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Genetic Parameters and Responses of Linear Type, Yield Traits, and Somatic Cell Scores to Divergent Selection for Predicted Transmitting Ability for Type in Holsteins[1]

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ABSTRACT

The objective was to examine the direct and correlated responses of linear type, yield traits, and somatic cell scores (SCS) to divergent selection for predicted transmitting ability for type (PTAT) in Holsteins, while maintaining selection for yield traits across lines. For four generations, one-half of the University of Nebraska research Holstein herd was bred to Holstein sires with PTAT > 1.50 and the other half to sires with PTAT < 1.25, with nearly equal predicted transmitting abilities for yield traits for both groups. Estimates of genetic and residual correlations and heritabilities were obtained from REML estimates of (co)variance components. Model for type traits included fixed effect of date cows were classified, effects of age in days at freshening, and stage of lactation at classification. Year-season when cows freshened was fixed effect in model for yield and SCS. Animal genetic and residual effects were random. Final score, milk, fat, and protein yields, and SCS had heritability estimates of 0.38, 0.13, 0.22, 0.09, and 0.38, respectively. Heritability estimates for type traits ranged from 0.04 to 0.52. Estimates of genetic correlations of final score with SCS and milk, fat, and protein yields were –0.64, 0.01, –0.18, and 0.06, respectively. Estimates of genetic correlations among linear type traits ranged from –0.77 to 1.00. Means of estimated breeding values for final score, stature, strength, body depth, fore udder attachment, rear udder height and width, udder cleft, udder depth, and front teat placement were significantly different between lines in the third generation. Milk, fat, and protein yields were not significantly different between lines in third generation, whereas SCS was significantly different. Estimate of genetic correlation between final score and SCS suggest that selection on PTAT would result in a change for SCS. In this study, divergent selection on PTAT of sires had a significant effect on udder and body traits, but little or no effect on feet and leg traits.
(**Key words:** milk yield, type score, correlated response, dairy cattle)

Abbreviation key: PTAT = predicted transmitting ability for type.

INTRODUCTION

Dairy producers select for yield, as highest producing cows are usually the most profitable. Funk (1993) reported that average milk production increased 3000 kg per cow from 1960 to 1990. Selection on yield traits alone could have a negative effect on secondary traits (Funk, 1993). Profitability depends on all economically important traits, whether yield or nonyield (Funk, 1993).

Direct and correlated responses from designed selection experiments for milk yield have been reported in previous studies (Legates and Myers, 1972; Hansen et al., 1979; Meland et al., 1982; Wautlet et al., 1990; Boettcher et al., 1993). Legates and Myers, (1972) reported an average response of 121 kg of milk per year. The experimental herd at the University of Minnesota had a genetic trend of 126 kg per year from 1967 to 1988 (Boettcher et al., 1993). Hansen et al. (1979) found that the selected lines had significantly higher incidences of problems associated with mammary and digestive health. Wautlet et al. (1990) reported no significant difference between the lines for udder edema, dystocia, and retained placenta in first-lactation cows. The regional project NC-2 also measured direct and correlated responses to single-trait selection for milk yield at various research stations (Kelm et al., 2000). The NC-2 project found selection for milk yield was effective for increasing milk production in selected lines compared with control lines (Kelm et al., 2000). The project also reported that selection for milk yield caused delayed estrus and increased health problems and costs;

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however, there was an increase of net income per lactation in the NC-2 project herds (Kelm et al., 2000).

Extreme emphasis on selection for yield may have a negative effect on linear type traits that contributes to overall fitness. Many AI and breed organizations maintain linear classification programs to measure and study these traits. The primary goal is to identify and emphasize traits associated with longevity and to select profitable and functional cows (Short and Lawlor, 1992). Many studies have reported on relationships between yield and linear type traits (Thompson et al., 1981; Foster et al., 1989; VanRaden et al., 1990; Short et al., 1991; Short and Lawlor, 1992; Misztal et al., 1992). Short and Lawlor (1992), using a sire model, reported a genetic correlation of 0.06 for milk yield and final score compared with 0.16 reported by Misztal et al. (1992) with an animal model. Traits associated with body size have a positive relationship with milk yield (Foster et al., 1989; Short and Lawlor, 1992; Misztal et al., 1992). Fore udder attachment, udder cleft, and udder depth have a negative association with milk yield, whereas rear udder height and rear udder width have a small positive relationship (Foster et al., 1989; Short and Lawlor, 1992; Misztal et al., 1992). Udder traits are also correlated with SCS (Monardes et al., 1990; Rogers et al., 1991; Welper and Freeman, 1992; Schultz et al., 1993; Boettcher et al., 1998). Boettcher et al. (1993) reported that cows selected for milk yield in the University of Minnesota experimental herd had significantly higher EBV for stature, body depth, angularity, rump width, leg set, rear-udder height and width, udder support, and udder depth than a control line. The NC-2 project reported that linear type traits in selected lines for increased milk yield did not drastically deteriorate compared with control lines; however, selected lines had cows with udders that were wider, longer, and slightly deeper (Kelm et al., 2000).

The objectives of this study were to estimate genetic parameters and responses (direct and correlated) of linear type, yield traits, and SCS to divergent selection for predicted transmitting ability for type (**PTAT**) of sires, while maintaining selection on yield traits across lines.

MATERIALS AND METHODS

A selection experiment was initiated in 1986 in the University of Nebraska dairy research herd to study effects of divergent selection for PTAT. The herd was split into two lines, designated as high and low lines. Holstein cows were assigned randomly to the lines. Cows in both lines were housed and managed in the same facilities. Lactating cows were fed a TMR based on nutritional requirements needed for yield, BW, and stage of lactation.

Selection was carried out on AI sires for PTAT. Sires selected for the high line had a PTAT greater than +1.50, and sires selected for the low line had a PTAT less than +1.25. An attempt was made to maintain production across the lines in order to study the response to selection for selecting solely on PTAT. Sires selected for both lines had to have a PTA greater than +860 kg for milk, greater than +20 kg for fat, and greater than +30 kg for protein. Sires used for a particular line were randomly mated to cows in that line. Over the course of the study, the genetic base for evaluations of registered Holstein cows changed. This did not change the selection criteria for type and yield traits, because of the difficulty of selecting for AI sires with low PTAT. Table 1 shows that the PTAT means of selected sires for the low line were higher in the later generations of selection. Previous selected sires were reevaluated each year to determine whether sires still met the selection criteria. If the sire of a particular line did not meet the criteria, they were discarded from the experiment. A total of 107 different sires were used in the high line, and 94 different sires were used in the low line.

Records for 783 cows in the research herd from 1987 to 1999 were obtained from Dairy Records Management Systems (Raleigh, NC). Milk, fat, and protein yields were 305-d, 2× milking, mature equivalent. Protein data were not available for some cows at the beginning of the study. To calculate 305-d mature equivalent for yields, a cow needs to have two valid milk tests and 60 DIM. Freshing cows with fewer than 60 DIM were removed from the analysis but were included in the pedigree. There were about the same number of records removed in each line—34 in the high line and 38 in the low line. Only first-lactation records were used for this study, because of different culling criteria for the two lines following the first lactation. After edits, there were 711 records for milk and fat yield and 561 records for protein yield. Data on SCS for 1992 to 1999 were obtained from the Animal Improvement Programs Laboratory of ARS-USDA, and records were not available for cows in the earlier part of the study. The scores were preadjusted for age, season of calving, and length of lactation, with factors developed by Wiggans and Shook (1987). As with lactation records, only first lactation SCS (n = 368) were used in the study. Data on final score and 16 linear type traits (scored on a 50-point scale) from 1989 to 1999 were obtained from the official evaluation program of the Holstein Association. At the beginning of the study, evaluators were only available to score cows in both lines once a year. This caused difficulty in getting data on transition or culled cows when the herd was evaluated in a particular year. Later

Table 1. Weighted[1] average predicted transmitting ability for type (PTAT), milk (PTAM), fat (PTAF), and protein (PTAP) of sires used in high and low lines by generation as of 1999.

	PTAT		PTAM		PTAF		PTAP	
Generation	High	Low	High	Low	High	Low	High	Low
0	–0.62	–0.47	–155.55	–78.36	–14.62	–11.41	–8.64	–4.56
1	–0.13	–1.04	687.30	714.77	15.64	25.06	16.83	22.18
2	0.52	–0.53	891.59	1042.78	26.80	38.76	26.55	32.12
3	1.06	–0.11	1132.84	1201.15	38.24	39.88	36.90	36.44

[1]Weighted by the number of progeny born in a particular generation.

in the study, evaluators were available to score cows in the herd every 8 mo. Evaluators were not told which cows were in a particular line. After edits, 511 linear type records were available for analysis.

Analysis was done using REML with a derivative-free algorithm developed by Boldman et al. (1995) to estimate (co)variance components using an animal model. Models for yield and SCS included year-season when a cow freshened as a fixed effect. Four seasons of calving were defined: December to February, March to May, June to August, and September to November. Models for linear type traits included date of classification as a fixed effect and effects of age at freshening and stage of lactation at classification (Funk et al., 1991). The random effects for both models included animal genetic and residual with variances G ⊗ A and E ⊗ I, respectively; G and E are (co)variance matrices for the animal and residual effects, respectively; and A is the numerator relationship matrix among animals. Convergence was assumed when the simplex variance was less than 1×10^{-6}. The analysis was restarted after the first convergence until the minimum –2 log-likehood value was constant. The delta method was used to find approximate standard errors for heritabilities and genetic correlations with balanced data (Searle et al., 1992).

For each individual cow within the herd, EBV were obtained from single-trait analyses after estimating genetic and residual variances. The EBV for lines were averaged and plotted by generation to identify trends for each trait. The mean difference for EBV between lines was tested by using a Student's t test of significance only at generation 3 because of the small number of fourth-generation cows with a first lactation.

RESULTS AND DISCUSSION

Genetic Parameters

Estimates of heritabilities, genetic variances, and residual variances for final score, yield traits, and SCS are in Table 2. Final score had a heritability estimate of 0.38 (0.09), which was larger than the estimate by Short and Lawler et al. (1992) but was comparable to the estimate reported by Misztal et al. (1992). Heritabilities for milk, fat, and protein yields were 0.13 (0.07), 0.22 (0.08), and 0.09 (0.09), respectively. The small sample size could explain the small estimates of heritabilities for milk and protein, which are not significantly different from zero at $P > 0.05$. These estimates within this herd were considerably smaller than estimates reported in previous studies with more lactation records across different herds (Van Vleck and Dong, 1988; Schultz et al., 1990; Short and Lawlor, 1992; Misztal et al., 1992; Welper and Freeman, 1992). Heritability of SCS (0.38) was larger than estimates from previous studies (Schultz et al., 1990; Rogers et al., 1991; Welper and Freeman, 1992; Schultz et al., 1993; Boettcher et al., 1998).

Estimates of genetic and residual correlations among final score, the yield traits, and SCS within the herd are in Table 3. Final score had low estimates of genetic

Table 2. Estimates of heritability (h^2) with standard errors (SE), genetic variance (σ_a^2), and residual variance (σ_e^2) for final score, first lactation yields, and SCS.

Trait	h^2	SE	σ_a^2	σ_e^2
Final score	0.38	0.09	17.88	29.08
Milk[1]	0.13	0.07	33.94	225.11
Fat[2]	0.22	0.08	75.35	260.61
Protein[2]	0.09	0.09	23.29	236.00
SCS	0.38	0.12	1.32	2.19

[1]Genetic and residual variances divided by 10^4.

[2]Genetic and residual variances divided by 10.

Table 3. Estimates[1] of genetic and residual correlations with standard errors[2] among final score, first lactation yields, and SCS.

Trait	Final score	Milk	Fat	Protein	SCS
Final score		0.01 (0.28)	–0.18 (0.22)	0.06 (0.30)	–0.64 (0.24)
Milk	0.22 (0.09)		0.36 (0.23)	0.34 (0.21)	–0.21 (0.60)
Fat	0.23 (0.10)	0.87 (0.03)		0.56 (0.29)	0.43 (0.40)
Protein	0.28 (0.10)	0.83 (0.04)	0.82 (0.03)		0.11 (0.53)
SCS	0.11 (0.19)	–0.26 (0.11)	–0.41 (0.12)	–0.30 (0.11)	

[1]Genetic above the diagonal and residual below the diagonal.
[2]SE in parentheses.

correlations of 0.01, –0.18, and 0.06 with milk, fat, and protein yields, respectively. These estimates were lower than estimates reported by Misztal et al. (1992). However, estimates of genetic correlation between final score and milk yield were comparable to estimates by Short and Lawlor (1992). Estimate of genetic correlation between final score and SCS was –0.64. This estimate indicates that selection for PTAT had a favorable effect on SCS within the herd. Rogers et al. (1991) reported a smaller genetic correlation between SCC and final score.

Estimates of heritability, genetic variance, and residual variance for the linear type traits within the herd are in Table 4. The heritability estimates ranged from 0.04 for foot angle to 0.52 for front teat placement. Type traits associated with body size, udder, and teats had higher heritabilities than estimates found in previous studies (VanRaden et al., 1990; Short et al., 1991; Short and Lawlor, 1992; Misztal et al., 1992). Heritability estimates for feet and leg traits were smaller than estimates in earlier studies (VanRaden et al., 1990; Short et al., 1991; Short and Lawlor, 1992; Misztal et al., 1992).

Estimates of genetic and residual correlations among linear type traits are in Table 5. Traits associated with body characteristics (stature, strength, body depth, and thurl width) had high positive genetic correlations among these traits. Dairy form had negative estimates of genetic correlations with body traits, except for stature (0.15) and rump angle (0.17). The only positive estimate of genetic correlation among feet and leg traits was between rear legs-rear view and foot angle, whereas the other estimates were negatively correlated. Udder and teat traits were positively genetically correlated with each other except for teat length. Teat length had negative genetic correlations with other udder traits that ranged from –0.07 with udder cleft to

Table 4. Estimates of heritability (h^2) with standard errors (SE), genetic variance (σ_a^2), and residual variance (σ_e^2) for linear type traits.

Trait	Direction[1]	h^2	SE	σ_a^2	σ_e^2
Stature	Tall	0.47	0.09	25.42	28.92
Strength	Strong	0.41	0.09	15.77	22.81
Body depth	Deep	0.36	0.09	12.92	22.83
Dairy form	Open ribbed	0.36	0.09	18.55	33.60
Rump angle	Sloped	0.36	0.09	29.28	51.88
Thurl width	Wide	0.30	0.09	11.68	27.41
Rear legs-rear view	No toe out	0.12	0.08	7.76	56.32
Rear legs-side view	Sickled	0.11	0.08	6.81	52.91
Foot angle	Steep	0.04	0.07	2.54	64.57
Fore udder attachment	Strong	0.37	0.09	20.81	35.97
Rear udder height	High	0.32	0.09	18.14	38.38
Rear udder width	Wide	0.30	0.08	15.83	36.80
Udder cleft	Strong	0.29	0.09	17.92	43.20
Udder depth	Shallow	0.23	0.08	15.01	48.91
Front teat placement	Close	0.52	0.09	31.11	29.04
Teat length	Long	0.29	0.10	17.81	42.87

[1]Direction of the largest score (i.e., 50 = tall).

Table 5. Estimates[1] of genetic and residual correlations with standard errors[2] among final score.

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 Final score		0.71	0.57	0.79	.38	0.45	0.62	0.21	–0.35	–0.15	0.85	0.81	0.88	0.66	0.76	0.84	–0.15
		(0.13)	(0.15)	(0.14)	(0.17)	(0.17)	(0.17)	(0.29)	(0.31)	(0.46)	(0.09)	(0.11)	(0.12)	(0.14)	(0.15)	(0.09)	(0.21)
2 Stature	0.13		0.68	0.85	0.15	0.01	0.69	–0.01	0.13	–0.24	0.37	0.39	0.55	0.42	0.78	0.38	–0.03
	(0.10)		(0.10)	(0.07)	(0.18)	(0.18)	(0.12)	(0.28)	(0.30)	(0.52)	(0.17)	(0.18)	(0.17)	(0.19)	(0.20)	(0.15)	(0.20)
3 Strength	0.17	0.60		0.96	–0.39	–0.34	1.00	0.40	–0.18	0.17	0.43	0.29	0.51	0.23	0.62	0.17	–0.10
	(0.09)	(0.07)		(0.03)	(0.18)	(0.18)	(0.11)	(0.29)	(0.29)	(0.45)	(0.17)	(0.18)	(0.16)	(0.20)	(0.22)	(0.16)	(0.21)
4 Body depth	0.16	0.60	0.77		–0.07	–0.25	0.91	0.38	–0.25	0.10	0.60	0.48	0.60	0.43	0.75	0.41	–0.20
	(0.09)	(0.06)	(0.04)		(0.20)	(0.19)	(0.10)	(0.31)	(0.31)	(0.48)	(0.18)	(0.19)	(0.17)	(0.21)	(0.25)	(0.17)	(0.22)
5 Dairy form	0.26	0.23	0.09	0.21		0.17	–0.38	–0.49	0.28	–0.57	0.08	0.62	0.55	0.58	–0.09	0.40	–0.15
	(0.09)	(0.10)	(0.10)	(0.09)		(0.19)	(0.23)	(0.35)	(0.30)	(0.55)	(0.20)	(0.16)	(0.17)	(0.19)	(0.23)	(0.15)	(0.22)
6 Rump angle	–0.09	0.12	0.04	0.02	0.03		–0.26	–0.73	0.20	–0.86	–0.48	–0.50	–0.29	–0.20	–0.43	–0.19	–0.39
	(0.09)	(0.10)	(0.10)	(0.09)	(0.10)		(0.21)	(0.21)	(0.33)	(0.54)	(0.17)	(0.20)	(0.20)	(0.21)	(0.20)	(0.17)	(0.21)
7 Thurl width	0.10	0.41	0.47	0.48	0.20	–0.13		0.98	–0.38	0.46	0.48	0.26	0.35	0.09	0.55	0.26	–0.21
	(0.07)	(0.08)	(0.06)	(0.07)	(0.09)	(0.09)		(0.39)	(0.32)	(0.57)	(0.20)	(0.21)	(0.20)	(0.23)	(0.26)	(0.18)	(0.24)
8 Rear legs-rear view	0.30	0.17	0.20	0.02	0.16	0.20	0.02		–0.58	0.43	0.61	0.61	0.65	0.20	0.18	0.05	0.35
	(0.08)	(0.09)	(0.08)	(0.08)	(0.09)	(0.10)	(0.08)		(0.48)	(0.68)	(0.35)	(0.31)	(0.31)	(0.35)	(0.36)	(0.28)	(0.33)
9 Rear legs-side view	0.05	–0.06	–0.02	0.01	0.07	–0.04	0.04	–0.05		–0.77	–0.37	–0.29	–0.17	–0.73	–0.34	–0.58	–0.01
	(0.08)	(0.30)	(0.09)	(0.08)	(0.08)	(0.08)	(0.08)	(0.07)		(0.77)	(0.29)	(0.32)	(0.33)	(0.38)	(0.35)	(0.39)	(0.37)
10 Foot angle	0.28	0.14	0.18	0.10	–0.01	0.07	0.03	0.37	–0.16		0.35	0.27	0.18	0.00	–0.13	0.29	0.33
	(0.08)	(0.09)	(0.08)	(0.08)	(0.08)	(0.08)	(0.07)	(0.06)	(0.07)		(0.57)	(0.54)	(0.53)	(0.53)	(0.54)	(0.50)	(0.63)
11 Fore udder attachment	0.84	0.10	0.04	–0.06	0.05	–0.01	–0.01	0.09	–0.04	0.16		0.58	0.74	0.39	0.89	0.69	–0.08
	(0.07)	(0.10)	(0.09)	(0.09)	(0.09)	(0.09)	(0.09)	(0.08)	(0.08)	(0.08)		(0.14)	(0.14)	(0.18)	(0.13)	(0.12)	(0.21)
12 Rear udder height	0.38	0.10	0.09	0.03	0.10	0.10	0.12	0.09	–0.06	0.16	0.38		0.86	0.60	0.37	0.52	–0.23
	(0.07)	(0.10)	(0.09)	(0.09)	(0.09)	(0.09)	(0.09)	(0.10)	(0.08)	(0.08)	(0.08)		(0.08)	(0.19)	(0.21)	(0.15)	(0.23)
13 Rear udder width	0.36	0.09	0.20	0.20	0.12	0.01	0.28	0.11	–0.04	0.17	0.26	0.65		0.62	0.48	0.52	–0.08
	(0.07)	(0.09)	(0.09)	(0.08)	(0.09)	(0.09)	(0.08)	(0.09)	(0.08)	(0.07)	(0.08)	(0.05)		(0.20)	(0.24)	(0.16)	(0.23)
14 Udder cleft	0.51	–0.12	–0.05	–0.09	0.02	–0.11	0.04	0.04	0.11	0.16	0.32	0.09	0.08		0.22	0.86	–0.07
	(0.07)	(0.10)	(0.09)	(0.09)	(0.09)	(0.09)	(0.09)	(0.08)	(0.08)	(0.08)	(0.08)	(0.09)	(0.08)		(0.22)	(0.12)	(0.24)
15 Udder depth	0.41	–0.19	–0.20	–0.24	–0.08	–0.12	–0.13	0.10	–0.01	0.18	0.50	0.18	0.04	0.47		0.75	–0.11
	(0.07)	(0.09)	(0.09)	(0.08)	(0.09)	(0.08)	(0.08)	(0.08)	(0.08)	(0.07)	(0.06)	(0.08)	(0.08)	(0.07)		(0.16)	(0.24)
16 Front teat placement	0.18	–0.12	0.02	–0.10	–0.03	0.03	0.05	0.01	0.07	0.11	0.27	0.08	0.02	0.10	0.17		–0.46
	(0.10)	(0.12)	(0.11)	(0.11)	(0.11)	(0.10)	(0.10)	(0.10)	(0.09)	(0.09)	(0.09)	(0.10)	(0.10)	(0.10)	(0.09)		(0.16)
17 Teat length	0.01	0.07	0.19	0.20	0.05	0.20	0.18	–0.08	–0.05	0.03	–0.06	0.16	0.20	–0.02	–0.08	–0.16	
	(0.10)	(0.10)	(0.10)	(0.09)	(0.10)	(0.10)	(0.09)	(0.08)	(0.08)	(0.08)	(0.09)	(0.09)	(0.09)	(0.09)	(0.09)	(0.10)	

[1]Genetic above the diagonal and residual below the diagonal.

[2]SE in parentheses.

–0.46 with front teat placement, indicating that shorter teats were associated with tighter attachments and closer teats. Final score was positively genetically correlated with body and udder traits with estimates that ranged from 0.38 for dairy form to 0.88 for rear udder width. These estimates indicate that selection for final score would increase body size and strengthen the overall composition of the udder in the herd. The estimates of genetic correlations among the linear type traits within the herd were similar to estimates reported in previous studies (VanRaden et al., 1990; Short et al., 1991; Short and Lawlor, 1992; Misztal et al., 1992).

Estimates of genetic and residual correlations among linear type traits, yield traits, and SCS within the herd are in Table 6. Estimates of genetic correlations between traits associated with body size and milk yield ranged from –0.10 (strength) to 0.91 (dairy form). Stature, strength, body depth, and thurl width had similar estimates of genetic correlations with milk yield compared to estimates reported by Short and Lawlor (1992) and Misztal et al. (1992). Dairy form and rump angle had larger estimates with milk yield compared to previous studies (Short and Lawlor, 1992; Misztal et al., 1992). Estimates of genetic correlations of feet and leg traits with milk yield ranged from 0.07 (rear legs-rear view) to 0.83 (rear legs-side view) and were considerably higher than earlier estimates (Misztal et al., 1992; Short and Lawlor, 1992). Rear udder height, rear udder width, and front teat placement had small positive genetic correlations. Negative estimates of genetic correlations were found between fore udder attachment, udder cleft, udder depth, teat length, and milk yield. The estimates of genetic correlations between udder and yield traits were generally similar to estimates reported from earlier studies (Misztal et al., 1992; Short and Lawlor, 1992).

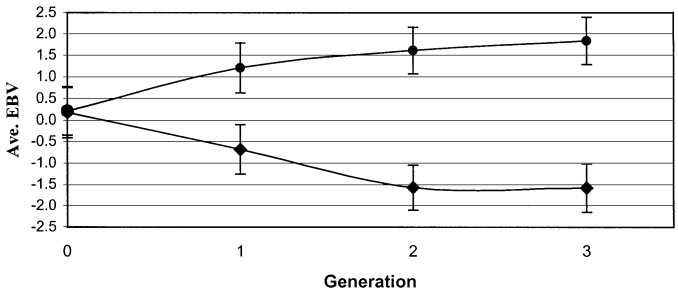

Figure 1. Average EBV for final score for cows in the high (●) and low (◆) lines by generation.

Estimates of genetic correlations between linear type traits and SCS in Table 6 were negative except for rump angle. Estimates between body size, feet, and leg traits and SCS ranged from –0.61 (rear legs-side view and rear legs-rear view) to 0.24 (rump angle). Negative correlations between udder traits and SCS ranged from –0.35 (udder cleft) to –0.16 (rear udder height). Because there were a small number of cows with SCS records, the standard errors for estimates of genetic correlations were large. These results were similar to those reported in earlier studies (Monardes et al., 1990; Rogers et al., 1991; Boettcher et al., 1993).

Response to Selection

Mean EBV for final score of cows in the high and low lines by generation are plotted in Figure 1. The graph clearly shows divergence between the lines. There was a steady increase of cow EBV in the high line, and cows

Table 6. Estimates of genetic and residual correlations with standard errors[1] among linear type traits, first lactation yields, and SCS.

	Genetic correlations				Residual correlations			
Trait	Milk	Fat	Protein	SCS	Milk	Fat	Protein	SCS
Stature	0.21 (0.28)	0.01 (0.21)	0.48 (0.29)	–0.27 (0.26)	–0.02 (0.10)	0.28 (0.10)	0.07 (0.11)	0.14 (0.18)
Strength	–0.10 (0.29)	–0.17 (0.21)	0.03 (0.32)	–0.21 (0.26)	0.13 (0.09)	0.19 (0.10)	0.12 (0.10)	0.20 (0.12)
Body depth	0.03 (0.32)	0.01 (0.23)	0.20 (0.33)	–0.30 (0.23)	0.15 (0.09)	0.21 (0.09)	0.14 (0.10)	0.24 (0.17)
Dairy form	0.91 (0.22)	0.60 (0.20)	0.91 (0.26)	–0.23 (0.27)	0.22 (0.08)	0.25 (0.09)	0.14 (0.10)	0.16 (0.17)
Rump angle	0.62 (0.27)	0.49 (0.21)	0.57 (0.32)	0.24 (0.28)	–0.03 (0.09)	–0.04 (0.10)	–0.03 (0.10)	–0.11 (0.17)
Thurl width	0.05 (0.34)	–0.17 (0.23)	0.02 (0.35)	–0.07 (0.35)	0.13 (0.08)	0.16 (0.09)	0.13 (0.09)	0.19 (0.14)
Rear legs-rear view	0.07 (0.49)	0.26 (0.34)	0.30 (0.54)	–0.61 (0.61)	0.05 (0.08)	0.02 (0.09)	0.04 (0.08)	0.01 (0.14)
Rear legs-side view	0.83 (0.52)	0.42 (0.51)	0.94 (0.47)	–0.61 (0.53)	–0.04 (0.08)	0.06 (0.08)	–0.09 (0.09)	0.02 (0.13)
Foot angle	0.39 (0.50)	–0.66 (0.58)	0.00 (0.67)	–0.48 (0.56)	–0.11 (0.09)	0.15 (0.08)	0.18 (0.08)	0.21 (0.14)
Fore udder attachment	–0.45 (0.27)	–0.41 (0.22)	–0.28 (0.29)	–0.24 (0.24)	0.11 (0.09)	0.20 (0.10)	0.12 (0.10)	–0.10 (0.17)
Rear udder height	0.16 (0.30)	–0.09 (0.23)	0.32 (0.30)	–0.16 (0.28)	0.12 (0.08)	0.18 (0.09)	0.19 (0.09)	0.31 (0.16)
Rear udder width	0.12 (0.31)	–0.17 (0.25)	0.20 (0.30)	–0.32 (0.32)	0.25 (0.08)	0.30 (0.09)	0.25 (0.09)	0.34 (0.14)
Udder cleft	–0.10 (0.33)	–0.22 (0.24)	–0.41 (0.37)	–0.35 (0.25)	0.03 (0.09)	0.01 (0.10)	0.04 (0.09)	0.01 (0.17)
Udder depth	–0.65 (0.31)	–0.51 (0.24)	–0.44 (0.33)	–0.20 (0.25)	–0.11 (0.08)	–0.09 (0.09)	–0.12 (0.09)	–0.20 (0.16)
Front teat placement	0.09 (0.26)	0.10 (0.19)	0.22 (0.28)	–0.19 (0.24)	0.01 (0.10)	0.03 (0.11)	–0.07 (0.11)	0.22 (0.19)
Teat length	–0.11 (0.35)	–0.38 (0.25)	0.02 (0.36)	–0.24 (0.33)	0.03 (0.09)	0.02 (0.10)	0.03 (0.10)	0.18 (0.16)

[1]SE in parentheses.

Table 7. EBV of cows within the herd for final score by generation and selection line.

	High line		Low line		Difference
Generation	n	Mean EBV	n	Mean EBV	Mean EBV
0	59	0.21	37	0.17	0.03
1	65	1.21	83	–0.68	1.89[1]
2	59	1.62	94	–1.57	3.19[1]
3	56	1.84	58	–1.58	3.42[1]

[1]$P < 0.01$.

in the low line had a decrease of EBV. Rate of response in the low line seemed to decrease from generation 2 to 3 compared with the rate from the base to second generation. Table 7 lists mean and differences of EBV by generation and line for final score. Lines at generation 3 were significantly ($P < 0.01$) different (EBV, 3.42). The results show that sires selected for PTAT did change EBV for final score in this herd.

Table 8 lists mean and differences of EBV for linear type traits of the lines at generation 3. Differences between lines for average EBV for the linear type traits are correlated responses from selecting for or against PTAT. Overall, the lines were significantly different for most of the traits in generation 3. For traits associated with body size, only stature, strength, and body depth were significantly ($P < 0.05$) different between lines. The differences in mean EBV for the other body traits were small. Feet and legs make up only 15% of final score, and estimates of heritabilities were low, which could explain the small and not significant difference of mean EBV between lines for feet and leg traits. The lines had significantly ($P < 0.01$) different mean EBV for fore udder attachment, rear udder height and width, udder cleft, udder depth, and front teat placement. Selection for PTAT did improve the overall udder composition as expected because udder traits make up 40% of final score.

Table 9 shows mean and differences of EBV for yield traits and SCS of the lines at generation 3. The line differences can be interpreted as a combination of correlated responses to divergent selection for final score and response to selection for yield in both lines. Cows in the low line did have higher average EBV for yield, but the mean EBV were not significantly different between the lines for the three yield traits. The high line had significantly ($P < 0.05$) lower EBV for SCS than the low line. The response of SCS indicates that selection for PTAT had a favorable effect on SCS.

CONCLUSIONS

Within the herd, genetic correlations between final score and yield traits were small, whereas final score was genetically associated with SCS. The genetic rela-

Table 8. EBV for linear type traits at generation 3 by selection line.

	High line	Low line	Difference
Trait	Mean EBV	Mean EBV	Mean EBV
Stature	0.17	–1.31	1.48[1]
Strength	0.55	–0.97	1.52[1]
Body depth	0.39	–0.93	1.32[1]
Dairy form	0.36	0.30	0.06
Rump angle	–1.01	0.14	–1.15
Thurl width	0.47	–0.52	0.99
Rear legs-side view	–0.19	0.14	–0.33
Rear legs-rear view	0.54	–0.19	0.73
Foot angle	0.15	–0.10	0.25
Fore udder attachment	1.57	–1.55	3.12[2]
Rear udder height	1.37	–0.42	1.79[2]
Rear udder width	1.39	–0.71	2.10[2]
Udder cleft	1.39	–0.66	2.05[2]
Udder depth	1.09	–1.47	2.56[2]
Front teat placement	2.14	–1.69	3.83[2]
Teat length	–0.01	–0.23	0.22

[1]$P < 0.05$.

[2]$P < 0.01$.

Table 9. EBV for yield traits and SCS at generation 3 by selection line.

Trait	High line Mean EBV	Low line Mean EBV	Difference Mean EBV
Milk yield, kg	15.80	93.48	–77.68
Fat yield, kg	–1.14	6.38	–7.52
Protein yield, kg	0.63	1.68	–1.05
SCS	–0.22	0.21	–0.43[1]

[1]$P < 0.05$.

tionship between body characteristics and milk yield was small, except for dairy form and rump angle. Traits related to udder attachment had a negative genetic relationship with milk yield, whereas udder capacity traits had a positive relationship with milk yield. The estimates suggest that selection for milk yield in the herd increased udder capacity, while causing the fore attachment and cleft to weaken. All udder traits had negative estimates of genetic correlations with SCS. These estimates indicate that selecting for higher udders with tighter attachments and closer teats would be favorable for reducing SCS.

This study showed a significant difference (3.42) in EBV for final score between the lines divergently selected on PTAT. For individual traits, udder and a few body traits were significantly different between the lines. The lines were not significantly different for yield traits, but they were for SCS. These results indicate that selection for final score could be used to improve body and udder characteristics.

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