Milk, Fat, Protein, Somatic Cell Score, and Days Open Among Holstein, Brown Swiss, and Their Crosses

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ABSTRACT

The objectives of this study were to compare Holstein (HO), Brown Swiss (BS), and their crosses for milk, fat, and protein yields, somatic cell score (SCS), days open (DO), and age at first calving (AFC), and to estimate the effects of heterosis and recombination. First through fifth lactation records were obtained from 19 herds milking crosses among BS and HO. The edited data set included 6,534 lactation records from 3,473 cows of the following breed combinations: 2,125 pure HO, 926 pure BS, 256 BS sire × HO dam (SH), 105 backcrosses to BS (SX), 18 HO sire × BS dam, and 43 backcrosses to HO. Least squares means for daily milk, fat, and protein yields, mature-equivalent milk, fat, and protein yields, SCS, DO, and AFC were calculated for breed combinations with a model that included fixed effects of age within parity (except for AFC), days in milk for daily yield and SCS, herd-year-season of calving, and breed combination. Cow and error were random effects. Breed combination was replaced with regressions on coefficients for heterosis and recombination in a second analysis. Last, data were analyzed with a 5-trait animal model that included a single pedigree file for both breeds and coefficients for heterosis and recombination. The least squares means for fat production were 1.21, 1.15, 1.27, and 1.16 kg for HO, BS, SH, and SX, respectively, which corresponds to a heterosis estimate of 7.30% and a recombination estimate of –3.76%. Heterosis and recombination estimates for protein production were 5.63% and –3.31%, respectively. Heterosis estimates increased for fat yield (10.38%) and protein yield (7.07%) when maternal grandsire identification from a known artificial insemination sire was required. Regression coefficients indicated an 11.44-d reduction in DO due to heterosis. Heterosis estimates for SCS were inconsistent. Regression on heterosis for SCS was significant and favorable (–0.22) when the

breed of sire was BS, but nonsignificant and unfavorable when sire breed was HO (0.43). Heterosis estimates were favorable for all traits, whereas recombination effects tended to be unfavorable for yield traits. Reduced performance of future generations did not appear to be the result of inseminating crossbred cows with inferior sires. Results indicated that first-generation crosses among BS and HO compared favorably with HO. Yield in subsequent generations was somewhat below expectations, perhaps due to recombination loss in HO.

Key words: Holstein, Brown Swiss, crossbred

INTRODUCTION

Tremendous gains in milk, fat, and protein yields have been realized in the US Holstein (HO) population due to successful genetic selection programs (AIPL, 2006). Shifts in herd management practices have resulted in shorter productive lives (Hare et al., 2006), and a 7.6% decline from 1980 to 2003 in the proportion of cows that survive to 48 mo of age (Cornell University Dairy Genetics, 2006). A severe decline in cow fertility has encouraged many producers to resort to heavy reliance on hormone therapy to establish pregnancy (Caraviello et al., 2006) at a time when consumers are increasingly concerned about the use of hormones in animal production. These trends in fertility and herd life, coupled with concerns over calving ease and shifts in milk pricing that place greater emphasis on fat and protein, have generated interest in crossbreeding (McAllister, 2002; Weigel and Barlass, 2003).

Recent crossbreeding research has been encouraging, particularly for reproductive fitness, survival, and calving traits. Crosses of HO cows with Scandinavian Red and Montbeliarde sires resulted in combined fat plus protein production levels that were 2.2 and 3.8% lower than pure HO, respectively (Heins et al., 2006a). However, Scandinavian Red × HO and Montbeliarde × HO crosses had 21 and 19 fewer days open (DO) than pure HO (Heins et al., 2006c). Survival to 150 d in the first lactation was also 5% higher for crossbred cows than pure HO. Calving difficulty and stillbirth rates for Scan-

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dinavian Red × HO and Montbeliarde × HO cows were significantly lower than for pure HO (Heins et al., 2006b).

First-generation crosses have been successful, but the performance of future generations is less clear. Small but favorable recombination effects have been reported by McAllister et al. (1994) and VanRaden and Sanders (2003), which would generate favorable performance for future generations. Rutledge (2001), in a meta-analysis of 80 studies, reported unfavorable recombination effects for yield in crosses of temperate dairy cattle breeds with indigenous tropical dairy breeds. Favorable heterosis for yield was completely counteracted by recombination in future generations of Red Danish, Finnish Ayrshire, Danish Friesian, and Holstein Friesian crosses (Pedersen and Christensen, 1989). Unfavorable recombination for yield has been reported for crosses among European Friesian and Holstein Friesian (Boichard et al., 1993; Wall et al., 2005).

Although much recent crossbreeding research has focused on non-US dairy breeds, Brown Swiss (**BS**) is the closest prevalent US breed to HO in production of milk, fat, and protein (AIPL, 2006) and is similar in body size to HO. Previous reports of performance for crosses among BS and HO have been encouraging. Brown Swiss × HO crosses yielded 3.8% less milk than pure HO, but 2.6% more fat and 1.8% more protein (McDowell and McDaniel, 1968). Heterosis for DO was favorable and ranged from 15 to 31% for crosses among BS and HO (Brandt et al., 1974). More recently, crosses of Jersey and BS with HO were demonstrated to be economically competitive with average purebred HO (VanRaden and Sanders, 2003).

The objectives of this study were to compare HO, BS and their crosses for yield, average lactation SCS, DO, and age at first calving (**AFC**), and to estimate the effects of heterosis and recombination for these traits.

MATERIALS AND METHODS

Data

Total lactation milk yield, fat yield, protein yield, mature-equivalent milk, fat, and protein yields, lactation average SCS, AFC, and DO were obtained from 19 herds milking BS, HO, and their crosses. Total lactation yield was divided by total DIM to derive average daily yield. Records were retrieved from Dairy Comp 305 (Valley Ag Software, Tulare, CA) for 5 herds. Records from 14 herds that participate in DHI and have their records processed at Dairy Records Management Systems (**DRMS**; Raleigh, NC) were downloaded from DRMS into the PCDART software (DRMS). Seventeen of 19 herds participated in DHI testing. The data collection method could create bias because only cows with

Table 1. Number of cows (n), cows with maternal grand-sire identification (n_{MGS}), and total lactation records for daily milk, fat, and protein yields, mature equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open, and SCS for breeds and crosses

Item	Breed or cross ¹					
	HO	HX	HS	BS	SX	SH
Cows, n	2,125	43	18	926	105	256
Cows, n_{MGS}	1,773	36	14	805	85	132
(Total lactation records, n)						
Milk yield	3,692	82	48	1,602	185	560
Fat yield	3,225	81	48	1,591	184	543
Protein yield	3,280	82	48	1,627	189	548
MEM yield	3,730	82	48	1,599	186	561
MEF yield	1,425	22	29	1,373	145	279
MEP yield	1,425	22	29	1,373	145	279
Days open	3,190	61	43	1,337	157	507
SCS	2,442	53	37	1,510	171	396

¹HO = Holstein, HX = Holstein backcross, HS = Holstein sire × Brown Swiss dam, BS = Brown Swiss, SX = Brown Swiss backcross, and SH = Brown Swiss sire × Holstein dam.

records available at the time of data retrieval could be included in the analysis. Records from culled cows were retained for approximately 1 yr for herds with PCDART records, whereas availability of records from culled cows in Dairy Comp 305 depended on frequency of data archiving. Culled cows may not have records available, whereas longer surviving birth-year contemporaries were still in the herd. To limit the potential effect of selection bias due to culling, 5% of cows from a herd were required to calve in the same year to retain records from any cow born in that year. Additionally, second and later lactations were only retained if a first-lactation record was available.

All cows were required to have a registered HO or BS sire and lactations 1 through 5 were retained. For analysis of DO, records with less than 25 DO were removed, and DO greater than 250 were set to 250 if 2 or more inseminations had been recorded. Cows open after 250 d that had been inseminated fewer than 2 times may have been designated as culling candidates for issues unrelated to reproductive performance, so these records were removed.

The total number of cows and the number of lactation records for daily milk, fat, and protein yields, mature-equivalent milk, fat, and protein yields, SCS, DO, and AFC are displayed in Table 1 for HO, BS, BS sire × HO dam (**SH**), HO sire × BS dam (**HS**), BS backcrosses (**SX**), and HO backcrosses (**HX**). Records were available from a total of 2,125, 926, 256, 18, 105, and 43 HO, BS, SH, HS, SX, and HX cows, respectively. A majority of SX cows (85) were BS sire × F₁ crossbred dams, whereas the remaining 20 cows were >50% and <100% BS. Of the HX cows, 34 were HO sire × F₁ crossbred dams. The number of records available for SH ranged from

279 for mature-equivalent fat and protein yields to 561 for mature-equivalent milk yield. Dairy Comp 305 provided mature-equivalent milk, fat, and protein for cows in their current lactation, but only provided mature-equivalent milk for previous lactations, creating a discrepancy in the number of mature-equivalent milk, fat, and protein records. The total numbers of records from cows with maternal grandsire (MGS) identification available are also displayed in Table 1. In total, 52% of SH cows had valid MGS identification.

Statistical Models

Records for all traits were analyzed by 3 different methods.

Method 1. All traits were analyzed with the MIXED procedure (SAS Institute, 2000) with the following model:

$$y_{ijkl} = HYS_i + b_0A_j + \sum_{x=1}^4 b_x DIM^x + BC_k + Cow_l + \varepsilon_{ijkl}, \quad [1]$$

where y = daily milk, fat, protein, and fat plus protein yield, mature-equivalent milk, mature-equivalent fat, mature-equivalent protein, SCS, AFC, or DO for cow l in herd-year-season (HYS) i , lactation group j , and breed combination (BC) k ; b_0 = fixed regression coefficient on age at calving nested within lactation group (parities 1, 2, and 3 to 5); b_x = regression coefficients for fixed fourth-order polynomials of DIM (daily yield and average SCS only); Cow_l = the random effect of cow l ; and ε_{ijkl} = random error. Least squares means (LSM) were calculated for BC. Least squares means for BC were also calculated after nesting BC within lactation group. Age at calving was not included in the analysis of AFC. Percentage heterosis for SH was calculated as $(LSM_X - LSM_\mu)/LSM_\mu$, where LSM_X is LSM for SH and LSM_μ is the average LSM for HO and BS. Percentage recombination for SX was calculated similarly, except that LSM_X is LSM for SX and LSM_μ is the average LSM for SH and BS.

Method 2. Coefficients for heterosis and recombination were calculated as in VanRaden and Sanders (2003). Heterosis was $1 - \sum s_i d_i$, where s_i is the proportion of sire genes from breed i , and d_i is the proportion of dam genes from breed i . Recombination coefficients were calculated as $1 - \sum (s_i^2 + d_i^2)/2$. All traits were analyzed with the MIXED procedure (SAS Institute, 2000) with the following model:

$$y_{ijk} = HYS_i + b_0A_j + \sum_{x=1}^4 b_x DIM^x + b_5HO + b_6H + b_7R + Cow_k + \varepsilon_{ijk}, \quad [2]$$

where y , HYS, b_0 , b_x , cow, and error terms are defined identical to model 1; b_5 = regression on percentage HO; b_6 = regression on heterosis (H); b_7 = regression on recombination (R). Heterosis and recombination were included with and without nesting the coefficient within breed of sire. Differences between heterosis when sire is HO (HET_{HO}) and heterosis when sire is BS (HET_{BS}) were estimated. Backcrossing to a BS sire resulted in recombination for HO (REC_{HO}), whereas recombination when sire is HO represented the recombination effect of BS (REC_{BS}).

Method 3. Method 3 was similar to method 2, except that a random animal effect was added. Two 5-trait animal models were analyzed with ASREML (Gilmour et al., 2006) with the following model:

$$Y = XB + Xa + Wu + \varepsilon, \quad [3]$$

where Y = a vector of milk, fat and protein yield, SCS, and DO; B = a vector of fixed HYS, age within parity, DIM, HET_{BS}, HET_{HO}, REC_{BS}, and REC_{HO}; X = design matrix for fixed effects; a = a vector of random animal effects; Z = design matrix for animal effects; u = a vector of random permanent environmental effects; W = design matrix for permanent environmental effects; and ε = random error. Daily milk, fat, and protein yields were included in the first 5-trait model, whereas mature-equivalent milk, fat, and protein yields were included in the second analysis.

RESULTS

LSM: Method 1

Least squares means (method 1) and percentage heterosis and recombination for BS, HO, SH, and SX cows for all traits are displayed in Table 2. Estimates for HS and HX are not included in Table 2 because of minimal observations for either breed combination, but both breed combinations contributed to regression on heterosis and recombination. Pure HO had the highest LSM for milk yield (mature-equivalent and daily), but SH had higher LSM for daily and mature-equivalent fat and protein yield. Heterosis for SH ranged from 4.43% (mature-equivalent fat) to 7.30% (daily fat) for yield traits. Heterosis was for lower AFC (2.06%), lower SCS (7.78%), and fewer DO (7.99%). Least squares means were not significantly different between BS and SX for any trait. Heterosis was higher for all yield traits (5.60% for mature-equivalent milk to 10.38% for daily fat) when a valid MGS was required (Table 3).

Least squares means for combined daily fat plus protein production, DO, and SCS within lactation group are displayed in Table 4. Combined fat plus protein

Table 2. Least squares means, heterosis, and recombination estimates for daily milk, fat, and protein yields, mature-equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open, SCS, and age at first calving (AFC) for breeds and crosses

Item	Breed or cross ¹				Estimate (%)	
	HO	BS	SH	SX	Heterosis	Recombination
Milk (kg)	33.31 ^a	28.34 ^b	32.37 ^c	29.30 ^b	5.01***	-3.49†
Fat (kg)	1.21 ^a	1.15 ^b	1.27 ^c	1.16 ^b	7.30***	-3.76*
Protein (kg)	1.00 ^a	0.93 ^b	1.02 ^a	0.95 ^b	5.63***	-3.31*
MEM (kg)	11,105 ^a	9,746 ^b	10,910 ^a	10,019 ^b	4.65***	-2.99
MEF (kg)	393 ^a	376 ^b	402 ^a	382 ^{ab}	4.43*	-1.78
MEP (kg)	326 ^a	314 ^b	340 ^c	319 ^{ab}	6.49***	-2.54
Days open	156.00 ^a	156.32 ^a	143.69 ^b	153.37 ^{ab}	7.99***	-2.24
SCS	2.73 ^{ab}	2.78 ^a	2.54 ^b	2.66 ^{ab}	7.78*	-0.16
AFC	25.85 ^a	26.58 ^b	25.68 ^a	26.58 ^b	2.06*	-1.71

^{a-c}Least squares means with different superscripts within rows are significantly different ($P < 0.05$).

¹HO = Holstein, BS = Brown Swiss, SH = Brown Swiss sire × Holstein dam, and SX = Brown Swiss backcross.

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

production for HO was 2.09, 2.24, and 2.25 kg/d for first, second, and third and higher lactations, respectively. Fat plus protein production for BS increased from 1.92 kg/d for first lactation, 2.13 kg/d for second lactation, and 2.22 kg/d for third and higher lactations. Heterosis for yield increased across lactations, from 4.43% for first lactation to 13.41% for third and higher lactations. The trend for heterosis in DO (15.08% for first lactation to 1.43% for third and higher lactations) was opposite that observed for yield. Least squares means for SCS also grew in magnitude as lactation progressed, from 3.17% in lactation 1 (nonsignificant) to 15.40% in third and higher lactations ($P < 0.05$).

Regression Coefficients: Method 2

Regression coefficients (method 2) for percentage HO, heterosis, and recombination are in Table 5. Coeffi-

cients for percentage HO were significant and positive for all yield traits. The regression coefficients indicate that pure HO produced (per day) 4.98 kg more milk, 0.07 kg more fat, and 0.07 kg more protein than pure BS. Regression on percentage HO was not significant for SCS or DO. Heterosis effects were significant and favorable (positive for yield and negative for DO, SCS, and AFC) for all traits. Recombination effects were negative, but generally not significant, for yield. The recombination effect for DO was positive, although not significant.

Results from regression on HET_{HO} , HET_{BS} , REC_{HO} , and REC_{BS} are in Table 6. Estimates for HET_{BS} tended to be greater in magnitude and more favorable than HET_{HO} , indicating that crosses of BS sire × HO cows performed favorably compared with crosses of HO sire × BS cows. Estimates for REC_{HO} were unfavorable for all traits except SCS, and approached significance ($P <$

Table 3. Least squares means, and heterosis and recombination estimates from cows with valid maternal grandsire for daily milk, fat, and protein yields, mature-equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open, SCS, and age at first calving (AFC) for breeds and crosses

Item	Breed or cross ¹				Estimate (%)	
	HO	BS	SH	SX	Heterosis	Recombination
Milk (kg)	33.69 ^a	28.59 ^b	33.23 ^a	29.58 ^b	6.70***	-4.29*
Fat (kg)	1.22 ^a	1.15 ^b	1.31 ^c	1.16 ^b	10.38***	-5.69**
Protein (kg)	1.01 ^a	0.94 ^b	1.05 ^c	0.95 ^b	7.07***	-4.49*
MEM (kg)	11,225 ^a	9,841 ^b	11,122 ^a	10,113 ^b	5.60**	-3.51
MEF (kg)	396 ^a	378 ^b	415 ^a	385 ^{ab}	7.23*	-2.89
MEP (kg)	329 ^a	317 ^b	350 ^c	324 ^{ab}	8.46**	-3.05
Days open	156.02 ^a	155.95 ^{ab}	144.60 ^b	153.45 ^{ab}	7.30*	-2.11
SCS	2.75	2.82	2.57	2.59	7.81	4.11
AFC	25.78 ^a	26.73 ^b	25.35 ^a	26.65 ^b	3.45**	-2.34

^{a-c}Least squares means with different superscripts within rows are significantly different ($P < 0.05$).

¹HO = Holstein, BS = Brown Swiss, SH = Brown Swiss sire × Holstein dam, and SX = Brown Swiss backcross.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4. Least squares means and heterosis estimates for combined daily fat plus protein yield, days open, and SCS for breeds and crosses by lactation group (1, 2 and 3 and higher)

Parameter and breed ¹	Lactation group		
	1	2	3+
Combined fat + protein yield (kg)			
HO	2.09 ^{a,x}	2.24 ^{b,x}	2.25 ^{b,x}
BS	1.92 ^{a,y}	2.13 ^{b,y}	2.22 ^{b,x}
SH	2.09 ^{a,x}	2.31 ^{b,x}	2.54 ^{c,y}
Heterosis (%)	4.43 ^{***}	5.45 ^{****}	13.41 ^{b****}
Days open			
HO	129.80 ^{a,x}	151.64 ^a	193.96 ^b
BS	137.01 ^{a,x}	142.75 ^a	188.11 ^b
SH	113.29 ^{a,y}	139.94 ^a	188.31 ^b
Heterosis (%)	15.08 ^{****}	4.93 ^{ab}	1.43 ^b
SCS			
HO	2.56	2.64 ^x	2.59 ^x
BS	2.52 ^a	2.86 ^{b,y}	2.58 ^{ab,x}
SH	2.46	2.47 ^x	2.19 ^y
Heterosis (%)	3.17	10.12 [*]	15.40 [*]

^{a-c}Estimates within rows with different superscripts are significantly different ($P < 0.05$).

^{x,y}Estimates within columns with different superscripts are significantly different ($P < 0.05$).

¹HO = Holstein, BS = Brown Swiss, SH = Brown Swiss sire $\times$ Holstein dam.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

0.10) for daily yield traits. Estimates of REC_{BS} were significant for SCS and AFC only, and were numerically favorable for all traits except mature-equivalent milk.

Mixed-Breed Animal Model: Method 3

Heritability and genetic and phenotypic correlations from 5-trait animal models among milk yield, fat yield, protein yield, DO, and SCS are in Table 7. Heritability estimates ranged from 0.03 for DO to 0.13 for daily milk yield. Daily milk yield was positively correlated with daily fat yield (0.46), daily protein yield (0.81), DO (0.23), and SCS (0.53). The genetic correlation estimate

Table 5. Coefficients for regression on percentage Holstein (HO_{PCT}), heterosis, and recombination for daily milk, fat, and protein yields, mature-equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open, and SCS

Item	HO _{PCT}	Heterosis	Recombination
Milk (kg)	4.98 ^{***}	1.48 ^{***}	-3.01
Fat (kg)	0.07 ^{***}	0.08 ^{***}	-0.11
Protein (kg)	0.07 ^{***}	0.05 ^{***}	-0.10 [†]
MEM (kg)	1,358 ^{***}	483 ^{***}	-1,078
MEF (kg)	17.42 ^{***}	13.78 [*]	-18.03
MEP (kg)	12.25 ^{***}	16.11 ^{**}	-30.59
Days open	-0.64	-11.44 ^{**}	3.67
SCS	-0.06	-0.16 [†]	-0.45
AFC	-0.77 ^{***}	-0.52 [*]	-0.15

[†] $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 6. Coefficients for regression on heterosis with a Brown Swiss sire (HET_{BS}) and a Holstein sire (HET_{HO}), and recombination for Brown Swiss (REC_{BS}) and Holstein (REC_{HO}) for daily milk, fat, and protein yields, mature-equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open, and SCS

Item	HET _{BS}	HET _{HO}	REC _{BS}	REC _{HO}
Milk (kg)	1.54 ^{***}	0.75	0.27	-3.95 [†]
Fat (kg)	0.09 ^{***}	-0.03	0.21	-0.17 [†]
Protein (kg)	0.05 ^{***}	0.00	0.04	-0.12 [†]
MEM (kg)	482 [*]	496	-848	-1,193
MEF (kg)	17.04 ^{***}	-16.22	57.62	-25.02
MEP (kg)	20.53 ^{***}	-23.36	26.13	-32.45
Days open	-12.55 ^{***}	-0.82	-45.05	15.36
SCS	-0.22 [*]	0.43	-2.41 [*]	-0.05
AFC	-0.55 ^{**}	-0.30	-4.96 [*]	1.76

[†] $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

between DO and SCS was 0.57. Estimates for regression on heterosis and recombination from method 3 (Table 8) were similar to those from method 2 (Table 6).

DISCUSSION

Production levels of SH crosses were similar to HO, and SH had significantly fewer DO. Total amount of combined fat plus protein yield were 0.08 kg greater for SH than for HO. Least squares means for DO were 12.3 d less, and SCS was 0.19 less for SH than HO. VanRaden and Sanders (2003) reported nearly identical fat and protein yields of SH compared with HO and demonstrated SH to be economically competitive with pure HO. Moreover, body size of BS and HO are similar, which reduces potential management challenges related to wide variation in body size that may result with crosses of breeds significantly smaller than HO.

Previous research has demonstrated favorable heterosis for yield traits. VanRaden and Sanders (2003) reported general heterosis estimates among US dairy breeds for milk, fat, and protein yields of 3.4, 4.4, and 4.1%, respectively. Heterosis estimates for SH were higher for yield in the current study (5.60 to 10.38% when MGS was required) than the estimates specific to SH (3.2 to 4.5%) reported by VanRaden and Sanders (2003). Heterosis estimates for SH were reported to be 9.9, 10.4, and 10.5% for milk, fat, and protein yields, respectively (McDowell and McDaniel, 1968). Brandt et al. (1974) reported no significant heterosis for yield for crosses among BS and HO with SH and HS group sizes of 13 cows each. McAllister et al. (1994) reported heterosis for lifetime yield in crosses among Ayrshire and HO of 16.6%. Touchberry (1992), in crosses among HO and Guernsey, reported a heterosis estimate of 8% for milk yield in first and second lactation.

Heterosis was stronger for all yield traits when a valid MGS was required. This may result from inconsis-

Table 7. Heritability¹ (on diagonal), genetic² (above diagonal), and phenotypic³ (below diagonal) correlations among daily milk, fat, and protein yields, mature-equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open (DO), and SCS

	Milk	Fat	Protein	MEM	MEF	MEP	DO	SCS
Milk	0.13	0.46	0.81	—	—	—	0.23	0.53
Fat	0.67	0.12	0.68	—	—	—	0.12	0.27
Protein	0.76	0.55	0.05	—	—	—	-0.25	0.51
MEM	—	—	—	0.12	0.40	0.73	0.17	0.38
MEF	—	—	—	0.81	0.09	0.55	0.35	0.34
MEP	—	—	—	0.94	0.83	0.09	-0.24	0.31
DO	-0.09	-0.05	-0.08	0.07	0.07	0.05	0.03	0.57 ⁴
SCS	-0.17	-0.14	-0.11	-0.16	-0.14	-0.14	0.14 ⁴	0.10

¹Standard errors for heritability estimates ranged from 0.02 to 0.03.

²Standard errors for genetic correlation estimates ranged from 0.08 (MEM and MEP) to 0.29 (protein and SCS).

³Standard errors for phenotypic correlation estimates ranged from 0.002 to 0.02.

⁴The genetic and phenotypic correlation estimates between DO and SCS were from a model that included daily yield. The corresponding genetic correlation and phenotypic correlation estimates from a model that included mature equivalent yield were 0.46 and 0.10, respectively.

tent methods of assigning breed code by producers. For example, any cow with a BS sire was identified as BS regardless of the breed of dam in some herds. In other herds, only pure BS were identified as BS. In contrast to VanRaden and Sanders (2003), a BS sire × HO dam appeared more favorable than HO sire × BS cow. However, only 18 HS cows were available in the current study so estimates for BS sire × HO cow are not precise.

Heterosis is often presumed to be larger for nonyield traits such as herd life and fertility measures than for yield. McAllister (2002), in a survey of previous crossbreeding results, summarized that heterosis estimates for lifetime traits can exceed 15%. Brandt et al. (1974) reported DO LSM estimates of 120, 131, 107 (15% heterosis), and 86 (31% heterosis) for HO, BS, HS and SH, respectively. McDowell and McDaniel (1968) reported

a DO heterosis estimate of 11.6% for SH. Others have failed to document large heterosis effects for fitness traits. VanRaden and Sanders (2003) reported general heterosis estimates of 1.2% for productive life and 0.7% for SCS.

Heterosis estimates for SH were favorable for the fitness-related traits (AFC, DO, and SCS) observed in this study, but they varied across lactations and varied depending on the breed of sire. Estimates for DO were stronger in first lactation, but near zero in third and higher lactations, whereas heterosis increased across lactation for SCS. The effect of heterosis on SCS was inconsistent and should be interpreted with caution. Heterosis was significant and favorable (-0.22) for HET_{BS}, but nonsignificant and unfavorable (0.43) for HET_{HO}.

The success of crossbreeding with BS could be affected by calf management effects associated with BS. Anecdotal evidence suggests that training BS calves to drink from buckets can be difficult, increasing labor devoted to weaning (Bulot, 2004). Data on calf management characteristics were not available in the current study. Least squares mean for AFC was 0.17 mo less for SH than HO, indicating that producers were able to adapt management systems to raise BS-sired calves successfully. Significantly lower calving difficulty scores and numerically lower stillbirth rates were reported for calvings with a BS sire compared with HO sire in California herds (Heins et al., 2006b), but measures of rearing difficulty were not available.

There was evidence that BS matured more slowly than HO. Differences between HO and BS for fat plus protein yield decreased as lactation number increased, whereas heterosis for fat plus protein yield increased. Fat plus protein yield was significantly different be-

Table 8. Coefficients from multiple-trait animal models for regression on percentage Holstein (HO_{PCT}), heterosis with a Brown Swiss sire (HET_{BS}) and a Holstein sire (HET_{HO}), recombination for Brown Swiss (REC_{BS}) and for Holstein (REC_{HO}) for daily milk, fat, and protein yields, mature-equivalent yields for milk (MEM), fat (MEF), and protein (MEP), days open, and SCS

Item	HO _{PCT}	HET _{BS}	HET _{HO}	REC _{BS}	REC _{HO}
Milk (kg)	5.16***	1.64***	0.75	0.65	-4.77*
Fat (kg)	0.07***	0.09***	-0.02	0.26	-0.26*
Protein (kg)	0.08***	0.07***	0.00	0.17	-0.15†
MEM (kg)	1,353***	482***	438	-826	-1,188
MEF (kg)	19.25***	13.00*	4.20	2.95	-16.27
MEP (kg)	13.73***	15.64***	-4.29	-15.05	-31.66
Days open ¹	-1.15	-12.24**	-2.02	-46.31	18.06
SCS ¹	-0.02	-0.18†	0.33	-2.25*	0.12

¹The estimates for days open and SCS were from a 5-trait model that included daily yield. The corresponding estimates from a 5-trait model that included mature equivalent yield were nearly identical and had the same level of significance.

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

tween BS and HO in first and second lactation, but not for third and higher lactations. Yield for SH was numerically (nonsignificant) higher than HO in lactation 2 and was significantly higher for SH than pure HO in lactation 3 and higher because heterosis increased across lactations. Touchberry (1992) also reported heterosis estimates that increased from first (4.34%) to second (12.0%) lactation for milk yield.

Backcrossing to BS resulted in lower yield for SX than would be expected, perhaps due to REC_{HO} . It did not appear that lower performance for SX was due to the use of inferior sires on crossbred vs. purebred cows because REC_{HO} estimates increased for daily yield traits when a pedigree effect was added. Evidence of recombination loss for yield in the literature is mixed. Brandt et al. (1974) reported no evidence of recombination among backcrosses to BS and HO. McDowell and McDaniel (1968) did not observe a reduction in yield for 3-breed crosses among Ayrshire, BS, and HO due to recombination. McAllister et al. (1994) reported favorable but generally nonsignificant effects for recombination. VanRaden and Sanders (2003) also reported evidence of slightly favorable recombination for yield when recombination effects were assumed to be constant across all 6 US dairy breeds. Rutledge (2001) reported recombination loss for crosses of temperate dairy breeds with indigenous tropical breeds in a meta-analysis of 80 studies. Unfavorable recombination has also been reported among closely related breeds. Boichard et al. (1993) and Wall et al. (2005) reported recombination estimates that were large and unfavorable for crosses among North American HO and European Holstein-Friesian. Pedersen and Christensen (1989) concluded that expected heterosis was near zero in 2- and 3-breed crossbreeding systems due to unfavorable recombination effects for yield among Red Danish, Finnish Ayrshire, Danish Friesian, and Holstein Friesian, particularly for crosses involving Holstein-Friesian.

The estimated recombination effect was approximately equivalent to heterosis for yield in SX, and REC_{HO} was more severe than REC_{BS} . As a result, LSM for SX were not significantly different than pure BS for any yield trait. Unfavorable REC_{HO} would be expected to reduce performance of 3-breed crosses as well as backcrosses. However, if REC_{BS} is not significant, the negative effect of recombination would be less than heterosis in a 3-breed cross. Crossbreeding systems will be optimal if breeds are identified that do not have significant nonadditive genetic effects for yield. Estimating recombination requires large numbers of second and higher generation crosses, which are often not available.

CONCLUSIONS

Crossbreeding will allow dairy producers to match the genotype of dairy herds to farm management conditions and BS is a viable choice for crossbreeding systems. Brown Swiss-sired cows from HO dams had higher fat and protein production than pure HO with fewer DO and lower SCS. Although F_1 crosses performed favorably, performance of future generations was depressed by the effects of recombination. Recombination effects were generally not severe and producers who want to capitalize on favorable heterosis for fitness traits should be able to do so with marginal losses of fat and protein yield. However, further exploration of future generations is warranted to define recombination effects more fully.

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