probability of bias from cows culled for mastitis, lactations later than first were considered only if a record from first lactation also was present. The maximum number of records per cow was 5 because of the relatively short time from earliest to most recent records (1987 to 1991). Numbers of records passing final edits are in Table 2 for breeds other than Holstein.

Holstein data were divided into 10 data files by last digit of herd code because estimation of

variance components with an animal model and all data would have required more than the 512 MB of computer memory available for computations. Three of the data files (last digit of herd code = 3, 6, or 9) were used for estimation of variance components, and all Holstein data were used to derive solutions for effects of age and month of calving and to obtain breeding values with BLUP. Numbers of all Holstein records and of those in the three data files used to estimate variance components are in Table 3.

The model used for analyses was similar to that currently used for USDA genetic evaluations for milk yield (23) except that effects of age and month of calving were included because records were not preadjusted for these two effects:

$$y_{ijklmno} = h_{ij} + r_{km} + t_{lm} + c_{in} + p_{no} + a_{no} + e_{ijklmno}$$

where $y_{ijklmno}$ = LSCS record adjusted for length of lactation of a cow (daughter o of sire n) that calved in region m, age class k, month l, year j, and herd i; h = effect of herd and calving year; r = effect of calving age class and region; t = effect of calving month and region; c = random herd-sire interaction effect; p = random permanent environmental effect; a = random additive genetic effect; and e = random residual effect.

Numbers of levels of effects are in Table 2 for breeds other than Holstein and in Table 3 for Holsteins. Because of overlap of sires for the Holstein data files used to estimate variance components, numbers of levels for additive genetic effect are much greater than .1 as many as for all Holstein data. The number of permanent environmental records is equivalent to the number of cows with records for each breed.

Sire and dam identification was complete for cows with records. Male pedigrees were

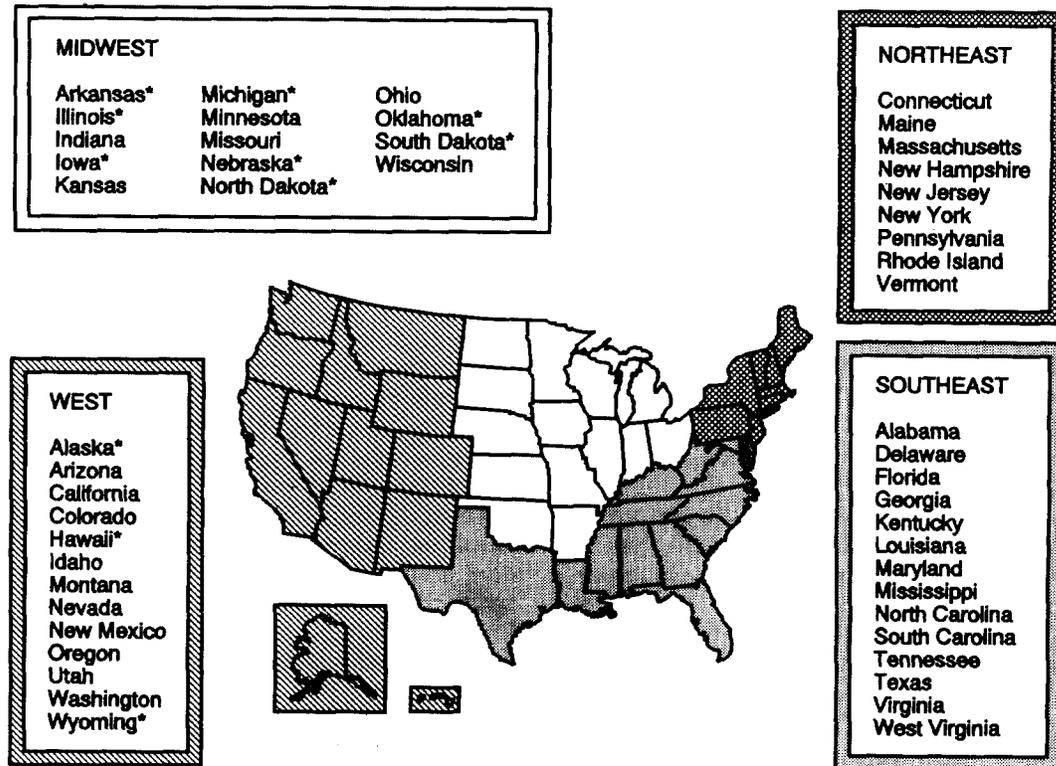


Figure 1. States in each of four geographic regions. Asterisk indicates that somatic cell score is not provided.

TABLE 1. Description of classes for age at calving.

Age class	Age at calving (mo)
1	18-21
2	22
3	23
4	24
5	25
6	26
7	27
8	28
9	29
10	30
11	31
12	32
13	33
14	34
15	35
16	36
17	37
18	38
19	39
20	40
21	41
22	42
23	43-44
24	45-46
25	47-48
26	49-50
27	51-52
28	53-54
29	55-57
30	58-60
31	61-63
32	64-66
33	67-71
34	72-77
35	78-83
36	84-89

included back to at least 1950 to account for most relationships. Female pedigrees were ignored except for dams of sires with >1 progeny because females would contribute relatively fewer relationships at a large cost in computational memory. Additive genetic effect also included unknown-parent groups (20).

Variance components for random additive genetic, permanent environmental, herd-sire interaction, and residual effects were estimated with an expectation-maximization type REML algorithm developed by Misztal (7). This algorithm inverts the coefficient matrix with sparse matrix techniques. Rate of convergence is improved by modified Aitken extrapolation. The convergence criterion was that variance estimates changed <.1% between rounds of iteration. Variances were first estimated for additive genetic, permanent environmental, and residual effects by using the model with herd-sire interaction effect excluded. Prior variances were .12 for additive genetic, .15 for permanent environmental, and .73 for residual effects relative to a phenotypic variance of 1.00. The expectation-maximization type REML estimates of variance from the model without herd-sire interaction effect were used as prior variances for the full model with 5% of the residual variance assigned to herd-sire interaction.

RESULTS AND DISCUSSION

Percentages of LSCS records from each region by breed are in Table 4. The largest

TABLE 2. Numbers of records and levels of effects to estimate components of variance for lactation mean of log₂-transformed SCC for breeds other than Holstein.

	Ayrshire	Brown Swiss	Guernsey	Jersey	Milking Shorthorn
Records	6785	12,423	29,223	117,854	1141
Effect					
Herd-year	431	792	1372	3764	90
Age-region	35	35	129	136	34
Month-region	48	48	48	48	45
Herd-sire interaction	2263	3523	7690	23,828	399
Permanent environment	4314	7845	18,115	67,862	787
Additive genetic	12,540	20,617	45,342	138,889	2535

TABLE 3. Numbers of records and levels of effects to estimate components of variance for lactation mean of log₂-transformed SCC for Holsteins.

	Last digit of herd code			All Holsteins
	3	6	9	
Records	186,280	189,001	160,013	1,832,366
Effect				
Herd-year	6161	6161	5659	60,842
Age-region	138	138	138	140
Month-region	48	48	48	48
Herd-sire interaction	53,708	54,035	47,407	528,588
Permanent environment	115,632	118,851	101,393	1,135,752
Additive genetic	212,316	215,890	196,294	1,368,277

percentage of records was from the Midwest for Brown Swiss, Guernseys, Holsteins, and Milking Shorthorns, although the distribution of Holstein records was more uniform among regions. The largest percentage of Jersey records was from the Southeast.

Table 4 also has LSCS means, standard deviations, and coefficients of variation by breed and region. Mean LSCS was highest in the Southeast for Guernseys, Holsteins, and Milking Shorthorns; in the Midwest for Ayrshires and Jerseys; and in the West for Brown Swiss. Means were lowest in the Northeast for all breeds except Holstein, which had its lowest mean in the West. Boettcher et al. (3) found for Holsteins highest means in the Northeast and lowest means in the Southeast, but the data included fewer years and fewer dairy records processing centers. Means for Jerseys and Guernseys were higher than for Ayrshires, Brown Swiss, and Holsteins. Means for Milking Shorthorns were difficult to interpret because of the larger sampling variance caused by the small number of records. Variability of LSCS was highest in the Southeast and lowest in the West for all breeds except Brown Swiss. Boettcher et al. (3) reported the same results for variability of Holsteins and suggested that the lower variability in the West might indicate a lower incidence of mastitis. Coefficients of variation were lowest in the West for all breeds. Further research may be justified to determine the impact of regional differences in variability on PTA.

Variance estimates for additive genetic, permanent environmental, herd-sire interaction, and cow repeatability (the sum of additive genetic, permanent environmental, and herd-

sire interaction) effects relative to a phenotypic variance of 1.00 are in Table 5 for breeds other than Holstein. If herd-sire interaction effect was not included in the model, heritability estimates ranged from .082 for Brown Swiss to .106 for Guernseys. Heritability differences for breeds were not as great as those reported by Emanuelson et al. (6) for Red and Whites and Friesians in Sweden. Estimates for the ratio of permanent environmental variance to phenotypic variance (.212 to .351) had a range larger than heritabilities or cow repeatability (.312 to .440). The high estimates for Milking Shorthorns may reflect the small number of records. Phenotypic standard deviations were similar for all breeds.

Herd-sire interaction expressed as a ratio to phenotypic variance ranged from .002 for Guernseys to .041 for Ayrshires. With herd-sire interaction included in the model, heritability estimates decreased but always by less than the amount of variation repartitioned to the herd-sire effect. When the full model was used, changes in permanent environmental and cow effects were small, <.01, compared with results from the model without herd-sire interaction.

Heritability estimates for the three Holstein data files used to estimate variance components ranged from .098 to .108 (Table 6) if herd-sire interaction was not included in the model. Mean of estimated heritabilities for LSCS was .103 with a standard error of .003. Previous estimates of heritability for US Holsteins from models without herd-sire interaction were slightly higher and averaged about .12 (2, 3, 5, 10, 19). In those studies, estimates were separate for parity, which may account

TABLE 4. Percentage of records, means, standard deviations, and coefficients of variation for lactation mean of log₂-transformed SCC (LSCS) by region within breed.

Breed	Region	Records	LSCS		
			\bar{X}	SD	CV
		(%)			
Ayrshire	Northeast	32	2.49	1.18	.47
	Midwest	31	2.81	1.35	.47
	Southeast	32	2.61	1.43	.55
	West	5	2.65	1.04	.39
Brown Swiss	Northeast	12	2.55	1.26	.50
	Midwest	53	2.76	1.44	.52
	Southeast	20	2.67	1.37	.51
	West	15	2.81	1.28	.46
Guernsey	Northeast	19	2.73	1.36	.50
	Midwest	47	2.89	1.41	.49
	Southeast	26	3.05	1.56	.51
	West	7	2.84	1.32	.46
Holstein	Northeast	21	2.72	1.37	.50
	Midwest	36	2.78	1.48	.52
	Southeast	23	2.79	1.54	.55
	West	20	2.58	1.11	.43
Jersey	Northeast	21	2.78	1.29	.46
	Midwest	12	3.20	1.36	.43
	Southeast	45	2.94	1.40	.48
	West	23	2.81	1.14	.41
Milking Shorthorn	Northeast	11	2.30	1.12	.49
	Midwest	79	2.58	1.49	.57
	Southeast	2	3.26	1.84	.57
	West	9	2.31	1.10	.48

for discrepancies if LSCS is influenced by some different genes in first and later parities, as has been suggested by Coffey et al. (4). Three of the studies (3, 10, 19) used multiple-trait models that included yield traits. Four studies (2, 5, 10, 19) used much less data from only a single region of the US. Estimates of heritability may have been higher in earlier studies (4, 10) because records with <4 sample d were excluded.

Estimates of Holstein heritability generally were lower with herd-sire interaction included in the model; the mean was .093 (SE = .002). Similarly, estimates of permanent environmental effects decreased if herd-sire interaction was included; mean was .210 (SE = .003) compared with a mean of .218 (SE = .004) if herd-sire interaction was not included. Herd-sire interaction accounted for a mean of .019 of phenotypic variance (SE = .002), which is higher than Holstein estimates from other studies (2, 5). With herd-sire interaction considered, additive genetic and permanent environmental effects accounted for somewhat

less variation than that reported by Da et al. (5). Their study included data primarily from the Southeast, which was the region with the highest mean and most variation of LSCS in this study. More variability could have contributed to larger estimates of additive genetic and permanent environmental effects. In their study (5), the amount of variation explained by herd-sire interaction was extremely small (.002). The mean estimate of .32 for cow repeatability (Table 6) was intermediate to estimates of .27 reported by Welper and Freeman (19) and .35 reported by Da et al. (5).

Evaluations for all Holsteins were computed with variance ratios averaged for the three Holstein data files. Mean PTA of animals for LSCS was near 0 and ranged from -.403 to .618 for cows with records and from -.479 to .657 for pedigree animals. A small genetic trend of .002 per year was estimated from mean breeding values of LSCS by birth year of cows with records. With a genetic standard deviation of .390, the trend was .005 standard deviations per year. Based on a standard devia-

TABLE 5. Variance estimates¹ for additive genetic, permanent environmental, herd-sire interaction, and cow effects relative to a phenotypic variance of 1.00 for lactation mean of log₂-transformed SCC for breeds other than Holstein.

Model effect	Ayrshire	Brown Swiss	Guernsey	Jersey	Milking Shorthorn
Additive genetic	.071 (.100)	.067 (.082)	.106 (.106)	.088 (.100)	.083 (.089)
Permanent environment	.247 (.255)	.259 (.266)	.221 (.223)	.203 (.212)	.350 (.351)
Herd-sire interaction	.041	.024	.002	.023	.012
Cow repeatability ²	.359 (.356)	.349 (.347)	.329 (.329)	.315 (.312)	.445 (.440)
Phenotypic SD ³	1.19	1.20	1.29	1.18	1.30

¹Estimations in parentheses for model without herd-sire interaction.

²Sum of additive genetic, permanent environmental, and herd-sire interaction effects.

³Phenotypic SD = Square root of sum of additive genetic, permanent environmental, herd-sire interaction, and residual variances.

tion for breeding value for milk yield of 544 kg and a genetic trend of 151.5 kg/yr (USDA, 1993, unpublished results for January 1993 USDA-DHIA genetic evaluations), annual genetic gain for Holstein milk yield is .278 standard deviations. If all selection were on milk yield with an actual genetic correlation between milk yield and LSCS of .20 [approximate mean of correlations for first lactation (2, 3, 10, 19)], expected annual genetic trend in Holstein LSCS would be .056 standard deviations (.278 × .20).

The actual annual increase in LSCS is smaller for several reasons. Selection for udder conformation traits that are negatively (favorably) correlated with LSCS (9, 11) often accompanies selection for milk yield. Selection on these traits (highly held, tightly attached udders with close teat placement) serves to slow the increase in SCS that would otherwise accompany selection for milk yield alone. Also, mastitis plays some role in culling decisions, whether voluntary or involuntary, on most farms. The correlation of LSCS with mastitis is about .62 (16). Hence, any selection against mastitis through related traits or culling would also decrease genetic trend for SCS. The genetic trend in SCS represents records collected over a relatively short period and should be monitored as more SCS records become available.

Smoothed (17) estimates of the fixed effect of age at calving by region from variance component estimation procedures are in Figure

2 for Holsteins and in Figure 3 for Jerseys. Solutions are reported relative to the mean solutions for age within region. Age solutions for Holsteins were quite similar for all regions except that LSCS was slightly higher for cows calving in the West from 35 to 55 mo of age. The small number of records for cows calving in the older age classes may explain the divergence of the age curves at calving ages >60 mo. Age curves for Jerseys also were similar

TABLE 6. Variance estimates¹ for additive genetic, permanent environmental, herd-sire interaction, and cow effects relative to a phenotypic variance of 1.00 for lactation mean of log₂-transformed SCC for Holsteins.

Model effect	Last digit of herd code		
	3	6	9
Additive genetic	.095 (.102)	.096 (.108)	.089 (.098)
Permanent environment	.212 (.216)	.204 (.213)	.215 (.226)
Herd-sire interaction	.013	.022	.021
Cow repeatability ²	.318 (.318)	.322 (.321)	.324 (.323)
Phenotypic SD ³	1.28	1.29	1.28

¹Estimates in parentheses for model without herd-sire interaction.

²Sum of additive genetic, permanent environmental, and herd-sire interaction effects.

³Phenotypic SD = Square root of sum of additive genetic, permanent environmental, herd-sire interaction, and residual variances.

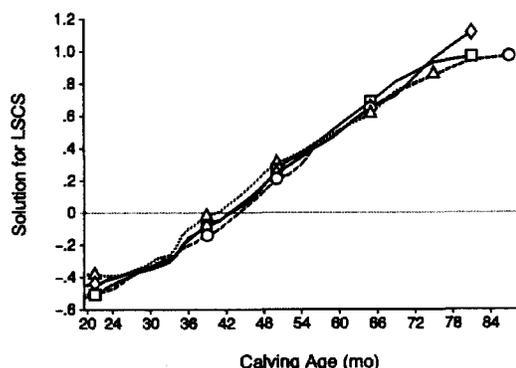


Figure 2. Smoothed solutions for effect of calving age on lactation mean of sample day, \log_2 -transformed SCC (LSCS) for Holsteins by region: Northeast (\diamond), Southeast (\circ), Midwest (\square), and West (\triangle).

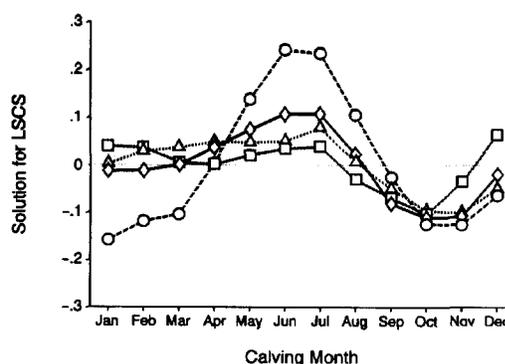


Figure 4. Solutions for effect of calving month on lactation mean of sample day, \log_2 -transformed SCC (LSCS) for Holsteins by region: Northeast (\diamond), Southeast (\circ), Midwest (\square), and West (\triangle).

across regions. However, in contrast to those for Holsteins, solutions differed little for cows calving from 20 to 40 mo of age, but regional differences increased quickly thereafter. Again, solutions from the West tended to be higher from 35 to 65 mo of age. Perhaps climate and management practices in the West cause cows to mature faster. Such cows would reach second calving at an earlier age, which could contribute to higher age solutions. Curves of estimates for other breeds were affected by small sizes of age classes and are not shown. In general, solutions for calving age of Guernseys were similar to those for Jerseys, but

solutions for Ayrshire, Brown Swiss, and Milking Shorthorn were more like those for Holsteins.

Solutions for calving month are in Figure 4 for Holsteins and in Figure 5 for Jerseys. Solutions are reported relative to the mean of monthly solutions within region. The ranges of solutions for calving month were smaller than those for calving age. Holstein LSCS tended to be highest for cows calving during the summer and lowest for cows calving during October and November. Seasonal impact was largest for cows in the Southeast. The curves show LSCS initiated during the designated month

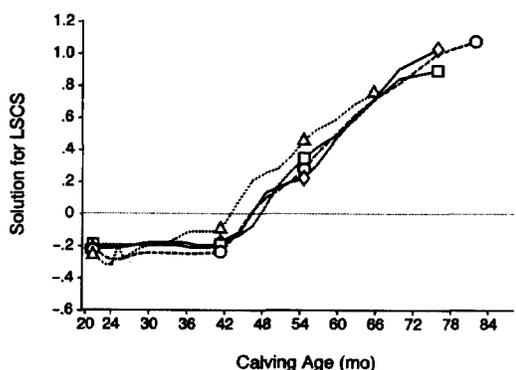


Figure 3. Smoothed solutions for effect of calving age on lactation mean of sample day, \log_2 -transformed SCC (LSCS) for Jerseys by region: Northeast (\diamond), Southeast (\circ), Midwest (\square), and West (\triangle).

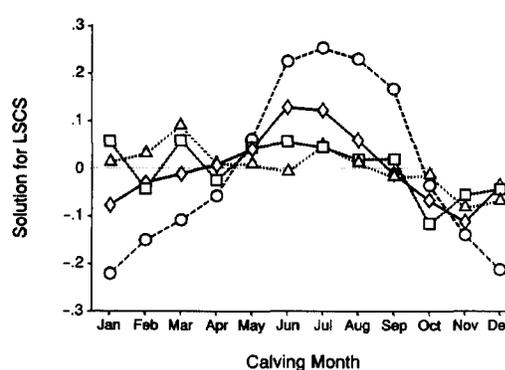


Figure 5. Solutions for effect of calving month on lactation mean of sample day, \log_2 -transformed SCC (LSCS) for Jerseys by region: Northeast (\diamond), Southeast (\circ), Midwest (\square), and West (\triangle).

rather than SCS from samples taken during only that month. Mastitis infection at calving probably is greater during summer and causes sample day SCS to be much higher early in lactation and somewhat higher throughout the remainder of lactation. Similar seasonal effects on SCS have been reported (3, 5, 18, 22). Solutions for Jerseys were similar to those for Holsteins, although curves were not as consistent.

CONCLUSIONS

Heritabilities and repeatabilities for LSCS were similar for six breeds of dairy cattle in the US. Techniques for estimation of variance components allowed for use of larger data files over a longer time, but estimates were similar to those in previous reports (2, 3, 5, 10, 18, 19). Multiple lactations were included by using single-trait repeatability models, which likely produced slightly lower estimates of heritability than in previous reports. Ultimately, animal evaluations should consider LSCS from different parities as multiple correlated traits, but initial evaluations based on a single trait and using repeated records are feasible and are expected to be nearly as effective. Estimates of genotype-environment (herd-sire) interaction were small, but inclusion of this effect for animal evaluations may still be needed to limit the impact of a single herd on the PTA of a particular sire. For genetic evaluations for milk yield, herd-sire interaction is assumed to be .14 of phenotypic variance (21), but actual estimates are about .02 (2). The variance assumed is considerably higher than estimated because it is thought to be effective for improving evaluations of bulls used in a limited number of herds. This study suggests that variances (standardized to a phenotypic variance of 1) are .09, .21, and .02 for additive genetic, permanent environmental, and herd-sire interaction effects, respectively, for genetic evaluation from repeated records of LSCS for Holsteins. The heritability of .09, although lower than heritabilities for other yield traits (10), would allow genetic progress in reducing LSCS. For genetic evaluation procedures, short records will be given less weight than complete records. If higher variation in short records reduced the estimate of heritability in this study, a slightly higher heritability of .10 to

.12 could be justified in implementation of evaluation procedures. The correct emphasis to place on LSCS in breeding programs has been discussed in other studies (8, 16).

Adjustments for age at calving should account for breed differences (Jersey and Guernsey versus other breeds). Effects of calving month were smaller than those for calving age and were similar for all breeds. The trait used in this study was the simple mean of sample day SCS from a lactation. If all sample day records were available, records could be adjusted more accurately for stage of lactation and sample month, which likely would reflect true climatic effects better than would calving month. The LSCS records could also be weighted according to the number of sample days that contribute to the lactation measure as previously proposed by Wiggans and Shook (22).

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