Is Crossbreeding the Answer to Questions of Dairy Breed Utilization?¹

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ABSTRACT

The current interest in crossbreeding in the commercial dairy industry, even though it is quite limited, raises questions of breed utilization. Fewer than 5% of US dairy cattle are other than purebred or grade Holsteins. The large advantage of Holsteins for additive genetic merit for lactation milk yield is apparently responsible for this trend. Why, then, this interest in crossbreeding? The economic importance of traits such as reproduction, health, and survival in dairy production systems is likely the basis for the interest in crossbreeding, even though these traits are secondary to milk yield. Several US studies and a Canadian study confirmed that while several crossbred groups were equivalent to Holsteins for lactation milk yield, none were superior. Two crossbred groups in the Canadian study had lifetime yields, milk value, and net returns equivalent to Holsteins. In the New Zealand study, Friesian-Jersey reciprocal crossbreds were predicted to exceed Friesians in first-lactation fat yield. Crossbred performance is dictated by a combination of additive and nonadditive genetic effects. Evidence exists for direct, maternal, heterosis, and cytoplasmic maternal effects. Heterosis of 15 to 20% for lifetime traits was found in two studies. Results from previous crossbreeding studies have something to recommend for inclusion of Holstein, Ayrshire, Brown Swiss, and Jersey breeds in a crossbreeding scheme. However, multiple-generation lifetime performance on an array of purebreds and crossbreds under US condition does not exist. Full unique identification of individual animals, including breed composition, would permit the use of DHIA data to estimate additive and nonadditive genetic parameters for the traits recorded therein. Survival data from birth and health data would need to be fully recorded

to provide complete data on lifetime performance. Self-propagation of crossbred replacements is mandatory if any crossbreeding system is to be successful. Based on current empirical data, a two-breed rotational crossing system appears to be the most viable system to maximize economic merit. The theoretical advantages of a three-breed rotational crossing system are clear, but the data to recommend the third breed and this system in practice are limited. Full-scale long-term breeding experiments or analysis of field data paired with a comprehensive modeling of alternative breed utilization strategies for US conditions are recommended.

(Key words: crossbreeding, dairy breed utilization)

Abbreviation key: ADNR = annualized discounted net returns.

INTRODUCTION

The rather limited but current interest in crossbreeding in commercial US dairy industry is an interesting development. The critical scientific debate regarding crossbreeding with dairy cattle populations, not surprisingly, was framed by Jay L. Lush. In his "Genetics of Populations" course notes (Lush, 1948), he lists a number of considerations involved in deciding to make a new breed. He states in these notes from over 50 years ago:

"The demonstrated commercial success of hybrid corn and hybrid chicks has made it seem biologically possible to make several new breeds, each good in some specific combinations although its own average phenotypic merit may be only mediocre. Using these breeds in rotational crossbreeding plans might be more profitable for commercial production than would raising any pure breeds which are available. This has been successful with chickens and (to a lesser extent) with pigs. Could it be extended profitably to other species which are less prolific and have longer generation intervals?"

The theoretical basis for crossbreeding effects in dairy cattle performance has been presented in previous symposia on this subject (Willham and Pollak, 1985; Swan and Kinghorn, 1992). It is sufficient here to reiterate that heterotic contributions to crossbred perfor-

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Table 1. Range in heterosis values for different types of dairy performance traits.¹

Trait	Heterosis (%)
Yields	5.0–6.6
Viability (livability)	3.7–4.6
Growth	3.2–5.7
Reproduction	0.8–5.0

¹Source: McDowell, 1982.

mance can be the result of dominance and epistasis and the differences in the frequencies of the different alleles at each locus that contributes to the trait. The total genetic makeup of crossbreds can include additive effects, dominance, maternal effects (both nuclear and cytoplasmic), maternal heterosis, and recombination effects. The particular kinds of crosses will determine what effects may be present and estimable.

A SURVEY OF RELEVANT DAIRY CROSSBREEDING STUDIES

Touchberry (1992) nicely summarized the dairy crossbreeding research and, hence, the scientific interest that preceded Lush's probing question. Three of these experiments were undertaken before 1920, some before routine collection of butterfat percentage data. Mendelian versus polygenic inheritance was also a focus of the analysis of milk yield, fat percentage, color, and color pattern.

The USDA crossbreeding study initiated in 1939 (Fohrman et al., 1954) sought to answer Lush's question with a study of two- and three-breed crosses involving Holstein, Jersey, Red Dane, and Guernsey using Holstein, Jersey, and Red Dane proved sires. The authors concluded that "there is sufficient evidence presented here to indicate that female progeny of crossbred cows when sired by production proved bulls will develop into very satisfactory dairy animals".

The four research herds whose results formed the S-49 regional project were used to determine whether hybridization would produce cattle of improved adaptability and productivity (McDowell, 1982). Heterosis was found for many types of dairy performance traits (Table 1). His conclusions affirmed many of those reported earlier (Fohrman et al., 1954). In particular, he concluded that: "Crossbreds may not exceed the best purebred for any single trait, yet the net economic merit of crossbreds may be superior to purebreds when all traits affecting or influencing net income are considered".

The Illinois crossbreeding study of Holsteins and Guernseys was conducted from 1949 to 1969. Touchberry (1992) described the objectives of the experiment

to assess the amount of heterosis for milk yield and its components and to estimate the importance of survival, reproduction, and growth in determining the total performance of crossbreds. Elegant and rigorous analyses showed various advantages of crossbreds over purebreds. He concluded:

"The measures of survival, growth, milk yield, and reproduction were appropriately combined into an index of income produced per cow. On a basis of income per lactation, crossbreds exceeded purebreds by 14.9%. On a basis of income produced per cow per year, crossbreds exceeded purebreds by 11.4%."

A Canadian study of dairy cattle selection and crossbreeding (McAllister et al., 1994) was begun before McDowell's summary of four crossbreeding trials was published. This study sought to extend the earlier studies with greater numbers of animals and to examine the use of selection and crossbreeding simultaneously with pureline cattle populations previously a part of a closed herd selection project for total solids yield. Further, multiple-lactation yield and lifetime performance of contemporary purebred and crossbred groups were foci of this project.

The Canadian Department of Agriculture study (McAllister et al., 1994), conducted in five herds, investigated use of a repeated hybrid male cross in a closed-herd breeding system. Purebreds and crossbreds were evaluated to estimate additive and nonadditive genetic influences on 1) lifetime yields, 2) a comprehensive array of growth, health, and reproductive traits and 3) the composite influence of these traits on lifetime annualized discounted net returns (ADNR). They reported large heterosis (>20%) for lifetime performance and a cytoplasmic maternal effect on ADNR that favored the Ayrshire based pureline. Some crossbred groups had lifetime performance equivalent to the superior Holstein pureline.

Analysis of New Zealand field data of primiparous Holsteins, Jerseys, and various crossbreds (Ahlborn-Breier and Hohenboken, 1991) revealed an individual breed effect favoring Holstein, a maternal effect on milk yield favoring Jersey, heterosis of 6.1% for milk yield and 7.2% for fat yield, a small negative maternal heterosis for fat percentage and a small cytoplasmic maternal effect favoring Holsteins on fat percentage. F₁ Jersey × Holstein and their reciprocal cross were estimated to exceed Holstein for fat yield (Figure 1).

Later studies of New Zealand field data (Harris, personal communication) reported significant heterotic effects of New Zealand Holstein Friesian × Jersey for milk, fat, and protein yields; live weight; reduced days to first mating; positive calving rate from successful AI; and survival from first to fifth lactations. In a study using survival analysis methods (Harris, personal com-

Figure 1. Relative performance of New Zealand Holsteins, Jerseys, and their crossbreds. All groups for each trait are statistically different ($P < 0.05$) from one another, except the two F_1 groups.

munication), 21% heterosis for mean residual life was reported. They also found beneficial heterosis for days to first mating and calving rate from AI.

A COMPREHENSIVE ASSESSMENT OF DAIRY CROSSBREEDING

Multi-Lactation Yield/Lifetime Performance/Economic Merit

Only two studies have attempted to characterize the additive and nonadditive genetic influences on multiple lactation or lifetime performance. Touchberry (1992) used the sum of the first two lactation yields. The Illinois study contained an analysis of the value of yield and animals sold per lactation and per year to account for reproductive rate, culling, BW, and yield. Whereas the heterosis values for total dollar value produced per cow per lactation were nearly 15%, it was estimated that the crossbreds earned only 92% of the income per cow per lactation and 90% of the income per cow per year of the better purebred. The inferior purebred was only 61% of the superior purebred for milk yield. Heterosis would have to have exceeded 25% for the crossbreds to exceed the superior purebred (Nagai and McAllister, 1982) if one assumes a genetic model which includes additive direct breed effects and direct heterosis.

The Canadian study (McAllister et al., 1994) used lifetime data for all animals until either culling, death, or the end of the project occurred. Complete lifetime survival and health, growth, reproduction, and lactation events had been recorded. Calf value at birth and salvage value were also included. Cost and income val-

Table 2. Estimated annualized discounted net returns (ADNR) from different breeding systems.

Genetic group (sire $\times$ dam) ¹	ADNR(\$)
H $\times$ H	234.8
H $\times$ A	292.5
A $\times$ H	210.8
RHMC (based on H $\times$ A)	225.4
TBRC ² (based on H $\times$ A)	
Cycle 1, H.H $\times$ A	304.5
Cycle 2, A.H.H $\times$ A	219.4
Cycle 3, H.A.H.H $\times$ A	301.5
Cycle 4, A.H.A.H $\times$ A	201.3
Cycle 5, H.A.H.A.H $\times$ A	300.8

¹Source: McAllister et al., 1994.

²TBRC = two breed rotational cross.

ues were assigned to form the basis of the ADNR calculation. Heterosis values for lifetime milk fat, protein, and lactose yields and lifetime milk value were 16.5, 20, 17.2, 16.6, and 17.9%, respectively. Heterosis for ADNR was 20.6 percent. Statistically significant genetic solutions for ADNR were: \$316.50 for direct additive (H minus A), \$134.30 for heterosis, and -\$81.70 for the cytoplasmic maternal (H minus A) effect. Predicted performance for ADNR of different breeding systems showed a two-breed rotational cross to be superior (Table 2) to the better purebred and the repeated hybrid male cross.

They performed nonorthogonal contrasts among the various pureline breeding and crossbred groups and found a difference between the purelines that favored Holsteins and an advantage for F_1 's compared with the parent purelines (Table 3). The F_1 's exceeded the second-generation crossbreds for lifetime milk, protein, and lactose yields. Examination of the breeding group solutions (Table 4) for lifetime milk value and ADNR showed no statistical difference between any of the crossbred groups and the Holstein pureline. In fact, the H $\times$ A F_1 and one of the third-generation crossbred groups had over \$100 more ADNR than the Holstein pureline. ADNR values give an annualized net return value per female born alive. Kulak et al. (1997) concluded that adjustment of lifetime profit for opportunity cost would provide an improved measure of profitability.

An examination of production of female replacements by purebreds and F_1 's gave an estimate of the total reproductive output of the breeding system (McAllister et al., 1994). The F_1 's generated 1.28 replacements per female born compared with 0.7 for the contemporary purelines.

Investigators in New Zealand have sought to evaluate the profitability of alternative breeding systems under New Zealand pastoral conditions (Lopez-Villalobos, et al. 2000). They developed a comprehensive determin-

Table 3. Significant nonorthogonal contrasts among breeding group means¹ and heterosis values for lifetime yields, milk value and annualized discounted net returns (ADNR).²

	Contrast			Heterosis %
	F ₁ vs. P	P _H vs. P _A	F ₁ vs. C ₁	
Lifetime milk (kg)	2018**	3284**	1300*	16.5
Lifetime fat (kg)	77.5**	72.7**	...	20.0
Lifetime protein (kg)	71.1**	96.4**	93.6*	17.2
Lifetime lactose (kg)	102.3**	161.4**	67.8*	16.6
Lifetime milk values (\$)	1112**	1465**	...	17.9
ADNR (\$)	134.9**	194.9**	...	20.6

¹H = Holstein pureline, C = crossbred line (i.e., F₁ × F₂), B = backcross, P = parental breeds and A = Ayrshire-based pureline.

²Source: McAllister et al. (1994).

istic model based on a 25-yr planning horizon that, on an annual basis, simulated nutritional, biological, and economic performance of straightbreeding, and rotational crossbreeding using two or three New Zealand breeds. Breeds considered were Holstein-Friesian, Jersey, and Ayrshires. Breed additive effects and heterosis for milk, fat, and protein yields, BW, and survival were taken from analyses of field data in New Zealand. The economic analysis revealed the largest advantage in net income per hectare for a Holstein-Jersey rotational cross (\$505 NZ \$/yr), which was only slightly larger than that for a Holstein-Jersey-Ayrshire rotational cross (\$493 NZ \$/yr). Rankings were similar among the various breeding groups for net income per cow. However, for milk income, Holsteins and these rotational cross groups were nearly identical.

Information Still Needed

The relatively recent crossbreeding results from Canada and New Zealand would seem to recommend cross-

breeding as a rational plan of breed utilization for the commercial dairy industry of the United States. However, criticisms and deficiencies of the studies thus far must be acknowledged:

None have directly involved current US genetics for any of the breeds studied except the current composition of New Zealand Holstein.

None have involved current US dairy production conditions, including market values.

None have involved a multi-generation economic comparison of Holsteins and a contemporary crossbred population.

Popular reports of crossbreeding being done by dairy producers confirm the interest in crossbreeding, but the degree is difficult to quantify except in DHI recorded populations (VanRaden and Sanders, 2001). One can only guess why producers are choosing crossbreeding as an option. A desire to improve component percentages, fertility, survival, longevity, and perhaps heat tolerance would appear to be key reasons.

Table 4. Pureline and crossline genetic group solutions and standard errors for value of lifetime milk production and annualized discounted net returns (ADNR).¹

Genetic group ²	Lifetime milk value		ADNR	
	Sol ³	SE ⁴	SOL	SE
	(\$)			
H	6948.5	542.8	753.7	54.2
A	5484.0	539.9	558.2	53.4
C ₀₁ = H × A	7621.6	663.6	857.7	66.1
C ₀₂ = A × H	7037.5	637.7	723.4	62.4
C ₁₁ = C ₀₁ × C ₀₂	6722.3	713.2	702.1	70.7
C ₁₂ = C ₀₂ × C ₀₁	6537.4	685.2	745.1	67.8
C ₂₁ = C ₀₁ × C ₁₁	6323.7	764.3	663.2	75.2
C ₂₂ = C ₀₂ × C ₁₂	6994.1	776.2	859.1	78.4
B ₁₁ = A × C ₀₁	5480.7	1383.6	669.7	136.2
B ₁₂ = A × C ₀₂	5619.9	1137.7	634.8	107.9
B ₁₃ = H × C ₀₁	5879.8	1138.6	725.8	117.0
B ₁₄ = H × C ₀₂	6504.9	1290.1	750.1	119.1

¹Source: McAllister et al. (1994).

²H = Holstein pureline, A = Ayrshire-based pureline, C = crossbred line, and B = backcross.

³Genetic group solution.

⁴Standard error.

Table 5. Four breed diallel of US dairy breeds to produce F_1 's, three-way crosses and backcrosses.¹

	Dam breed			
	Ayrshire (150)	Brown Swiss (150)	Holstein (150)	Jersey (150)
Sire breed	No. Females			
Ayrshire	150	150	150	150
Brown Swiss	150	150	150	150
Holstein	150	150	150	150
Jersey	150	150	150	150

¹Each reciprocal F_1 group could be divided randomly to produce three way crosses or backcrosses.

Obtaining the Information Needed

A multi-generational breeding experiment where life-time performance was measured on Ayrshires, Brown Swiss, Holsteins, and Jerseys could provide the information needed. Such an experiment could require a total of 2400 females (Table 5) if a full diallel mating plan were used. A full diallel is the simplest design that would provide estimates of breed additive effects, heterosis effects and breed additive maternal effects. From such a full diallel mating scheme of the breeds, each reciprocal F_1 group could then be divided into two groups; one to produce three-way crosses and the other to produce equal numbers of backcrosses of the two types possible for that particular F_1 . The production of three-way crosses and backcrosses would be recommended and would permit a direct comparison of these breeding groups, which are the candidate groups dairy producers practicing crossbreeding could produce. Backcrosses to both parent breeds would permit the estimation of breed cytoplasmic maternal effects. However, backcrossing versus three-way crosses provides no opportunity to estimate additional genetic parameters. A further benefit of such a design would be the opportunity to examine heat tolerance and genotype by environment interaction. Locations in northern and southern US regions would permit comparison with their accompanying cooler and warmer seasonal climates. Comparison of intensive dry-lot production systems versus extensive pasture based grazing could be built into the design.

Molecular genetic techniques could also be used with such a design for the detection of major genes across breeds. Are there university or government research herds or combinations thereof composed of the requisite breeds and of sufficient size? Are there fully pedigreed private herds willing to submit to a common experimental protocol and recording scheme for a minimum of 12 yr to collect first-lactation data and at least five more years for lifetime data? Unfortunately, a project of this scale and scope is not likely to materialize.

The combination of field data analysis and a modeling approach (Lopez-Villalobos et al., 2000) is more proba-

ble. Full capture of all data from herds practicing crossbreeding would be desirable to be able to take advantage of all the analytical tools available to examine data on crossbreds and contemporary purebreds (VanRaden and Sanders, 2001).

Straightbreeding, virtually exclusively, defines the current utilization of dairy breeds to achieve the maximum economic merit from dairy production. Exploitation of additive genetic differences through selection within breeds is responsible for the genetic change of US dairy breeds (VanRaden and Wiggans, 2000). Differences among breeds in the magnitude of change is apparent. The additive genetic contribution of individual sires to crossbred performance was emphasized in a much earlier summary of dairy crossbreeding research (Fohrman et al., 1954). This genetic fact is immutable. As straightbreeding and perhaps increasingly crossbreeding is practiced by the US dairy industry, this will continue to be an extremely important component.

IMPLICATIONS AND CONCLUSIONS

The studies reviewed herein clearly establish the merit of dairy cattle crossbreeding. Even though some questions remain to be answered, evidence shows benefits of a crossbreeding system to improve the overall economic merit of US dairy cattle production over generations.

How Can Crossbreeding Be Used Practically?

The adoption of crossbreeding in a dairy herd begins with the choice of sire(s) of one or more breeds to mate with an existing female population of a single breed. The choice of sires based on their genetic evaluations for individual traits or indexes such as Net Merit\$ (www.aipl.arsusda.gov) is the single most important element once the desired breed has been chosen. Choice of sires in the 80th percentile for NM\$ is recommended. The predominant breed in the US is obviously Holstein, and they will most likely be used as the dam breed, the evidence for Ayrshires for ADNR and Jerseys for milk yield not withstanding.

Each of the four breeds proposed for the diallel has merit to recommend them:

1. Their rates of genetic progress for yield traits, which indicates the strength of their within breed selection programs. Admittedly, the Ayrshire breed lags behind the other three breeds.

2. Yield levels competitive with Holstein (i.e., $\geq 75\%$ of Holstein level).

3. Demonstrated heterosis with Holsteins for yield traits and nonyield traits especially fitness traits.

4. Demonstrated superiority in maternal performance as shown the Ayrshire breed in one study that can offset a disadvantage in breed additive genetic merit.

These criteria would, in fact, serve as a standard for consideration of inclusion of any breed in a crossbreeding program. Practically, one would also require availability of high genetic quality breeding animals and semen.

By the time F_1 females have reached breeding age, the future structure of the crossbreeding program must have been decided. One option is the use of F_1 bulls to mate to the F_1 females. Progeny testing of crossbred dairy bulls has become a possibility with the existence of a crossbred bull in an AI organization. The repeated hybrid male cross scheme used in the Canadian study produced a crossbred female not statistically different from Holstein for overall economic merit, but with predicted merit less than the average generation of a two-breed rotational crossing scheme. The fluctuation in generation means from rotational crossing systems depending on the magnitude of additive breed differences raises the question of whether composite populations might be considered. Combinations of two-, three-, and four-breed crosses could be used to form a composite population. Results from research in beef cattle indicate that optimum performance levels for major economic traits can be achieved with composite populations, but that the resource requirement for their formation is extremely high.

The use of crossbreeding presents many options to the US dairy industry. The production of F_1 's followed

by production of three-way crosses and backcrosses from them would provide the greatest opportunity for practitioners of crossbreeding to fully evaluate the merits of alternative crossbreeding systems.

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