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Economic Merit of Crossbred and Purebred US Dairy Cattle

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ABSTRACT

Heterosis and breed differences were estimated for milk yield traits, somatic cell score (SCS), and productive life (PL), a measure of longevity. Yield trait data were from 10,442 crossbreds and 140,421 purebreds born since 1990 in 572 herds. Productive life data were from 41,131 crossbred cows and 726,344 purebreds born from 1960 through 1991. The model for test-day yields and SCS included effects of herd-year-season, age, lactation stage, regression on sire's predicted transmitting ability, additive breed effects, heterosis, and recombination. The model for PL included herd-year-season, breed effects, and general heterosis. All effects were assumed to be additive, but estimates of heterosis were converted to a percentage of the parent breed average for reporting. Estimates of general heterosis were 3.4% for milk yield, 4.4% for fat yield, and 4.1% for protein yield. A coefficient of general recombination was derived for multiple-breed crosses, but recombination effects were not well estimated and small gains, not losses, were observed for yield traits in later generations. Heterosis for SCS was not significant. Estimated heterosis for PL was 1.2% of mean productive life and remained constant across the range of birth years. Protein yield of Brown Swiss × Holstein crossbreds (0.94 kg/d) equaled protein yield of purebred Holsteins. Fat yields of Jersey × Holstein and Brown Swiss × Holstein crossbreds (1.14 and 1.13 kg/d, respectively) slightly exceeded that of Holsteins (1.12 kg/d). With cheese yield pricing and with all traits considered, profit from these crosses exceeded that of Holsteins for matings at breed bases. For elite matings, Holsteins were favored because the range of evaluations is smaller and genetic progress is slower in breeds other than Holstein, in part because fewer bulls are sampled. A combined national evaluation of data for all breeds and crossbreds may be desirable but would require an extensive programming effort. Animals should receive credit for heterosis when considered as mates for another breed.

(**Key words:** crossbreeding, heterosis, breed difference)

Abbreviation key: PL = productive life.

INTRODUCTION

Crossbreeding provides a simple method to increase the health and efficiency of many plants and animals, by introducing favorable genes from other breeds, by removing inbreeding depression, and by maintaining the gene interactions that cause heterosis. Few dairy cattle in the United States are crossbred because high milk yields made purebred Holsteins the preferred breed (Young, 1984). Crossbreeding of strains within breeds has been a common practice outside the United States, where Holstein and other specialized dairy bulls often were mated to Friesian and other dual-purpose cows (Cunningham, 1983). Crossbreeding of Jerseys with Holsteins is common in New Zealand (about 20% of milk-recorded cows) and in Australia (about 5% of cows). Crossbreeding is also common in tropical climates (McDowell, 1985) where higher producing European dairy breeds are less adapted to the environment than local breeds.

Designed studies in North American research herds indicated that some crossbreds were more profitable than Holsteins (Touchberry, 1992; McAllister et al., 1994). A study of Holstein crossbreds in a commercial herd also showed that some crossbreds may be more profitable than Holsteins (Lesmeister et al., 2000). Data from the larger numbers of crossbred and purebred dairy cows in commercial herds may provide more current or more accurate estimates of heterosis for recorded traits and include more breeds than previous designed studies. Lopez-Villalobos et al. (2000) concluded that rotational crossbreeding is profitable for commercial milk production in New Zealand.

Genetic evaluations traditionally have considered data from different breeds separately. Cows with sire and dam of different breeds are excluded from USDA-DHIA evaluations unless identified as part of a breed association "grading-up" program. This strategy avoids biased evaluations within breeds but provides no evalu-

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ations for crossbreds and no method of making unbiased comparisons across breeds. If crossbreds are on the average more profitable than their parents, it may be desirable to include them in genetic evaluations. Methods for evaluation of crossbred cows were presented by Swan and Kinghorn (1992) with a discussion of the use of crossbreeding in dairy cattle.

When animals of different breeds are mated or are managed together in the same herds, a combined evaluation may be preferred (Harris, 1994). Evaluations that account for heterosis and include all breeds and crossbreds in a combined dataset are used in New Zealand and The Netherlands. Belgium, Denmark, France, Great Britain, Hungary, Ireland, and The Netherlands adjust for heterosis of North American Holsteins crossbred with European Friesians (Interbull, 2000). Most also adjust for recombination losses in later generations (Boichard et al., 1993; Van der Werf and de Boer, 1989). Dairy goat evaluations in the United States have included all breeds and crossbreds since 1987 but without accounting for heterosis (Wiggans, 1989).

Objectives were 1) to document the numbers and types of crossbred dairy cattle in the United States, 2) to estimate breed differences, general and specific heterosis, and recombination losses in herds containing both purebred and crossbred cows, and 3) to predict the net economic merit of each breed or breed cross.

MATERIALS AND METHODS

Data sent to USDA for November 2000 genetic evaluations included records from 16,810 crossbred and nearly 3 million purebred cows. Cows were considered to be crossbred if sire and dam were both known but had different breed codes. For birth year 1997 (first-lactation cows), records were available from 3480 crossbreds (compared with 612,771 Holsteins and 35,530 Jerseys). About one-third of crossbred cows had at least one parent with a breed code of XX, indicating that the parent was crossbred and that the cow was a three-fourths or some other non-F_1 cross. The most numerous cross (924 cows) for 1997 births was Jersey sire by Holstein dam; however, the reciprocal cross numbered only 167 cows. Holstein sire by XX dam was second most numerous (799 cows). The number of crossbreds reported from each dairy records processing center was proportional to population size, indicating that all centers were sending crossbred data.

For USDA evaluations, if the sire is identified but the dam is not, and cow breed identification matches sire breed, the cow was assumed to be purebred. Also, Holstein and Red and White are considered one breed. Because most crossbred cows (97%) are not evaluated, farmers may supply parent identification less often for crossbreds than for purebreds, resulting in an undercount of crossbred cows. Crossbreeding of dairy cows to beef bulls is not reported within DHIA.

Heterosis and breed differences for yield and SCS data were estimated using data from the national test-day database available in May 2001. This database includes test-day yields for calvings since 1990 but is incomplete in the earliest years because only lactation records were reported for some herds until 1997. The study of heterosis and breed differences for productive life (**PL**) reported here was computed and reported in abstract form by VanRaden (1995). Thus, the study of yield and SCS included only very recent data, whereas PL data were from an earlier and more extended period and data edits for PL differed slightly from those for yield and SCS.

Yield Traits

Total number of crossbreds with sire and maternal grandparent breeds identified was 12,565, which included F_1 crossbreds and F_1 progeny. Sire was required to have a PTA that included at least 10 daughters and was assumed purebred for the breed of evaluation. Unknown maternal grandparent breed was determined from dam breed when possible. Pedigree for cows with dam coded XX (crossbred) and unknown grandparent breed, or grandparent breed XX, were incomplete, and the cows' records were excluded.

Test-day yields were obtained from cows in 572 herds, each containing at least five crossbred cows born since 1990. This subset of herds included 10,442 crossbreds (83% of the total), but greatly reduced the number of herd-year-seasons, significantly reducing computing time. The selected herds included a total of 140,421 purebred cows of all breeds. The majority (80%) of these other cows were Holsteins.

A total of 92,471 cows had yield records in multibreed contemporary groups within the selected herds. Numbers of F1 crossbreds are presented on the off-diagonals of Table 1 and numbers of purebreds on the diagonal. Jersey and Brown Swiss appeared as the sire breed more often than the dam breed for crosses with Holsteins. Thus, "grading up" to Holstein was not the reason for producing most of these crossbred animals. Some Holstein breeders have used crossbreeding to increase protein and fat percentages or believe that the benefits of heterosis outweigh breed differences. In some cases, harmful recessives were avoided by mating carrier sires to cows of a breed without the defect. Also, easier births may result from mating Holstein heifers to sires of a smaller breed. Numbers of some backcrosses are presented in Table 2. Only backcrosses in-

Table 1. Numbers of purebred and F_1 crossbred cows born since 1990, with yield records in contemporary groups having both purebreds and crossbreds.

	Sire breed					
Dam breed	Ayrshire	Brown Swiss	Guernsey	Jersey	Milking Shorthorn	Holstein
Ayrshire	**933**	. . .	1	26	2	477
Brown Swiss	. . .	**2537**	8	22	5	242
Guernsey	8	31	**1763**	23	4	1228
Jersey	18	22	11	**6593**	8	507
Milking Shorthorn	. . .	11	1	. . .	**1509**	175
Holstein	145	819	130	1631	162	**71,836**

volving Holstein are listed because backcrosses among the other breeds each included fewer than 10 cows.

The model for yield traits included effects of herd-year-season of freshening, age, lactation stage, a regression on the coefficient of heterosis, and on the coefficient of recombination, and a regression on sire's PTA. Adjustment for sire's PTA was included in case sires of crossbreds were more highly or less highly selected than sires of purebred herdmates. To obtain estimates of specific heterosis, the general effects of heterosis and recombination were replaced in the model by a three-way interaction of sire breed with maternal grandsire breed with maternal grandam breed. Paternal grandparents were not needed because all sires were purebred. With this second model, separate solutions for the two reciprocal crosses were obtained for each F_1 cross and for each backcross and three-breed cross. Because pedigrees extended only two generations and crossbred grandams were excluded, no breed fraction was <1/4 and no pedigree included more than three breeds.

All effects in the models were assumed additive, but specific heterosis for each reciprocal cross is reported as a percentage of the mean of parent breeds (a multiplicative effect). Estimates of general heterosis and general recombination are also reported as multiplicative factors. Parent breed averages weighted by the number of contributing cows were the denominator for converting from additive to multiplicative factors. Breed effects were estimated relative to Holstein by including Holstein as the last breed and setting its effect to zero. Solutions were obtained by PROC GLM of SAS (SAS Institute, 1999). Because correlated test-day yields were treated as independent observations, the calculated standard errors were too low and had to be adjusted upward. Standard errors were multiplied by the ratios of number of tests to effective number of tests (2.4 for first lactations and 3.5 for all lactations). Effective number was defined as the number of cows each with one test that would provide information equivalent to the multiple correlated tests for an average cow.

Table 2. Numbers of backcross cows with 25 or 75% Holstein genes, born since 1990, with yield records in contemporary groups having both purebreds and crossbreds.

Second Breed	25% Holstein	75% Holstein
Ayrshire	17	124
Brown Swiss	124	196
Guernsey	32	367
Jersey	171	321
Milking Shorthorn	14	48

Component yields sometimes were missing. Test-day fat yields were available for 87% of the milk tests and test-day protein yields were available for 84% of the milk tests. The three yield traits were analyzed separately with single-trait methods.

Somatic Cell Score

High SCS indicates higher incidence of clinical mastitis and results in lower milk prices in many markets. Test-day SCS was available for 77% of the test-day milk yields. The models for SCS were the same as those for yield traits.

Productive Life

Longevity has a large effect on dairy cattle profit because multiple lactations are needed to pay for the cost of raising replacements. One measure of longevity is PL, which is computed as total months of milk production limited to 10 mo per lactation and 7 yr of age (VanRaden and Klaaskate, 1993). Projected records are included for cows still alive and for cows sold to untested herds for dairy purposes. The PL data for US cows born at least 3 yr ago are routinely evaluated by BLUP with an animal model (VanRaden and Wiggans, 1995).

Productive life records of crossbred cows and their herdmates were from national data files available July 1994 and results were reported earlier as an abstract (VanRaden, 1995). Included were cows born from 1960 through 1991. Cows with sire breed differing from dam breed (F1 crossbreds) and with sire or dam breed code of XX (crossbred) were included. Numbers of F1 cross-

Table 3. Numbers of purebred and F_1 crossbred cows with productive life records.

	Sire breed					
Dam breed	Ayrshire	Brown Swiss	Guernsey	Jersey	Milking Shorthorn	Holstein
Ayrshire	**15,465**	40	58	98	27	1455
Brown Swiss	41	**24,566**	50	166	29	2002
Guernsey	171	243	**42,727**	282	59	3746
Jersey	94	560	221	**70,966**	31	2356
Milking Shorthorn	21	23	19	33	**6893**	423
Holstein	1347	3258	2205	4188	774	**596,276**

breds are presented on the off-diagonals of Table 3 and numbers of purebreds on the diagonal. Breed composition was calculated for each crossbred animal. Pedigrees were traced to a maximum of five generations. For the oldest generation, breed composition was assumed to equal 100% for the breed coded for that animal. For each descendant, breed composition was set equal to the mean of its parents' breed compositions. If either parent was unknown, the corresponding half of its breed composition was determined from its own breed code. If the progeny breed code was XX and either parent was unknown, breed composition was incompletely known, and the record was excluded. Also, if the parent breed codes matched but the progeny breed code did not the record was excluded. For example, a pedigree was considered invalid if two Holsteins were mated to produce a Jersey.

Herdmates were selected by first sorting the crossbred file by birth year within herd. Cows born between 1 yr prior to the first crossbred birth and 1 yr after the last crossbred birth within a herd were then extracted. When the master data file reached the end of a breed, the crossbred file was reset to the first cow (rewound) so that herdmates of any breed would be extracted for each crossbred cow. This strategy avoided a new sort of the master data file by herd instead of breed and herd. Two seasons were defined: January through June and July through December. Seasonal effects on PL records may be smaller than for yield records because PL is expressed across several years rather than within a year.

The first model for PL included an effect for herd-year-season, a regression on the fraction of genes contributed by each breed, and a regression on the coefficient of heterosis. Regression on Holstein breed content was omitted to avoid linear dependencies and so that all other breeds would be compared with Holstein. Observations were weighted by age, which reflects the cow's opportunity to be culled (VanRaden and Klaaskate, 1993). Solutions were obtained by PROC GLM of SAS (SAS Institute, 1999).

The second model for PL was used to estimate changes in genetic parameters over time. As inbreeding accumulates within each breed, heterosis between breeds could also increase. Interactions of birth year with breed composition and with heterosis were added to the first model. Birth years were coded as differences from 1990 and included in a simple linear regression. Estimated breed differences for 1990 were then updated to 1995 births by adding the genetic trend that occurred over the period 1990–1995 from the national PL evaluation. Again, age weights were applied, and regression and interaction for Holstein breed content were both omitted to make Holstein the standard of comparison.

Economic Comparison

The overall profit from any breed or breed cross depends on yield traits and on several other traits. Net Merit (NM$), Cheese Merit (CM$), and Fluid Merit (FM$) economic values from August 2000 (VanRaden, 2000) were applied to the estimated breed differences and general heterosis to provide an economic analysis of purebreds and crossbreds. Trait values in each index are the same except for milk pricing. Protein receives a higher price in CM$ than in NM$ and a price of zero in FM$, while the fluid volume of milk receives a penalty in CM$ but a reward in FM$. Thus, breeds with higher fat and protein percentages are more profitable with CM$ pricing and less profitable with FM$ pricing.

Breed differences and heterosis for linear composite traits were not available. Estimates of zero were used for udder composite, and feet and legs composite. Assumed breed means for mature body weight were converted to size composite units using the formula 11 kg = 1 size composite unit (Heins et al., 2000). Heterosis of 3% for mature BW was assumed based on an average of literature estimates (Lopez-Villalobos, 1998). Although heterosis results in an increase in BW, larger BW has a negative economic value because the additional feed costs for growth and maintenance exceed the value of the additional beef produced.

Later Generations

First-generation crosses have half of their genes from each of two parent breeds, but later generations may have a range of breed compositions and express less heterosis than the F_1. A coefficient of general heterosis can be calculated as $1 - \Sigma s_i d_i$, where s_i and d_i are fractions of the sire's and dam's genes from breed i, respectively (VanRaden, 1992). Heterosis equals one unless both the sire and dam have genes from the same breed. For this study, summation is over six breeds: Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey, and Milking Shorthorn. In later generations, several of these breeds could be present in one pedigree.

Recombination loss in two-breed crosses was discussed by Van der Werf and de Boer (1989) and Rutledge (2001). The coefficient of recombination loss can be generalized to $1 - \Sigma(s_i^2 + d_i^2)/2$ for multiple-breed crosses. The coefficient of heterosis measures the expression of the dominance effect, plus half of the additive × additive (**A × A**) interaction between the breeds. The coefficient of recombination loss is twice the coefficient of A × A interaction expression, minus the coefficient of heterosis. The coefficient for A × A interaction is the probability that two genes at unlinked loci are from different breeds, or $1 - \Sigma p_i^2$, where p_i is the breed composition of the progeny. Substitution of the simple identity $p_i = (s_i + d_i)/2$ and cancellation of $\Sigma s_i d_i$ gives the formula above for recombination loss. With estimates of general heterosis and general recombination loss, the nonadditive merit of any breed mix can be predicted.

RESULTS AND DISCUSSION

Yield Traits

Means of test-day yields for Holsteins, across all lactations were 31.5 kg of milk, 1.12 kg of fat, and 0.94 kg of protein. These are equivalent to actual 305-d yields of 9608 kg of milk, 342 kg of fat, and 287 kg of protein. Estimated breed differences from Holstein ranged from –7.5 to –4.7 kg/d for milk, –0.19 to –0.07 kg/d for fat, and –0.16 to –0.06 kg/d for protein. Means of yields for Holsteins, for first parity were 28.5, 1.01, and 0.85 kg/d for milk fat and protein, respectively. Estimated breed differences for first parity were slightly less, on average, across traits. Estimated yields for other breeds were obtained by adding estimated breed differences to the Holstein breed mean.

Standard deviations of test-day yields across all breeds were 9.6 kg of milk, 0.37 kg of fat, and 0.27 kg of protein across all parities; and 7.5 kg of milk, 0.28 kg of fat, and 0.21 kg of protein in first parity. Residual standard deviations after removing all effects in the model were 6.5 kg of milk, 0.29 kg of fat, and 0.19 kg of protein across all parities; and 5.2 kg of milk, 0.23 kg of fat, and 0.15 kg of protein in first parity.

Estimates of general heterosis were 1.03 kg of milk, 0.048 kg of fat, and 0.037 kg of protein across all lactations. When expressed as percentages of weighted parent breed averages, the heterosis estimates were 3.4, 4.4, and 4.1%, respectively, for milk, fat, and protein. A model without the regression on sire's PTA gave slightly lower estimates, indicating that the sires of crossbreds had slightly lower merit than the sires of their purebred herdmates. Analysis of first-lactation records gave slightly higher estimates of heterosis, ranging from 4.0 to 4.9%.

Estimates of specific heterosis are in Table 4. Only crosses of Holstein with the other breeds are given because these represent such a large majority of the total number of crossbreds. Solutions for fat yield ranged from 7% heterosis for Holstein sire × Guernsey dam to –2% for Ayrshire sire × Holstein dam. Solutions for protein yield ranged from 7% heterosis for Holstein sire × Jersey dam to –2% for Ayrshire sire × Holstein dam. Estimates were always higher when Holstein was the sire breed rather than the dam breed. A negative maternal breed effect for Holstein could be the cause, but maternal effects were not studied directly. Another possible cause is that regression of yield on sire PTA was assumed constant but could differ for crossbred vs. purebred progeny. Finally, the two reciprocal crosses would tend to have herdmates of different breeds.

Regressions of actual test-day yields on sire's PTA for standardized lactation yield were multiplied by 305 to make results more interpretable. Regressions for milk, fat, and protein were 0.91, 0.96, and 0.93, respectively. These regressions were expected to be less than 1.00 because age adjustment of test-day yields was by additive rather than multiplicative factors.

Somatic Cell Score

Mean SCS for Holsteins was 2.95 across all parities and 2.63 in first parity. Estimated breed differences from Holstein ranged from –0.29 to +0.18. These breed differences in SCS obtained from within herd comparisons were generally smaller than breed differences obtained from national means. In first parity, Jerseys and Guernseys had higher SCS than Holsteins (2.82 and 2.80 vs. 2.63, respectively), but not across all parities. Age adjustment factors of Schutz et al. (1995) also indicate that Jerseys have higher SCS in first parity but not in later parities. Other breeds had SCS lower than Holsteins.

Standard deviation of SCS across all breeds was 1.90 across all parities and 1.77 in first parity. Residual standard deviation after removing all effects in the model was 1.76 across all parities and 1.64 in first parity.

General heterosis for SCS (0.016) was small and positive (unfavorable). Expressed as a percentage of

Table 4. Specific heterosis as a percentage of parent breed averages (H%), general heterosis, and general recombination estimates for yield traits.

	Milk				Fat				Protein			
	Holstein sire		Holstein dam		Holstein sire		Holstein dam		Holstein sire		Holstein dam	
Second breed	H%	SE	H%	SE	H%	SE	H%	SE	H%	SE	H%	SE
Ayrshire	2.4	1.0	–2.0	1.9	2.7	1.3	–1.8	2.3	2.9	1.1	–2.4	1.9
Brown Swiss	5.6	1.3	3.2	0.8	4.8	1.6	4.5	1.0	4.7	1.3	3.8	0.8
Guernsey	5.2	0.7	2.4	2.0	7.1	0.9	4.4	2.3	5.5	0.8	4.0	2.0
Jersey	7.5	1.1	1.6	0.6	6.6	1.4	4.5	0.8	7.2	1.1	4.1	0.7
Milking Shorthorn	2.8	1.8	0.3	1.9	3.2	2.4	1.3	2.4	3.6	1.9	1.2	1.9
General heterosis	3.4% (SE = 0.3)				4.4% (SE = 0.4)				4.1% (SE = 0.4)			
General recombination	2.2% (SE = 1.2)				2.2% (SE = 1.6)				1.9% (SE = 1.3)			

weighted parent breed average, the estimate becomes 0.66% (SE = 0.92). Crossbreeding often leads to increased health, but the higher yields of crossbreds also may increase the stress on the udder and could be the cause of the small net increase in SCS. The slightly higher heterosis for fat and protein yield than for milk yield indicates a more concentrated milk in the crossbreds, which could also raise SCS as a correlated response.

Regressions of actual test-day SCS on sire's PTA for standardized lactation SCS were 0.86 in first lactation and 0.92 in all lactations. These SCS regressions were not multiplied by 305 because lactation SCS is an average rather than a total of daily SCS. Again, regressions were expected to be less than 1 because additive age adjustments were used rather than the multiplicative factors used in calculating PTA SCS.

Productive Life

Mean PL for Holsteins born in 1990 was 23.8 mo. Holsteins had longer ($P < 0.0001$) PL than all other breeds when compared within herd-year-seasons and over the full 32-yr period. Guernseys stayed in the milking herd 6.0 mo less than Holstein herdmates ($P < 0.0001$), whereas Jerseys compared more favorably at 1.7 mo less ($P < 0.0001$). Mean PL was 24.3 mo for F1 crossbred cows and 25.1 mo for herdmates, with standard deviations of 13.5 and 13.3 mo, respectively. Statistics for herdmates are similar to those reported previously for Holsteins (VanRaden and Klaaskate, 1993) because most herdmates were Holsteins.

The estimate of general heterosis for PL was positive but small compared with breed differences and remained constant across time at 0.3 mo. Matings among the Jersey, Brown Swiss, and Holstein breeds can produce crossbred progeny that on average will stay in the herd as long or longer than purebred Holsteins. The heterosis estimate of 1.2% obtained here was very small compared with the 9% estimate reported by Hocking et al. (1988) in research herds.

Some breed differences changed significantly across time. Jerseys, Ayrshires, and Brown Swiss have improved relative to Holsteins ($P < 0.0001$). In more recent years, Jerseys slightly exceeded Holsteins in genetic merit for PL. Positive phenotypic trend for Jersey herd life was noted earlier by Nieuwhof et al. (1989).

Economic Analysis

Breed means for traits used in computing merit indexes are summarized in Table 5.

Breed differences relative to Holstein for the three merit indexes are in Table 6 and are reported as BV (the effect of all the genes) rather than as TA (the effect of half the genes). Holsteins were more profitable than any other purebreds under all three pricing systems. Estimates of general heterosis for NM$, CM$, and FM$ were $197, $207, and $163, respectively. Merit of F1 crosses equals the mean of the parent breed effects plus the heterosis. For example, Jerseys had an additive value of –$305 for NM$ as compared with Holsteins. Thus, the NM$ for F1 Jersey × Holstein crosses is (0–$305)/2 + $197 or $44. Jersey × Holstein and Brown Swiss × Holstein crosses both had higher NM$ and CM$ than Holsteins. Two other crosses (Brown Swiss × Jersey and Ayrshire × Holstein) had CM$ only slightly less than Holsteins (–$14 and –$21, respectively). Holsteins had higher $FM than any F1 crossbred. Average merit estimates for F1 Holstein crosses are given on the Holstein scale in Table 7.

Genetic evaluations that include crossbreds often have subtracted the heterosis and reported only the remaining additive effects. An alternative is to provide multiple rankings where each animal is considered as a potential mate within each breed. Such predictions include the additive genetic merit of each animal and the nonadditive genetic merit of the cross. Animals of

Table 5. Breed means and general heterosis for traits used in merit indexes.

	Milk (kg/d)	SE of diff[1]	Fat (kg/d)	SE of diff[1]	Protein (kg/d)	SE of diff[1]	SCS	SE of diff[1]	PL (mo)	SE of diff[1]	Mature size[2] (kg)
Ayrshire	26.3	0.24	0.99	0.01	0.81	0.008	2.86	0.07	23.2	0.2	550
Brown Swiss	26.8	0.14	1.04	0.01	0.87	0.004	2.96	0.04	23.8	0.2	680
Guernsey	24.1	0.21	1.01	0.01	0.77	0.007	3.01	0.06	18.2	0.2	520
Jersey	23.9	0.04	1.04	0.01	0.81	0.004	3.14	0.04	25.8	0.1	450
Milking Shorthorn	25.6	0.39	0.92	0.02	0.78	0.012	2.98	0.12	19.5	0.5	590
Holstein	31.5	. . .	1.12	. . .	0.94	. . .	3.10	. . .	24.3	. .	680
General heterosis	3.4%		4.4%		4.1%		0.7%		1.2%		3.0%

[1] SE of the estimated difference from Holstein.

[2] Values obtained from literture estimates.

different breeds receive credit for heterosis but animals of the same breed do not. For example, if a purebred Holstein sire and purebred Jersey sire are compared as potential mates for a Holstein cow, the progeny of the Jersey sire will receive half of the breed difference plus heterosis. If the same two sires are compared as potential mates for a Jersey cow, the progeny of the Holstein sire will receive the heterosis but the progeny of the Jersey sire will not. Thus, when gene action is nonadditive, the ranking of an animal depends on the target population.

Crossbreds may have additional advantages for traits not included in the merit indexes. Specifically, fertility, calving ease, and calf mortality were not considered. Also, the above comparisons are for animals at the 2000 genetic base for each breed (cows born in 1995). A comparison of the highest animals available for selection in each breed would favor Holsteins because more extreme animals are available in a larger population.

The very best available sires of the other breeds did not rank as high as the best available Holstein sires as potential mates for Holstein cows. For example, the highest NM$ among Jersey sires in May 2001 was $472. Addition of $44 for the effect of heterosis and breed difference provides an estimate of $516 on the Holstein scale, which was lower than 93 Holstein sires. Similarly, the top Brown Swiss sire at $546 converted to $564 on the Holstein scale, which was lower than 29 Holstein sires. Thus, the use of crossbreeding will be limited in practice by the lower number of bulls being progeny tested in the other breeds and the reduced range of evaluations that result. This reduced selection intensity and slower expected genetic progress in the other breeds will cause breed differences to increase over time.

Heterosis is also expected to increase over time as relationships increase within breeds but not across breeds. Inbreeding coefficients currently are increasing by 2 to 3% per decade in most US dairy breeds, and the corresponding inbreeding depression that accumulates is all removed by crossing. Using estimated regressions from Wiggans and VanRaden (1995), heterosis for yield traits should increase by 0.6 to 0.9% per decade. Thus, future profits from crossbreeding could increase or decrease as heterosis, breed differences, and economic values of traits change across time.

Later Generations

General recombination effects for milk, fat, and protein were about half as large as corresponding estimates of general heterosis and positive, not negative (gains instead of losses). Lopez-Villalobos (1998) reported a wide range of recombination effects across literature estimates but generally negative and smaller than heterosis in absolute value. Rutledge (2001) reported on the large recombination losses that often occur in wide crosses. The recombination effects estimated from our

Table 6. Breed differences for merit indexes expressed as the breeding value difference from Holstein.

	Net merit ($)	Cheese merit ($)	Fluid merit ($)
Ayrshire	–510	–469	–728
Brown Swiss	–355	–256	–808
Guernsey	–761	–692	–1117
Jersey	–305	–186	–865
Milking Shorthorn	–892	–862	–1073
Holstein	. . .	. . .	. . .
General heterosis	$197	$207	$163

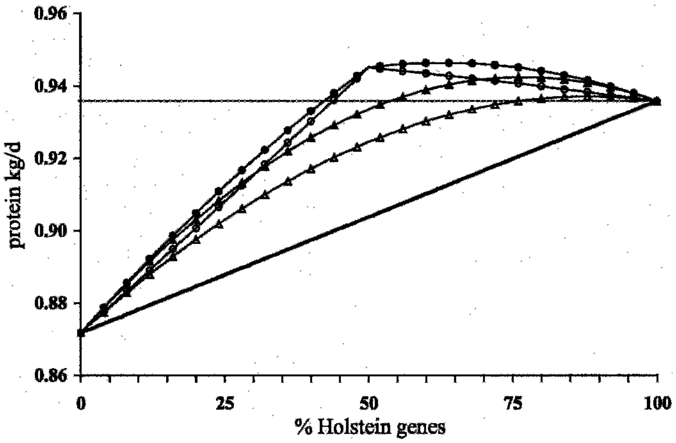

Figure 1. Predicted protein yields for all possible Brown Swiss × Holstein crosses in models with additive, dominant, and epistatic breed effects (--- Holstein mean; —— additive effects; ○ additive + dominance effects, with maximum heterosis; ● additive + dominance + epistatic effects, with maximum heterosis; △ additive + dominance effects, with minimum heterosis; ▲ additive + dominance + epistatic effects, with minimum heterosis.

data indicate that if F1 crosses are superior to purebred Holsteins for protein yield, then backcrosses to Holstein will also be superior.

Predicted additive and nonadditive merits can be displayed graphically for all possible crosses between two breeds. Maximum heterosis occurs when parent breed compositions are the most different and minimum heterosis occurs when the two parents have identical breed composition. Thus, for progeny of a particular breed composition, minimum heterosis occurs with a synthetic population. Figure 1 provides examples of maximum and minimum heterosis for two different models. With a model containing only additive and dominance effects, the F1 and all possible backcrosses are represented by the upper, jointed straight lines. These jointed straight lines become jointed quadratic curves if A × A effects are added to the model. Additive breed effects are displayed on the bottom, straight line.

Predicted merits for all possible synthetic populations are represented by the two lower, smooth curves in Figure 1. The lower of the two is for the model including only additive and dominance effects because A × A interaction was positive in this study. Predicted merits for any other crosses lie between the upper and lower curves. The merit of any particular cross is the sum of the breed fractions multiplied by the breed additive effects, the heterosis coefficient multiplied by the heterosis estimate, and the recombination coefficient multiplied by the recombination estimate.

CONCLUSIONS

Currently, <0.5% of US milk recorded cows are crossbred. Breed differences and heterosis were estimated from 572 DHI herds each containing 5 or more crossbred cows. General heterosis for yield traits was 3.4 to 4.4% of the purebred mean. Heterosis for SCS was <1% of the purebred mean and unfavorable. Heterosis for PL was positive, but only 1.2% of the purebred mean. Milk yield of Holsteins (31.5 kg/d) was higher than all other breeds and crossbreds. Fat yield (1.12 kg/d) and protein yield (0.94 kg/d) of Holsteins was similar to that of Brown Swiss × Holstein crossbreds (1.13 kg/d of fat and 0.94 kg/d of protein), and Jersey × Holstein crossbreds (1.14 kg/d of fat and 0.92 kg/d of protein). Breeds and breed crosses were compared at genetic bases of 0 using three merit functions that differed in milk pricing method and included SCS, productive life, and cow size but did not directly include fertility, mortality, calving ease, or other health and conformation traits. F1 crosses of Brown Swiss or Jerseys with Holsteins were more profitable than purebred Holsteins with two of the three pricing methods. Breeds with smaller mature body size were credited for their higher efficiency. A joint evaluation of all breeds could estimate genetic merit of each animal regardless of breed and include crossbred animals but would require an extensive programming effort. Simple formulas and graphs were developed to predict recombination effects in all possible crosses, but estimates for recombination were positive instead of negative and SE were large. Heterosis for yield could increase by 0.6 to 0.9% per decade because inbreeding coefficients are increasing by 2 to 3% within most breeds, making crossbreeding more attractive over time. Currently, elite Holstein matings have higher economic merit than elite crossbred matings because of

Table 7. Average merit of F_1 Holstein crosses on the Holstein scale.

Second breed	Net merit ($)	Cheese merit ($)	Fluid merit ($)
Ayrshire	–58	–27	–201
Brown Swiss	18	79	–241
Guernsey	–184	–138	–395
Jersey	44	113	–269
Milking Shorthorn	–249	–223	–373

the Holstein breed's larger population size and greater range of genetic evaluations than the other breeds.

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REFERENCES

Boichard, D., B. Bonaiti, and A. Barbat. 1993. Effect of Holstein crossbreeding in the French black and white cattle population. J. Dairy Sci. 76:1157–1162.

Cunningham, E. P. 1983. Structure of dairy cattle breeding in western Europe and comparisons with North America. J. Dairy Sci. 66:1579–1587.

Harris, B. L. 1994. Animal model for New Zealand dairy cattle evaluation. Open Session INTERBULL Annu. Mtg., Ottawa, Canada, Aug. 5–6, 1994. Int. Bull Eval. Serv. Bull. No. 10. Dep. Anim. Breed. Genet., Uppsala, Sweden.

Heins, B. J., L. B. Hansen, A. J. Seykora, and G. D. Marx. 2000. Impact on body weight of divergent selection for body size. J. Dairy Sci. 83(Suppl. 1):74. (Abstr.)

Hocking, P. M., A. J. McAllister, M. S. Wolynetz, T. R. Batra, A. J. Lee, C. Y. Lin, G. L. Roy, J. A. Vesely, J. M. Wauthy, and K. A. Winter. 1988. Factors affecting length of herdlife in purebred and crossbred dairy cattle. J. Dairy Sci. 71:1011–1024.

Interbull. 2000. National genetic evaluation programmes for dairy production traits practiced in Interbull member countries. Bull. 24, SLU, Uppsala, Sweden.

Lesmeister, K. E., D. W. Kellogg, A. H. Brown, Jr., Z. B. Johnson, and A. G. Lane. 2000. Effects of crossbreeding and season of calving on production of milk fat and protein of primiparous dairy cows. J. Dairy Sci. 83(Suppl. 1):52. (Abstr.)

Lopez-Villalobos, N. 1998. Effects of crossbreeding and selection on the productivity and profitability of the New Zealand dairy industry. Ph.D. thesis, Massey University, Palmerston North, New Zealand.

Lopez-Villalobos, N., D. J. Garrick, C. W. Holmes, H. T. Blair, and R. J. Spelman. 2000. Profitabilities of some mating systems for dairy herds in New Zealand. J. Dairy Sci. 83:144–153.

McAllister, A. J., A. J. Lee, T. R. Batra, C. Y. Lin, G. L. Roy, J. A. Vesely, J. M. Wauthy, and K. A. Winter. 1994. The influence of additive and nonadditive gene action on lifetime yields and profitability of dairy cattle. J. Dairy Sci. 77:2400–2414.

McDowell, R. E. 1985. Crossbreeding in tropical areas with emphasis on milk, health, and fitness. J. Dairy Sci. 68:2418–2435.

Nieuwhof, G. J., H. D. Norman, and F. N. Dickinson. 1989. Phenotypic trends in herdlife of dairy cows in the United States. J. Dairy Sci. 72:726–736.

Rutledge, J. J. 2001. Greek temples, tropical kine, and recombination load. Livest. Prod. Sci. 68:171–179.

SAS Institute Inc., SAS Online Doc, Version 8, Cary, NC: SAS Insitute Inc., 1999.

Schutz, M. M., P. M. VanRaden, G. R. Wiggans, and H. D. Norman. 1995. Standardization of lactation means of somatic cell scores for calculation of genetic evaluations. J. Dairy Sci. 78:1843–1854.

Swan, A. A., and B. P. Kinghorn. 1992. Evaluation and exploitation of crossbreeding in dairy cattle. J. Dairy Sci. 75:624–639.

Touchberry, R. W. 1992. Crossbreeding effects in dairy cattle: The Illinois experiment, 1949 to 1969. J. Dairy Sci. 75:640–667.

Van der Werf, J. H. J., and W. de Boer. 1989. Estimation of genetic parameters in a crossbred population of black and white dairy cattle. J. Dairy Sci. 72:2615–2623.

VanRaden, P. M. 1992. Accounting for inbreeding and crossbreeding in genetic evaluation of large populations. J. Dairy Sci. 75:3136–3144.

VanRaden, P. M. 1995. Merits of purebred and crossbred dairy cows for productive life. J. Dairy Sci. 78(Suppl. 1):159. (Abstr.)

VanRaden, P. M. 2000. Net Merit as a measure of lifetime profit. AIPL Research Report NM$1. Available: http://aipl.arsusda.gov/memos/html/nm2000.html.

VanRaden, P. M., and E. J. H. Klaaskate. 1993. Genetic evaluation of length of productive life including predicted longevity of live cows. J. Dairy Sci. 76:2758–2764.

VanRaden, P. M., and G. R. Wiggans. 1995. Productive life evaluations: Calculation, accuracy, and economic value. J. Dairy Sci. 78:631–638.

Wiggans, G. R. 1989. Animal model evaluation of dairy goats for milk, fat, and protein yields with crossbred animals included. J. Dairy Sci. 72:2411–2416.

Wiggans, G. R., and P. M. VanRaden. 1995. Calculation and use of inbreeding coefficients for genetic evaluation of United States dairy cattle. J. Dairy Sci. 78:1584–1590.

Young, C. W. 1984. Systems of mating—problems and opportunities. Page 61–72 in Proc. Natl. Inv. Workshop on Genet. Impr. Dairy Cattle, Milwaukee, WI. Cornell Univ., Ithaca, NY.