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Heterogeneous Within-Herd Variance. 2. Genetic Relationships Between Milk Yield and Calving Interval in Grade Holstein Cows¹

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ABSTRACT

Genetic and phenotypic (co)variances for mature equivalent yield of 4% FCM and calving interval were simultaneously estimated by REML for grade Holstein cows in first and second parity. Data were 305-d mature equivalent lactation records and calving dates for 299,441 daughters of 2489 AI sires first calving from 1970 to 1985 in California, New York, or Texas. Data were divided into three time periods, and herds were partitioned into three within-herd-year phenotypic SD classifications for milk yield.

Average FCM yield and calving interval increased with SD in all time periods for both parities. Genetic variance of calving interval showed no trend with SD of yield, although residual variances increased as SD of yield increased. Heritability of calving interval was less than .06 in all time periods and SD classes. Genetic correlations between first and second calving interval increased as SD of yield increased (.33 to .63), but phenotypic correlations were uniformly small. Genetic correlations between FCM and calving interval were largest in the highest SD class and for second lactations. Phenotypic correlations were small in every SD class. Even though milk yield and calving interval were positively (un-

favorably) correlated genetically, the correlated response in calving interval was only about 1 d for each 100-kg increase in genetic merit for FCM yield.

(Key words: milk yield, calving interval, heterogeneous variance)

INTRODUCTION

Most studies of the association between milk yield and reproductive measures in dairy cattle showed an unfavorable relationship between them (2, 8, 12, 23, 27), although others showed either no association (24) or a favorable one (16). High milk yield per lactation has been associated with longer postpartum intervals to first service (2, 15), longer service period (2, 12), more open days (2, 12, 23, 27), and longer calving intervals (8). From designed selection experiments differences were not detected in fertility measures (e.g., service interval to conception or conception rate) between daughters of sires selected for milk and daughters of sires with average transmitting ability (24). Differences in health costs associated with treatment of reproductive disorders did not differ between high and low genetic lines for milk (24, 25).

Dachir et al. (7) did not detect a relationship between measures of ovarian activity and actual yield or transmitting ability for FCM in Holsteins. However, with more information from the same experiment, Gonzalez (11) obtained ($P < .05$) unfavorable regression coefficients for postpartum intervals to first and second ovulation on 60-d and 90-d FCM yields of Holsteins, but not for third ovulation, which occurred on average 67 d postpartum. Postpartum interval to first estrus increased with 305-d yield for Holsteins and Jerseys (11). Although cows commence ovarian activity early in the postpartum period, the probability of identifying cows in estrus is less for high yielding than for low yielding individuals. Butler and Smith (6) re-

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ported that postpartum interval to first ovulation was influenced by negative energy balance in early lactation. Normal ovarian activity is initiated as cows move from greatest negative energy balance toward positive balance (7). Butler et al. (5) reported that first ovulations occurred an average of 10 d after greatest negative energy balance.

Most estimates of heritability of reproductive traits are less than .10 (2, 12, 15, 22, 27), thus indicating that relatively slow improvement in fertility would result from selection. Even though most reproductive traits have low heritabilities, monitoring reproductive performance has merit because, after low milk yield, poor fertility is the leading reason for culling dairy cows (2).

There have been numerous studies on the effects of heterogeneous within-herd variation in milk yield on the accuracy of selection and on genetic progress for milk yield (4, 13, 18, 30). Most studies on the effect of heterogeneous herd variation in milk yield showed that genetic parameters for yield differed with herd average milk. Few estimates of genetic and environmental parameters are available for environments in which herds were classified by variation in milk yield (26). Furthermore, other studies of heterogeneity of within-herd variation for milk yield did not estimate parameters of reproductive performance.

Therefore, the objectives of this study were 1) to estimate the genetic and environmental (co)variances of milk yield and calving interval for nonregistered (grade) Holstein dairy cows in production environments classified by within-herd variation in yield, and 2) to determine change of these parameters with time.

MATERIAL AND METHODS

Data

Data were lactation and calving interval records from grade Holstein cows in California, New York, and Texas that calved for the first time from 1970 through 1985. Lactation records were 305-d, mature equivalent, 4% FCM yields in first (FCM1) and second (FCM2) lactations. Calving intervals were the periods between first and second (CI1), and second and third (CI2) parturitions, omitting observations exceeding 700 d.

Data were divided into nine subsets based on herd-year SD of ME milk yield and time period. The within-herd SD were calculated using all lactations in herd-years with at least 25 cows. To account for sampling variance and minimize the chance of placing a herd in the incorrect SD class, gaps were left between SD classes. Within herd SD classes were low (less than 1018 kg), medium (1131 kg to 1357 kg), and high (greater than 1471 kg). Time periods were chosen to balance number of sires and were 1970 to 1975, 1977 to 1981, and 1982 to 1985. Numbers of observations, sires and herd-year-seasons for each data set and trait are in Table 1.

Statistical Model

A multiple-trait mixed model was used to analyze FCM yield and calving interval records. The model equation was

$$y_i = X_i\beta_i + Z_iu_i + e_i$$

where y_1 is the vector of FCM1, y_2 is the vector of CI1, y_3 is the vector of FCM2, and y_4 is the vector of CI2. The X_i and Z_i are incidence matrices relating y_i to β_i and u_i , respectively. β_i is a vector of contemporary group effects for trait i , u_i is a vector of sire transmitting abilities for trait i , and e_i is a vector of residuals for trait i . Contemporary groups were defined as cows calving in the same herd, year, and season. Seasons were January through April, May through August, and September through December. All u and e are considered multivariate and normally distributed with $E(u) = 0$, $E(e) = 0$, $\text{var}(u) = G$, $\text{var}(e) = R$, and $\text{cov}(u, e') = 0$. Then $E(y) = X\beta$ and $\text{var}(y) = ZGZ' + R$. For a sire model that accounts for relationships among sires, the genetic and residual variance-covariance matrices G and R can be written $G = G_0 * A$, where G_0 represents the 4×4 matrix of additive genetic (co)variances of sire effects, A represents the numerator relationship matrix, and the asterisk denotes the direct product, and $R = R_0 * I_n$, where R_0 is a 4×4 variance-covariance matrix of residual effects for each cow and I_n is an identity matrix of order n , the number of cows. When an animal has a missing observation, the elements of R in the row and column corresponding to the missing observation are replaced by zeros.

A sequential data pattern (10) was required so that a transformation could be applied to make uncorrelated the residual effects on each animal [i.e., transform R_0 , the residual (co)variance matrix, to an identity matrix]. Residuals on each cow were made uncorrelated using elements from the inverse of the Cholesky decomposition of matrix R_0 , where $R_0 = L_0 L_0'$ and $L_0^{-1} R_0 L_0'^{-1} = I$.

Genetic (co)variance components were estimated by REML methods using an expectation-maximization algorithm described for the specific case of sequentially missing data by Garlick (10). A successive approximations algorithm (10) was used to estimate residual (co)variance components. Standard errors of genetic correlations were approximated by the method presented by Robertson (21). Standard errors of heritabilities were estimated using the approximation of Swiger et al. (28).

TABLE 1. Numbers of herd-year-seasons (HYS), sires, and cows with records for each time period and within-herd standard deviation class.

Period and parameter	Within-herd SD class ¹		
	Low	Medium	High
1970 to 1975			
HYS	2632	4097	1283
Sires	398	493	509
Lactation 1	14,671	32,920	13,927
Calving interval 1	11,616	23,662	9139
Lactation 2	11,144	22,941	8850
Calving interval 2	8371	15,711	5789
1977 to 1981			
HYS	1475	8417	10,198
Sires	397	872	985
Lactation 1	8049	43,019	72,223
Calving interval 1	6463	32,658	51,787
Lactation 2	6291	31,837	50,185
Calving interval 2	4846	23,596	35,143
1982 to 1985			
HYS	1285	6376	10,015
Sires	386	1071	968
Lactation 1	6857	30,715	77,060
Calving interval 1	4259	22,571	54,965
Lactation 2	3361	21,277	51,127
Calving interval 2	1831	12,669	30,219

¹Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

RESULTS AND DISCUSSION

Table 2 has average FCM yields and calving intervals for subsets of data. Average yields across parities, time, and SD classification ranged from 6080 to 8654 kg. Average calving intervals correspondingly ranged from 381 d to 399 d. For each subset, average yields were greater for second than for first lactations, but calving intervals tended to be longest in the first parity. Yields of FCM increased with time within each SD class. Calving interval increased across SD classes within each time period but did not change noticeably with time.

Variance Components and Heritability of Calving Interval

Estimates of sire and residual components of variance for calving interval are in Table 3. No pattern in sire variance was discernible with SD class. Sire variances were greatest in the most variable herds from 1970 to 1975, in the medium variance herds from 1977 to 1981, and in the least variable herds from 1982 to 1985. Seykora and McDaniel (23) reported that sire variance for days open increased with time, especially in the 1970s. Within each SD class, trends were not detected across time. Average sire variances within each time period weighted by number of sires were 28, 37, and 31 d², respectively, for the three periods. Sire variances in this study for calving interval were similar to those reported for days open by Strandberg and Danell (27) for two Swedish dairy breeds (20 to 34 d²), and Jansen et al. (14) for Dutch Friesians (up to 23 d²). Variances for calving interval and days open should be similar, because calving interval only differs from days open by the length of gestation, which varies little within breeds ($\bar{X} = 280$, SD = 6.1 d for Holsteins, (29)).

Sire components of variance for calving interval did not show the same trend as those for FCM yield across SD classes, even though mean calving interval increased with SD of yield in all time periods and parities (Table 2). Sire variances tended to be greater for C12 than for C11, although differences were small. Residual variances for calving intervals did not show a trend with time, although residual variation increased with SD of milk yield in both parities within each time period. When weighted by number of sires, estimates of resid-

TABLE 2. Average 4% FCM yield and calving intervals (CI) in first and second parities for each time period and within herd standard deviation class.¹

Period	Parity	FCM			CI		
		Low	Medium	High	Low	Medium	High
		(kg)			(d)		
1970 to 1975	1	6080	6981	7467	388	394	397
	2	6397	7347	7906	385	389	391
1977 to 1981	1	6648	7430	8104	387	392	398
	2	7017	7711	8239	388	390	394
1982 to 1985	1	6711	7610	8326	385	392	399
	2	7031	8005	8654	381	385	389

¹Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

ual variances for CI1 were 3651, 4322, and 4184 d² for the three time periods. Residual variation was consistently less for CI2 than for CI1. This might be expected since average CI2 were 4.6 d shorter than CI1. Nieuwhof et al. (20) reported average calving intervals were 2.5 d shorter in second than in first lactation grade Holsteins. Apparently, dairy farmers are prone to allow first-calf heifers to have more days open than older cows.

Heritabilities of first and second calving interval are in Table 4. Heritabilities were .05 or less in all analyses, which is consistent with

most genetic studies of calving interval (9, 17, 19) and days open (2, 12, 14, 27) using sire models. Heritability of calving interval was highest from 1982 to 1985 (.051 and .054) for low SD class, from 1977 to 1981 (.037 and .040) for medium SD class, and from 1970 to 1975 (.039 and .053) for high SD class. Within each time period, trends were not detected across SD classes. Dong and Van Vleck (8) reported a much larger heritability of first calving interval in New York Holstein herds using an animal model (average of .15 from four data sets). For this study, heritability of CI2 was

TABLE 3. Estimates of sire (σ_s^2) and residual (σ_e^2) components of variance (days²) for first and second calving intervals for each time period and within-herd standard deviation class.

Period	Component	Parity	Within-herd SD class ¹		
			Low	Medium	High
1970 to 1975	σ_s^2	1	21	21	41
		2	24	25	44
	σ_e^2	1	3048	3605	4168
		2	2780	3071	3345
1977 to 1981	σ_s^2	1	29	41	36
		2	23	41	37
	σ_e^2	1	3293	4043	4983
		2	3129	3511	3890
1982 to 1985	σ_s^2	1	36	26	34
		2	38	25	31
	σ_e^2	1	2748	3990	4807
		2	2742	2995	3335

¹Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

TABLE 4. Heritabilities of first and second calving intervals by time period and within-herd standard deviation class.¹

Period	Parity	Within-herd SD class ¹					
		Low		Medium		High	
		h ²	SE	h ²	SE	h ²	SE
1970 to 1975	1	.028	.012	.023	.007	.039	.017
	2	.034	.016	.032	.010	.053	.026
1977 to 1981	1	.035	.020	.037	.007	.029	.019
	2	.029	.026	.040	.009	.037	.007
1982 to 1985	1	.051	.030	.026	.009	.028	.004
	2	.054	.071	.033	.017	.038	.008

¹Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

larger than CI1 for eight of the nine subsets, which agreed with other reports of greater heritability of days open in later parities than for first parity (1, 2, 27).

Correlations Between Milk Yield and Calving Interval

Genetic correlations between FCM yield and calving interval by SD class for the three time periods are in Tables 5, 6, and 7. All but one genetic correlation of FCM and calving interval indicated an unfavorable relationship (the exception was $r_{FCM1:CI2}$ for the period 1977 to 1981). Genetic correlation coefficients ranged from $-.24$ to $.29$ for the low SD class, from $.27$ to $.58$ for the medium class, and from $.41$ to $.61$ for the high SD class. Figure 1 shows genetic correlations of FCM1 with CI1 by herd SD

class. The trend of increasingly larger correlations with herd SD class resulted from increases of genetic covariance relative to the variances for FCM1 and CI1. The antagonistic relationship between milk yield and calving interval in the two largest SD classes was greater than from most reports, although van Arendonk et al. (1) reported similar correlations between days open and milk yields in first (.64) and second (.65) lactations of Dutch Friesian cows. Genetic correlations between FCM1 and either calving interval were generally smaller for the latter time periods than for the period 1970 to 1975.

Genetic correlations between CI1 and FCM2 also were positive and increased with increasing SD in the first two periods (see Figure 2), indicating that cows with genetic merit for longest first calving interval were those with

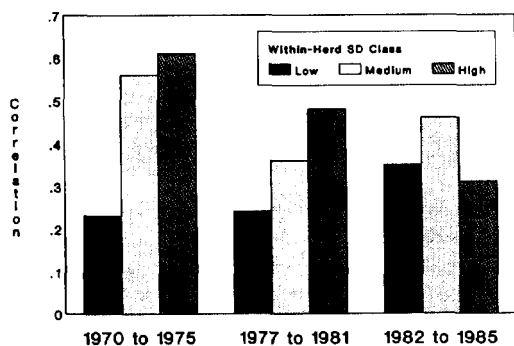


Figure 1. Estimates of genetic correlations between 4% FCM yield and first calving interval for each herd standard deviation class and time period.

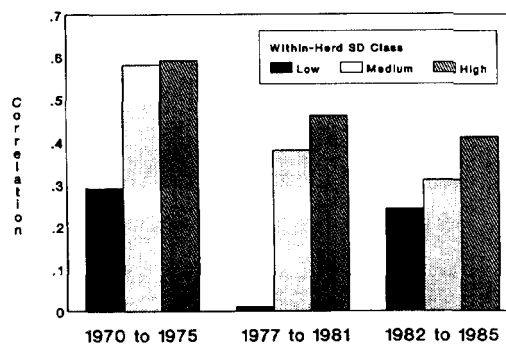


Figure 2. Estimates of genetic correlations between first calving interval and 4% FCM yield in second lactation for each herd standard deviation class and time period.

TABLE 5. Genetic and phenotypic correlations¹ between FCM yield and calving interval (CI) in first and second parities for each within herd standard deviation class in the period 1970 to 1975.

Within-herd SD class ²		FCM1	CI1	FCM2	CI2
Low	FCM129 (.14)	.88 (.02)	.09 (.14)
	CI1	.2423 (.17)	.33 (.28)
	FCM2	.42	.1909 (.19)
	CI2	.09	.07	.27	. . .
Medium	FCM158 (.07)	.97 (.00)	.51 (.08)
	CI1	.2256 (.06)	.45 (.09)
	FCM2	.55	.1855 (.08)
	CI2	.13	.07	.27	. . .
High	FCM159 (.09)	.99 (.00)	.61 (.10)
	CI1	.2361 (.10)	.62 (.20)
	FCM2	.61	.2165 (.10)
	CI2	.17	.12	.27	. . .

¹Genetic correlations are above diagonals and phenotypic correlations are below diagonals. Approximate standard errors are in parentheses (21).

²Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

highest genetic merit for yield in second lactation. For the latest period this correlation was highest for the medium SD class (.46). The genetic correlations between CI1 and FCM2 were smaller in the time periods 1977 to 1981 and 1982 to 1985 than in 1970 to 1975 for the medium and high SD classes. Estimates of these correlations are considerably higher than those of Dong and Van Vleck (8), who reported

a genetic correlation of .10 using an animal model. In that study, data were only from 15 herds in each of two replicates. They attributed differences in the genetic correlation between CI1 and subsequent milk yield from sire models vs. animal models to differences in heritabilities of calving interval from the models (.03 vs. .15). However, this requires that estimates of the genetic covariance be-

TABLE 6. Genetic and phenotypic correlations¹ between FCM yield and calving interval (CI) in first and second parities for each within-herd standard deviation class in the period 1977 to 1981.

Within-herd SD class ²		FCM1	CI1	FCM2	CI2
Low	FCM101 (.23)	.86 (.04)	-.24 (.27)
	CI1	.2324 (.26)	.50 (.38)
	FCM2	.40	.1301 (.23)
	CI2	.06	.17	.27	. . .
Medium	FCM138 (.07)	.88 (.01)	.44 (.07)
	CI1	.2236 (.08)	.54 (.10)
	FCM2	.51	.1645 (.08)
	CI2	.12	.17	.28	. . .
High	FCM146 (.11)	.86 (.01)	.47 (.06)
	CI1	.2148 (.12)	.58 (.17)
	FCM2	.57	.1360 (.05)
	CI2	.15	.10	.27	. . .

¹Genetic correlations are above diagonals and phenotypic correlations are below diagonals. Approximate standard errors are in parentheses (21).

²Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

TABLE 7. Genetic and phenotypic correlations¹ between FCM yield and calving interval (CI) in first and second parities for each within-herd standard deviation class in the period 1982 to 1985.

Within-herd SD class ²		FCM1	CI1	FCM2	CI2
Low	FCM124 (.24)	.75 (.09)	.13 (.37)
	CI1	.2435 (.28)	.39 (.53)
	FCM2	.42	.1320 (.46)
	CI2	.05	.07	.30	. . .
Medium	FCM131 (.10)	.93 (.01)	.27 (.13)
	CI1	.2646 (.11)	.53 (.21)
	FCM2	.52	.1637 (.14)
	CI2	.12	.07	.31	. . .
High	FCM141 (.05)	.84 (.01)	.44 (.06)
	CI1	.2331 (.07)	.63 (.07)
	FCM2	.59	.1752 (.06)
	CI2	.16	.10	.30	. . .

¹Genetic correlations are above diagonals and phenotypic correlations are below diagonals. Approximate standard errors are in parentheses (21).

²Standard deviation of 305-d mature equivalent milk yield: low, less than 1018 kg; medium, 1131 to 1357 kg; high, greater than 1471 kg.

tween calving interval and milk yield be the same for both models.

Genetic correlations between FCM2 and CI2 were near zero for the low herd SD classification, except in the last time period, and increased to .65 for the high SD class. For the low SD class, FCM2 and CI2 were correlated genetically less than FCM1 and CI1. However, correlations were slightly larger between FCM2 and CI2 in the medium and high SD herd classes than between FCM1 and CI1. Positive (unfavorable) genetic correlations in first and second parities signify pleiotropic effects by the genes controlling physiological pathways of milk secretion on the mechanisms of fertility and reproduction, although the specific mechanisms are unknown (16). Berger et al. (2) reported a smaller correlation between days open and 305-d milk yields in second and later parities than in first lactation.

Genetic correlations between CI1 and CI2 ranged from .33 to .50 in the low herd SD class, from .45 to .53 in the medium herd SD class, and from .58 to .63 for the high herd SD class (Tables 5, 6, and 7). Genetic correlations are similar to those reported by Strandberg and Danell (27). Reproductive performance in CI2 appears to be influenced by many of the same pleiotropic pathways that affect CI1. Sire components of variance were similar for CI1 and CI2.

Phenotypic correlations between FCM yields and calving intervals also are in Tables 5, 6, and 7. Phenotypic correlations of FCM1 with CI1 or CI2 were smaller (.05 to .26) than genetic correlations. Correlations between FCM1 and CI2 were smaller than for FCM1 and CI1 in each SD class and remained uniform with time for each SD herd class. Correlations between FCM1 and CI2 were smallest in the low SD class. Phenotypic correlations between CI1 and FCM2 were less than .21 and did not vary with SD class or time. Dong and Van Vleck (8) obtained phenotypic correlations averaging .16 between CI1 and FCM2. Phenotypic correlations between FCM2 and CI2 were slightly larger than those between FCM1 and CI1 in all SD classes and time periods.

Phenotypic correlations between CI1 and CI2 were slightly positive, .07 to .17, which agreed with results by Strandberg and Danell (27) and Jansen et al. (14). No trend was detected across time or SD class.

Correlated Response in Calving Interval

Using estimates of the parameters from a joint analysis of all SD classes in the period 1981 to 1985, the expected correlated response in calving interval from selection for FCM yield was calculated. The genetic correlation

between FCM1 and CI1 was .53, and the heritabilities and phenotypic variances were .18 and .03, and 1,700,000 kg² and 4500 d², respectively, for FCM1 and CI1. A 100-kg increase of genetic merit for 4% FCM would genetically lengthen calving interval by about 1 d. These results are similar to the conclusion of Seykora and McDaniel (23) that a 1000-kg response in milk yield would increase days open by 5 to 10 d.

CONCLUSIONS

The genetic variance of calving interval was small and was greatest in herds with most variability for milk yield, except in the period 1982 to 1985. This result agreed with most studies of reproductive traits. Low heritability and genetic variances of calving interval in this study support the idea that genetic selection to reduce calving interval is probably unwarranted. As reported by Blake (3), increased economic returns from direct responses in milk yield dominate the relatively small cost of correlated increases in calving interval.

Fat-corrected milk yield and calving interval were unfavorably related and more so in herds with greatest variability in yield. Genetic correlations were greater than phenotypic correlations in all herd SD classes. Trends associated with time were not detected for genetic and residual variances or heritability of calving interval, although genetic correlations with FCM yield were smaller from 1977 to 1985 compared with 1970 to 1975.

The expected correlated increase in calving interval was about 1 d/100 kg genetic increase in FCM, which is similar to previous estimates of correlated change in days open (12, 23). Because yield of milk and its components are the most economically important traits in a selection program, coupled with low heritability and small genetic variance of calving interval, there is no immediate incentive to genetically manage calving interval because selection intensity for milk yield would be reduced.

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