

GENETICS AND BREEDING

Comparison of United States and Danish Strains of Jerseys for Yield Traits¹

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ABSTRACT

Eleven US and 11 Danish young bulls were AI sampled in the US and Denmark. The milking daughters of these sires provided an opportunity for comparison of the US and Danish Jersey populations. Danish age and month of calving and DIM adjustment factors were developed so that Danish and US records could be compared on a standardized basis (305-d lactation, mature equivalent). Least squares and animal model analyses were used to estimate strain differences and effects of heterosis. Jerseys from the US had superiority over Danish Jerseys of approximately 1000 kg for milk and 17 kg for protein. However, Danish Jerseys had an advantage of 20 kg for fat. Estimates of heterosis from crosses of US and Danish Jerseys were 1.5 to 3% of the mean for milk, fat, and protein yields. Correlations

of EBV from official genetic evaluations of the US and Denmark were high, ≥ 0.78 , for the project bulls, providing little evidence of an interaction of genotype and environment.

(Key words: heterosis, Jerseys, yield traits)

INTRODUCTION

Two of the most influential populations of Jersey dairy cattle in the world are those of Denmark and the US. During 1992, Denmark had 83,693 Jersey cows enrolled in official production recording that averaged 5018 kg for milk, 313 kg for fat, and 201 kg for protein (7); the US had 131,411 Jersey cows enrolled in official production recording that averaged 5891 kg for milk, 280 kg for fat, and 224 kg for protein (H. D. Norman, 1993, personal communication). Furthermore, Denmark had 98 Jersey sires from their AI progeny-testing program that received their first genetic evaluations for yield (7) during 1992; the US had 113 Jersey bulls similarly sampled through AI (G. R. Wiggans, 1992, personal communication).

Heterosis may result when strains of Jerseys are crossed. Jerseys from the US and Denmark are essentially unrelated since the time of im-

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portation to their respective countries, prior to 1900, from the Isle of Jersey (J. C. Wilk, 1992, personal communication). Prior to 1985, little exchange of genetic material had occurred, other than limited amounts of frozen semen for a small number of bulls (19). Several studies involving crosses of strains within a breed found positive heterosis for yield traits. Crosses of Dutch-Friesians and Holstein-Friesians had heterosis of 2.3, 2.6, and 2.4% for milk, fat, and protein yields, respectively, in a study by Van der Werf and De Boer (21). Boichard et al. (3) found heterosis of 2 to 2.5% of the mean for milk, fat, and protein yields when North American Holsteins and French Black and White cattle were crossed. Heterosis averaged 2.2 and 2.1% for milk and fat yields when Holstein or Friesian bulls from nine countries were crossed with Polish Black and White cows (24).

Bulls potentially can rank differently in countries because of interactions of genotype and environment. Mao and Burnside (9) reported a significant interaction of sire PTA and amount of grain fed during summer in a study of Canadian herds. Studies involving various environments in the US and including different regions (5, 8), levels of yield (6), SCC (2), and proportions of concentrate fed (23) have found no convincing evidence of interactions of genotype and environment. Other studies involving various countries (4, 14, 15, 18) found high genetic correlations of PTA for sires from those countries. However, two studies (4, 14) considered fat yield and found lower correlations for fat yield than for milk yield.

During 1983 and 1984, Jersey breed representatives and dairy scientists from the US and Denmark had discussions that resulted in the exchange of frozen semen between the two countries. During 1985, 6 US and 5 Danish young bulls were sampled in both countries. Similarly, 5 US and 6 Danish young sires were sampled in both countries during 1986. The milking daughters that resulted allow comparison of the two Jersey populations.

The objectives of this study were 1) to compare US and Danish Jerseys for milk, fat, and protein yields; 2) to estimate the amount of heterosis that resulted from crossing US and Danish strains of Jerseys; and 3) to determine whether an interaction of genotype and en-

vironment existed for the two strains of Jerseys.

MATERIALS AND METHODS

Lactational DHI records of milk, fat, and protein yields that were used for genetic evaluations for January 1992 were from the Animal Improvement Programs Laboratory, USDA (Beltsville, MD). Records were from Jersey cows born during 1973 or later, and yields were standardized (305-d lactation, twice daily milking, mature equivalent). Records of lactational yield for milk, fat, and protein were from the Danish Agricultural Advisory Centre, Arhus, Denmark. Records were for Jersey cows calving from January 1981 to December 1991. Genetic evaluations from January 1993 (US) and March 1993 (Danish) for the 22 project bulls also were from the Animal Improvement Programs Laboratory, USDA, and the Danish Agricultural Advisory Centre.

Danish Adjustment Factors for Age and Month of Calving

Danish data originally included 1,249,523 lactational records. Edits removed records for lactations with <305 DIM or without a record for protein. Yields were required to be from 1818 to 18,182 kg for milk, 91 to 909 kg for fat, and 68 to 727 kg for protein. Furthermore, age at calving was required to be from 18 to 95 mo. Following these edits, 276,906 lactational records remained. An additional edit that required 15 records per herd-year left 184,648 records from 7288 herd-years.

Effects of age at calving and month of calving were estimated by ordinary least squares with the following model:

$$Y_{ijklm} = \mu + hy_i + m_j + g_k + (m \times g)_{jk} + c_l(g_k) + e_{ijklm}$$

where

$$Y_{ijklm} = \text{the milk, fat, or protein yield of record } m \text{ in age class } l \text{ nested within age group at calving } k \text{ in month of calving } j \text{ in herd-year } i,$$

$$\mu = \text{the overall mean,}$$

- hy_i = the fixed effect of herd-year i (absorbed),
 m_j = the fixed effect of month of calving j ,
 g_k = the fixed effect of age group at calving k ,
 $(m \times g)_{jk}$ = the fixed effect of the interaction of month of calving j and age group at calving k ,
 $c_l(g_k)$ = the fixed effect of age class at calving l nested within age group at calving k , and
 e_{ijklm} = the random residual, assumed to have a normal distribution.

TABLE 1. Description of groups and classes (nested within groups) for age at calving.

Age group	Number of classes	Months per class	Age
			(mo)
1	11	1	18-28
2	6	1	29-34
3	3	1	35-37
4	5	1	38-42
5	18	1	43-60
	1	2	61-62
6	14	1	63-76
7	1	3	77-79
	2	2	80-83
	3	4	84-95

Age groups at calving were similar to those of Miller (11) and are in Table 1. Least squares solutions for age at calving were smoothed by medians of 7 and by hanning as described by Tukey (20), which involves taking consecutive and successive means of two estimates. Because variance tended to increase with mean of yield, multiplicative adjustment factors were developed. The weighted mean of age groups 6 and 7 based on frequencies was considered to be mature equivalent. The adjustment factor for each age at calving and month of calving combination was calculated from solutions with the following: factor = $(\mu + \text{weighted mean of age groups 6 and 7}) / [\mu + \text{month} + \text{age group} + (\text{month} \times \text{age group}) + \text{age class (age group)}]$.

Danish Adjustment Factors for DIM

An attempt was made to develop DIM adjustment factors for Danish records from the lactational records provided. However, almost all Danish lactational records of <305 DIM were terminal records rather than records in progress. Because terminal records are usually from cows with lower yields, the factors were large and inappropriate for expansion of records in progress.

Average daily yields for Danish Jerseys from 5 to 305 DIM in 15-d intervals were provided by the Danish Agricultural Advisory Centre. Daily yields within 15-d intervals were from interpolation. Yields for the first 15 DIM were calculated using the methods of Wiggins (22). Cumulative yields for DIM after 15 d were by summation of average daily yields. A

multiplicative factor for each DIM (15 to 305 DIM) was from the following:

$$\text{factor} = (\text{total 305-d yield}) / (\text{cumulative yield for the DIM considered}).$$

Danish yield records were standardized using the Danish adjustment factors for age and month of calving and DIM. Requirement for lactational records were 15 to 305 DIM and age at calving of 18 to 95 mo. Yields were required to be from 1 to 18,182 kg for milk, 1 to 909 kg for fat, and 0 to 727 kg for protein. Following these edits, the remaining 305-d records on a mature equivalent basis totaled 1,137,256.

Comparison of Strains and Crosses

Least Squares Analysis. Initially, data included the 1,137,256 standardized records of yield for Danish Jerseys as described plus the 1,442,555 records of US Jerseys, which had been previously standardized by the Animal Improvement Programs Laboratory, USDA. Preliminary edits required that sires of cows be registered, that protein be recorded for daughters, and that daughters be born after January 31, 1983 and have calved after October 31, 1985. Standardized milk, fat, and protein yields were required to be >0. Furthermore, fat and protein percentages were required to be >2 and 1.5%, respectively. Following these edits, 421,586 US and 365,173 Danish records remained. Only first lactations were considered

for this study because many daughters of project bulls had only enough time to complete one lactation, which reduced the data to 192,524 US and 154,129 Danish records.

Additionally, records from daughters of all foreign sires and their sons (other than the 22 project sires) were removed, which left 188,666 US and 143,228 Danish lactational records. This removal allowed comparisons among purebred US Jerseys, purebred Danish Jerseys, and their crosses. Elimination of foreign sires other than the project bulls also removed records for proven US or Danish sires that may have been mated nonrandomly to cows from the other country.

Further edits required records to be from herd-years with first-crop daughters of the 22 project sires. Remaining records were 20,566 US lactations from 666 herd-years and 12,425 Danish lactations from 930 herd-years. An additional edit required a minimum of three records per herd-year. This edit reduced the data to 20,502 US lactations from 620 herd-years and 12,315 Danish lactations from 857 herd-years. Evidence for strain differences and heterosis were tested with a model similar to that of Ahlborn-Breier and Hohenboken (1) using the general linear models procedure of SAS (16):

$$Y_{ijkl} = \mu + hy_i + b_1A_j + b_2H_j + e_{ijkl}$$

where

Y_{ijkl} = the first lactation standardized milk, fat, or protein yield of record l ,

μ = the overall mean,

hy_i = the effect of herd-year i (absorbed),

b_1 = the partial regression coefficient of yield on additive genetic effect of strain,

A_j = the additive genetic effect of strain composition (US parent \times US parent, $A_1 = 1$; US parent \times Danish parent, $A_2 = 0$; and Danish parent \times Danish parent, $A_3 = -1$),

b_2 = the partial regression coefficient of yield on the effect for heterosis,

H_j = the effect for level of heterosis (US parent \times US parent, $H_1 = 0$; US parent \times Danish parent, $H_2 = 1$; and Danish parent \times Danish parent, $H_3 = 0$), and

e_{ijkl} = the random residual, assumed to have a normal distribution.

Animal Model Analysis. The data were the same as those used for the least squares analysis prior to editing on ancestor information (first lactations for 192,524 US and 154,129 Danish Jerseys). To identify maternal grandsires of cows, the original data were searched for the dam of each cow. Because a registered maternal grandsire was required, the data were reduced to 168,923 US and 126,705 Danish records. Records for daughters and maternal granddaughters of foreign sires and their sons, except for sons of US and Danish bulls, were removed from the data, and 164,536 US and 112,164 Danish records remained. Because records were required to be from herds with first-crop daughters or maternal granddaughters of the 22 project bulls, 57,302 records in 453 US herds and 38,876 records in 731 Danish herds remained.

Herd-year-seasons were defined using the clustering procedure of Schmitz et al. (17). Parameters used were a maximum season interval of 1 yr, a minimum of three records per season, and a minimum season interval of 2 mo.

The following edits were successively performed until the data converged. Records of daughters and maternal granddaughters of sires with <10 daughter equivalents [daughters + (.5 \times maternal granddaughters)] were removed.

Following edits, 44,916 records from 2844 US herd-year-seasons with 913 "primary" sires remained; all sires and maternal grandsires of cows in this study are hereafter referred to as primary sires. Similarly, 31,795 records from 3814 Danish herd-year-seasons with 735 primary sires remained.

The EBV for the primary sires were obtained with the animal model program of Mistral and Gianola (12) with the model:

$$Y_{ijkl} = \mu + hys_i + h_j + a_k + e_{ijkl}$$

where

- Y_{ijkl} = the standardized milk, fat, or protein yield of cow k ,
 μ = the overall mean,
 h_{ys_i} = the fixed effect of herd-year-season i ,
 h_j = the fixed effect of heterosis (separate fixed effects for the two strain crosses and the two purebreds),
 a_k = the random effect of individual cow k , and
 e_{ijkl} = the random residual, assumed to have a normal distribution.

All cows with yield records had a sire and maternal grandsire, each of which had ≥ 10 daughter equivalents in the data. The maternal grandam of each cow was assigned to a phantom group based on the birth year of the grandam's daughter. Pedigrees of the primary sires were traced to approximately 1955 using all relationships among sires and maternal grandsires. Three phantom groups were defined: 1) a male pathway based on the birth year of his son, 2) a female pathway based on the birth year of her son, and 3) a female pathway based on the birth year of her grandson. Separate phantom groups were defined for US and Danish cattle. Some birth years were combined to gain sufficient numbers of offspring for a phantom group. The smallest phantom group had 21 offspring or grandoffspring. The data included 71,609 cattle in the US pedigree file and 53,051 in the Danish file. The convergence criterion of 1×10^{-9} was the sum of the squared differences of the animal model solutions from the present and previous rounds of iteration divided by the sum of squared solutions from the present round.

Mean EBV of the primary and project bulls were compared.

An interaction of genotype and environment would cause bulls to rank differently in the US and Denmark or change the variance of response. Correlations of official EBV from the US and Denmark for the project bulls were used to detect evidence of interaction of genotype and environment.

RESULTS AND DISCUSSION

Danish adjustment factors for age and month of calving for milk, fat, and protein yields are available on request from the authors. The factors were very similar to factors for age and month of calving currently used by the USDA (13) to adjust lactations to a mature equivalent basis. Danish factors for summer were slightly smaller, suggesting that summer in Denmark may be milder and have a less detrimental effect on yield than in the US.

Danish expansion factors for DIM (for 5-d intervals) based on Danish lactation curves also are available on request from the authors. The factors were larger than those of McDaniel et al. (10), but smaller than those based on Danish terminal records, suggesting that Danish Jerseys are more persistent than the US Jerseys included in the data of McDaniel et al. (10).

Unadjusted means for US and Danish Jerseys and their crosses from the data used for the least squares analysis are in Table 2. For milk yield, US purebreds were highest, Danish purebreds were lowest, and the strain crosses were intermediate. However, Danish purebreds were higher than US purebreds for fat yield. Crosses sired by US bulls were higher than the Danish purebreds for milk and protein yields,

TABLE 2. Unadjusted means for milk, fat, and protein yields of US and Danish Jerseys and their crosses from data used for the least squares analysis.

Yields	US sire	Danish sire	US sire	Danish sire
	US dam	Danish dam	Danish dam	US dam
	(n = 20,227)	(n = 11,918)	(n = 397)	(n = 275)
	(kg)			
Milk	6133	5218	5962	5792
Fat	291	330	332	313
Protein	225	209	228	226

TABLE 3. Parameter estimates for genetic effects from the least squares analysis.

Yields	Additive strain effect ¹			Heterosis effect ²		
	Estimate	SE	P ³	Estimate	SE	P
	————— (kg) —————			————— (kg) —————		
Milk	540.0	40.9	.0001	103.4	40.9	.0116
Fat	-11.1	2.0	.0001	4.9	2.0	.0127
Protein	9.5	1.4	.0001	5.0	1.4	.0004

¹Estimates for strain effects represent one-half of the additive genetic strain difference of US and Danish Jerseys.

²Estimates for heterosis effects represent the difference of the mean of US and Danish crosses and the mean of purebreds.

³P is probability from F test of significance.

but the Danish sired crosses were intermediate to Danish and US purebreds for milk and fat yields. For protein yield, both strain crosses were superior to Danish purebreds. Similar to milk yield, protein yield of US purebreds was higher than that of Danish purebreds. The US sired crosses in Denmark had higher phenotypic yields than the Danish sired crosses in the US for milk and fat yields. These means are unadjusted, and differences were not tested for significance.

The parameter estimates for additive strain and heterosis effects on milk, fat, and protein yields from the least squares analysis are in Table 3. For milk yield, additive strain effect was significant ($P < .0001$); US Jerseys had an advantage of 1080 kg. Heterosis was significant ($P < .012$); the strain crosses had an advantage of 103 kg over the purebreds. Additive strain effect was significant ($P < .0001$) for fat yield; Danish Jerseys had an advantage of 22 kg. Heterosis also was significant ($P < .013$); the strain crosses showed an advantage of 5 kg over the purebreds. For protein yield, additive strain effect was significant ($P <$

.0001); US Jerseys had an advantage of 19 kg. Heterosis also was significant ($P < .001$); the strain crosses showed an advantage of 5 kg over the purebreds for protein yield. The estimates for heterosis were equivalent to 1.8, 1.6, and 2.3% of the mean of purebred US and Danish Jerseys (from Table 2) for milk, fat, and protein yields, respectively. These estimates of heterosis were similar to those from other studies involving strain crosses from a single breed (3, 21, 24).

Estimates of additive strain effect and heterosis were deviated from the phenotypic means of purebred yields in Table 2 to estimate the expected phenotypic yields of crosses. Crosses in the US were 96, 6, and 6 kg higher than expected for phenotypic milk, fat, and protein yields, respectively. Similarly, crosses in Denmark were 101, 8, and 4 kg higher than expected for milk, fat, and protein yields, respectively. Therefore, the superior performance of crosses in Denmark compared with the US (Table 2) was expected, based on parameter estimates in Table 3.

Unadjusted means for US and Danish Jer-

TABLE 4. Unadjusted means for milk, fat, and protein yields of US and Danish Jerseys and their crosses from data used for the animal model analysis.

Yields	US sire	Danish sire	US sire	Danish sire
	US dam	Danish dam	Danish dam	US dam
	(n = 44,691)		(n = 31,477)	
	————— (kg) —————			
Milk	6196	5198	5962	5819
Fat	294	329	332	314
Protein	228	208	228	227

TABLE 5. Solutions for effects of heterosis from the animal model analysis.

Yields	Crosses	Purebreds	Difference
Milk	151.4	-1.3	152.7
Fat	7.4	0	7.4
Protein	6.4	0	6.4

seys and their crosses from data used for the animal model analysis are in Table 4. Means for milk, fat, and protein yields of the purebreds and strain crosses were similar to those from the least squares analysis.

Estimates of heterosis from the animal model analysis are shown in Table 5. Appropriately, solutions for the purebreds were near zero. Crosses of US and Danish Jerseys had an advantage over purebreds of 153 kg of milk, 7 kg of fat, and 6 kg of protein, which is 2.7, 2.4, and 2.9% of the purebred mean from Table 4. The estimates for heterosis within breed were similar to those of previous studies (3, 21, 24).

Mean EBV for the project and primary sires are in Table 6. The US project sires had superiority of 1033 kg for milk and 17 kg for protein over the Danish project sires. The Danish project sires, however, had EBV for fat yield that averaged 26 kg higher than those of US project sires. The EBV for primary sires gave similar results. Primary sires from the US were 848 kg higher for milk and 11 kg higher for protein yield than primary sires from Denmark. Primary sires from Denmark were 22 kg higher for fat than their US counterparts.

The EBV in Table 6 provide estimates of the additive genetic difference for the two male populations. Weighting of the EBV of each sire by the number of daughter equivalents in the data provides an estimate that more closely represents the additive genetic difference for

the two populations. Weighted means of EBV for the primary sires are in Table 7. The additive strain differences of US and Danish Jerseys were 960 kg for milk and 16 kg for protein in favor of US Jerseys. However, Danish Jerseys had an advantage of 18 kg for fat yield.

Means and medians of daughter information from official genetic evaluations of the two countries for the 22 project sires are in Table 8. As expected, the project sires had more daughters in their country of origin than in the foreign country. Project sires from the US had more daughters in their US genetic evaluations than in their Danish genetic evaluations. Likewise, the Danish project sires had more daughters in Denmark than in the US. However, US project sires had more daughters in Denmark than the Danish project sires had in the US. As expected, the US project sires had higher EBV for milk and protein yields, but the Danish project sires had higher EBV for fat yield.

Product-moment correlations of the official US and Danish EBV for the project sires are in Table 9. These correlations are of national EBV, not EBV from the present study. When sires were correlated within country of birth, all correlations were ≥ 0.82 . When combined across countries, all correlations were ≥ 0.78 . Expected correlations were not estimated because accuracies of EBV were calculated differently for the two countries. With such a small sample of sires examined, correlations < 1 may simply be due to sampling variation or prediction error rather than interaction of genotype and environment.

CONCLUSIONS

Estimates for additive strain differences and heterosis were similar from least squares and animal model analyses. Jerseys from the US

TABLE 6. Means of EBV for milk, fat, and protein yields of project and primary sires.

Yields	Project			Primary		
	US	Dane	Difference	US	Dane	Difference
	(n = 11)	(n = 11)		(n = 902)	(n = 724)	
	(kg)					
Milk	535.9	-497.2	1033.1	275.5	-572.5	848.0
Fat	-4.6	21.6	-26.2	-13.3	8.4	-21.7
Protein	13.0	-3.7	16.7	2.3	-8.6	10.9

TABLE 7. Weighted means of EBV for milk, fat, and protein yields of the primary sires.

Yields	US	Dane	Difference
	(n = 902)	(n = 724)	
	(kg)		
Milk	491.5	-468.9	960.4
Fat	-2.5	15.1	-17.6
Protein	10.6	-5.3	15.9

had higher EBV than Danish Jerseys of approximately 1000 kg for milk and 17 kg for protein. However, Danish Jerseys had an advantage of 20 kg for fat.

Crosses of US and Danish Jerseys were superior to means of purebreds by approximately 125 kg of milk, 6 kg of fat, and 6 kg of protein. Estimates of heterosis for the three yield traits ranged from 1.5 to 3% of the purebred mean. Although estimates of heterosis expressed as a percentage of total yield were low, estimates of heterosis as percentages of additive genetic differences seem larger. The impact of this degree of heterosis on genetic evaluations that ignore nonadditive genetic variation may be substantial.

Correlations of official, national US, and Danish EBV of the project bulls were high enough to provide little evidence of interaction of genotype and environment.

TABLE 8. Mean and median daughters, reliabilities, and EBV¹ of the project sires.

	US		Dane	
	Mean	Median	Mean	Median
US				
Daughters	148.2	99.0	26.9	25.0
Reliability	87.7	87.0	67.3	65.0
EBV Milk, kg	547.4	587.0	-139.8	-127.0
EBV Fat, kg	21.6	17.0	48.0	55.0
EBV Protein, kg	18.0	21.0	9.4	3.0
Dane				
Daughters	39.8	39.0	79.7	74.0
Repeatability	72.6	75.0	86.5	85.0
EBV Milk, kg	1335.3	1257.0	271.6	242.0
EBV Fat, kg	16.1	16.0	24.8	24.0
EBV Protein, kg	31.3	33.0	8.9	5.0

¹Official genetic evaluations from USDA and Danish Agricultural Advisory Centre.

TABLE 9. Product-moment correlations of official US and Danish EBV¹ of the project sires.

Yields	US	Danish	Combined
Milk	.82	.83	.86
Fat	.86	.85	.83
Protein	.84	.86	.78

¹Official genetic evaluations from USDA and Danish Agricultural Advisory Centre.

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