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Abstract

Nine measures related to breeding efficiency were used for comparisons among purebred Ayrshires, Brown Swiss, Holsteins, and Jerseys and between purebreds and 32 crossbred groups representing 2-breed, 3-breed, 5/8, and backcrosses by purebred sires and progeny of crossbred sires. There were four herds with Holsteins common to all, Brown Swiss and Jerseys in three herds and Ayrshires in one herd. Four 2-breed, two 3-breed, and two backcross groups were common to two or more herds. Among purebreds, breed effects were significant in 16 of 72 tests, but there was no consistent trend favoring one breed. Generally, Jerseys were better than Holsteins, and Brown Swiss were poorer than Holsteins. Purebred females bred to their breed required similar services for conception (1.77 versus 1.79) as when bred to a different breed of sire. Least squares estimates of differences between purebreds and crossbreds favored crossbreds in 86 of 144 tests suggesting advantages for breeding efficiency; however, few were significant. Standard errors frequently exceeded estimates of differences. Parity was not associated with superiority in the crosses. Average heterosis in % was (2.0) for days from calving to first heat, (11.1) days first breeding to conception, (1.7) days open, (.8) calving interval, (6.4) percent pregnant <90, (8.4) <120, (−.2) <145, (1.6) <200 days postpartum, and (−1.3) in services for conception. The average overall was 3.2%. Numbers of sterile heifers were similar for crosses and purebreds, but fewer crosses completed two gestations. Crosses by purebred sires were poorer than the mean of parent breeds in percentage of reproductive disorders (7.8 versus 5.5), calving troubles (6.2 versus 5.0), and termination of lactation for health (10.1 versus 9.6), sterility (6.6 versus 5.7), and death (2.2 versus 2.0). Daughters of crossbred sires had slightly fewer reproductive disorders than crosses by purebred sires. Progeny of crossbred sires were similar to other crosses in death losses but had higher frequencies than crosses by purebred sires in the other traits.

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Introduction

Reports from several investigations (1, 3, 5, 7, 9, 12, 14) involving single herds have indicated some degree of heterosis may occur in measures of breeding efficiency in females when two or more European breeds of dairy cattle are crossed. Some studies show heterosis for reproduction equal to that for milk yield and growth rate, and economic significance as great as gains in fertility for crossbred swine, sheep, and beef cattle. Most studies with dairy breeds suggest the possible advantages of crossbreds over purebreds lie primarily in a shorter breeding period, fewer days open in lactation, an earlier age for puberty, a larger proportion of females born which live to complete one or more lactations, and a higher percentage which conceive during any breeding period. Possible superiority among crossbreds over the pure breeds must, however, be interpreted with caution as sampling variances for measures of reproductive efficiency from single herds are large.

The objectives of our study were to use nine measures related to breeding efficiency to: (a) determine possible differences among four pure breeds, (b) estimate heterosis expected from various crossbred combinations, and (c) compare crosses to purebred herdmates.

Materials and Methods

Sources of data. Breeding records were from four experimental investigations on the use of interbreed matings as a system of breeding for improving traits economically important in commercial dairying. The herds were located at Clemson University, Clemson, South Carolina; Georgia Coastal Plain Experiment Station at the State Prison Farm, Reidsville, Georgia; Iberia Livestock Experiment Station, Jeanerette, Louisiana; and the USDA Agricultural Research Center, Beltsville, Maryland. (Herds are identified as Beltsville, Jeanerette, Reidsville, and Clemson.)

The breeding plans for the various stations have been reported previously – Clemson (2), Reidsville (8), Jeanerette (6), and Beltsville (10). The breeding records were for 1957 to 1969 in all herds. There were 1,162

TABLE 1. Numbers of cows, records, sires, and daughters per sire for various groups.

	Beltsville		Jeanerette		Reidsville		Clemson		No.	Avg
Breed group	Cows	Rec.	Cows	Rec.	Cows	Rec.	Cows	Rec.	sires	dtr/sire
					Purebreds					
1. Ayr (A)	87	283	...	...	...	...	...	...	53	1.6
2. Swiss (S)	95	308	...	...	124	364	75	272	119	2.4
3. Hol (H)	97	320	127	405	162	491	92	403	158	3.0
4. Jer (J)	...	...	29	99	216	696	58	155	65	4.7
					2-breed crosses					
5. A × S[a]	43	126	...	...	...	...	...	...	22	2.0
6. A × H[a]	44	136	...	...	...	...	...	...	27	1.6
7. H × J	...	...	18	79	76	273	...	...	36	2.6
8. S × H[a]	28	120	22	66	...	...	72	180	54	2.2
9. S × J	...	...	9	33	53	180	...	...	26	2.4
					3-breed crosses					
10. A × SH[b]	41	89	...	...	...	...	...	...	25	1.6
11. H × AS[b]	42	101	...	...	...	...	...	...	24	1.8
12. H × SJ	...	...	24	58	42	130	...	...	31	2.1
13. H × RJ[c]	...	...	33	138	...	...	...	...	22	1.5
14. S × AH[b]	35	65	...	...	...	...	...	...	25	1.4
15. S × HJ	...	...	56	175	71	180	...	...	42	3.0
16. S × RJ[c]	...	...	10	37	...	...	...	...	8	1.2
					Backcrosses					
17. H × SH[b]	...	...	13	39	...	...	17	45	19	1.6
18. J × SJ	...	...	...	...	30	71	...	...	12	2.5
19. J × HJ	...	...	...	...	36	83	...	...	13	2.8
20. S × HS	...	...	...	...	...	...	11	34	10	1.1
					5/8 crosses					
21. J × HSJ[b]	...	...	...	...	34	102	...	...	20	3.0
22. A × SHA[b]	23	37	...	...	...	...	...	...	15	1.5
23. S × AHS[b]	13	24	...	...	...	...	...	...	9	1.4
24. S × SAH[b]	12	19	...	...	...	...	...	...	9	1.3
					Daughters crossbred sires					
25. Dtrs ×-bred	...	...	97	198	...	...	...	...	13	7.4

[a] Includes reciprocal crosses.
[b] Includes reciprocal crosses on dam side.
[c] R = Red Sindhi.

purebred cows of four breeds with 3,796 parities. Holstein females were common to all stations, Brown Swiss and Jerseys were in three herds, but Ayrshires were only at Beltsville (Table 1). There were 2,620 parties for 908 2-breed, 3-breed, backcross, and ⅝ crossbred groups representing 32 groups by 415 purebred sires of the Ayrshire, Brown Swiss, Holstein, and Jersey breeds. Also included were 97 daughters of 13 crossbred sires.

All crossbred groups were included in the general comparisons between crossbreds and purebreds, but groups 7, 9, 12, 13, 14, 15, 16, 17, 20, 23 and 25 (Table 1) were not in the statistical analyses because either purebred females of all parental breeds were not in the same herds or reciprocal crossbred combinations were not made at a station.

Breeding schedules. Estrus was recorded continuously after the females reached 12 mo of age. Reproductive tracts were palpated for abnormal conditions before each expected breeding.

Heifers at Beltsville, Clemson, and Reidsville were bred at the first estrus following 15 mo of age and at Jeanerette after 17 mo regardless of body weight. Breedings continued during each observed estrus until conception or until the heifers reached 20 mo at Reidsville, 24 mo at Beltsville and Clemson, and 26 mo at Jeanerette. Heifers not pregnant by these ages were culled.

Lactating cows were bred at the first estrus following 60 days post-partum except for first lactations at Beltsville where breeding was delayed until first estrus after 70 days postpartum. Cows not pregnant by 305 days after parturition were culled at all locations. Pregnancies, abortions, and stillbirths were verified by veterinarians. Within a breeding period, each female was bred to one service sire up to three services with subsequent breedings to alternate sires.

All females were allowed an opportunity to complete at least one production record of 305 days. In the Jeanerette herd, cows were culled for low milk yield without regard to breed after completing one lactation with later cullings for reasons of health, sterility, or to reduce numbers in which case the oldest cows were removed without regard to breed group. At Clemson all females remained in the herd for two gestations irrespective of production. Cows were not culled except for health problems or sterility until they completed three gestations in the Beltsville project. At Reidsville, cows were culled for low production following second lactation; otherwise the oldest cows were removed to maintain a stable herd size. With breeding schedules based on age or a fixed postpartum interval, service periods and calvings were randomly distributed among seasons.

Sire selection. Inseminations were frozen semen, except for 1957-58 at Reidsville when liquid semen was used. The semen came from 29 AI organizations offering semen for public distribution. At Reidsville and Beltsville three sires per breed were selected at random each year from all bulls available for service with the restrictions that quality of semen be good, sires have at least 10 daughters with lactation records, and sires be unrelated in the first two generations. Holstein sires for Jeanerette were required to have at least 100 AI daughters with an average for milk yield at least one-half genetic standard deviation above breed average and fat test of at least 3.6%. Brown Swiss sires were selected on a similar basis except that each sire needed only 25 daughters with an average fat test of 4.0%. Brown Swiss and Holstein sires used at Clemson were selected at random from three AI studs serving South Carolina.

With few exceptions, sires were used for no more than 1 yr to service both purebreds and crossbreds; thus, the average number of daughters per sire was small except for crossbred sires at Jeanerette (Table 1). Sires were a representative sample of those in service within a year. In the main analyses, breed of service sire was ignored. The hypothesis was that fertility of females was equal and fertility among males was similar since semen was required to be average or better in motility. Also, it was assumed there was no interaction between breed of sire and breed of cow.

Feeding. In all herds heifers were fed to sustain a good rate of development with the main sources of nutrients being pasture in season or silage and hay plus concentrate supplement. Pastures were used as partial roughage for lactating cows in all herds except during first lactation at Beltsville where complete drylot feeding was used. Silages made from grass, cereal grains, or corn were fed free choice in all herds with hay usually restricted to a given amount. Concentrates were allocated according to milk yield, fat content, and body weight. Feeding during first lactation at Beltsville was 100 to 115% of Morrison's Feeding Standards (11) while at the other stations it was 100 to 110% of the same standards.

Measures of reproductive performance. Measures of reproductive performance were number of days from calving to first observed estrus, date of first breeding to date of conception or service period, days from parturition to conception or time open (up to 305 days), days between successive calvings, and numbers of services when pregnancy occurred. Also included were proportions of those females exposed to breeding which were pregnant prior to 90, 120, 145, or 200 days postpartum. One or zero observations were used for the latter measures – one for conception and zero for nonconception for the periods indicated.

Parity was used to designate various breeding periods. For calving interval, interval from calving to first heat, and days open, parity one was assigned to the interval between first and second calving, parity two to periods between the second and third calvings, and later parities to all periods after third calving. In days from first breeding to conception, parity one was the interval before first conception, parity two corresponded to the interval during first lactation, and later parities included conceptions in second and later lactations. The groupings of parities corresponded to recommendations from other studies (3, 7, 9, 12, 14) and reflect effects due to age and culling according to production and reproduction.

The proportion of records with reproductive disorders or calving problems during parturition were evaluated along with the proportion of lactations terminated due to problems of health or physical injury, sterility, and death.

Methods of analysis. Since there were few crossbred groups common to more than two locations, purebreds were used to evaluate effects due to years, parity, and their interactions. The model for each trait was:

$$X_{ijkh} = \mu + s_i + y_j + l_k + sy_{ij} + sl_{ik} + yl_{jk} + syl_{ijk} + e_{ijkh}$$

where the fixed main effects and interactions are as indicated in the listing of how differences in reduction were computed.

Sums of squares of the analysis of variance were differences between reductions due to fitting models including the indicated main effects and interactions:

Source	Sums of Squares
Station	$R(\mu,s,y,l,yl) - R(\mu,y,l,yl)$
Year	$R(\mu,s,y,l,sl) - R(\mu,s,l,sl)$
Parity	$R(\mu,s,y,l,sy) - R(\mu,s,y,sy)$
Station × Year	$R(\mu,s,y,l,sy,sl,yl) - R(\mu,s,y,l,sl,yl)$
Station × Parity	$R(\mu,s,y,l,sy,sl,yl) - R(\mu,s,y,l,sy,yl)$
Year × Parity	$R(\mu,s,y,l,sy,sl,yl) - R(\mu,s,y,l,sy,sl)$
Station × Year × Parity	$\Sigma_{ijk} \frac{X^2_{ijk\bullet}}{n_{ijk}} - R(\mu,s,y,l,sy,sl,yl)$
Error	$\Sigma_{ijkh} X^2_{ijkh} - \Sigma_{ijk} \frac{X^2_{ijk\bullet}}{n_{ijk}}$

n_{ijk} = number of observations from the i^{th} station in the j^{th} year during the k^{th} parity. The degrees of freedom for each sum of squares was the difference in the ranks of the two matrices that entered in the computation of that sum of squares.

The basic model to evaluate differences among purebreds – Holsteins and Brown Swiss at Beltsville, Reidsville, and Clemson; Holsteins and Jerseys at Jeanerette, Reidsville, and Clemson; and Holsteins, Brown Swiss, and Jerseys at Reidsville and Clemson – was:

$$X_{ijkh} = \mu + s_i + y_j + b_k + sy_{ij} + sb_{ik} + yb_{jk} + syb_{ijk} + e_{ijkh}$$

where the elements of the model correspond to the fixed effects of station, year, breed, and their interactions plus random error.

The sums of squares for main effects and interactions were obtained in a manner similar to the analysis of purebreds at four locations.

Estimates for heterosis were from the following model:

$$X_{ijkhl} = \mu + y_i + p_j + g_k + m_h + s_{kh} + \text{2-way and 3-way interactions} + e_{ijkhl}$$

where the elements of the model correspond to fixed effects of year, station, breed of sire, breed of dam, interaction effect (heterosis) due to breed of sire and dam, and other interactions plus a random error term.

Separate analyses were made for: Holstein, Brown Swiss, H × S, and S × H at Beltsville and Clemson; Holstein, Ayrshire, H × A, and A × H at Beltsville; and Brown Swiss, Ayrshire, S × A, and A × S at Beltsville. In the latter two analyses, effects of station were excluded from the model.

Sums of squares were differences in reductions using models that included the following effects:

Source	Sums of Squares
Station	$R(\mu,p) - R(\mu)$
Years	$R(\mu,p,y) - R(\mu,p)$
Breed of sire	$R(\mu,p,y,g) - R(\mu,p,y)$
Breed of dam	$R(\mu,p,y,g,m) - R(\mu,p,y,g)$

Source	Sums of Squares
Heterosis	
	$\Sigma_{ijkh} \frac{X^2_{ijkh\cdot}}{n_{ijkh}} - R(\mu,p,y,g,m,s)$
Error	
	$\Sigma_{ijkhl} X^2_{ijkhl} - \Sigma_{ijkh} \frac{X^2_{ijkh\cdot}}{n_{ijkh}}$

Interactions, effects due to heterosis, and other effects nonsignificant were deleted from the remaining reductions.

To test the significance of the difference between purebreds and crossbreds having the same breed of sire the following model was used:

$$X_{ijkh} = \mu + a_i + l_j + g_k + al_{ij} + ag_{ik} + lg_{jk} + alg_{ijk} + e_{ijkh}$$

where the elements of the model correspond to fixed effects of year, parity, purebred or crossbred group, and 2-way and 3-way interactions plus a random error term.

Analyses were separate for each breed of sire. Sums of squares for the analysis of variance were as follows:

Source	Sums of Squares
Years	
	$R(\mu,a) - R(\mu)$
Breed groups	
	$R(\mu,a,g) - R(\mu,a)$
Parity	
	$R(\mu,a,g,l) - R(\mu,a,g)$
Interactions	
	$\Sigma_{ijk} \frac{X^2_{ijk\cdot}}{n_{ijk}} - R(\mu,a,g,l)$
Error	
	$\Sigma_{ijk} X^2_{ijkh} - \Sigma_{ijk} \frac{X^2_{ijk\cdot}}{n_{ijk}}$

n_{ijk} = number of observations during the i^{th} year of the j^{th} parity for k^{th} breed group. Degrees of freedom and parities were defined the same way as for the analysis of purebred data at the four stations.

Results and Discussion

Location comparisons. The importance of location, year, parity, and the interactions were tested with purebreds. From unadjusted means (Table 2) location differences were largest for interval from calving to first heat and from first breeding to conception, but insofar as tests could be made, there was no strong indication, based on the frequency of significance for the main effects (L, Y and P), Table 3, that the breeds responded differently at the various locations. This statement must be made with reservations as the main effects due to station, year, and parity could not be interpreted in most traits because of the significant F-values for interaction. The 3-way interactions among stations, years, and parities were significant ($p<.01$) for calving interval of Holsteins and Brown Swiss and for interval from first breeding to conception of Brown Swiss and Jerseys. There were other significant comparisons at $P<.05$. The significance of the interactions was attributed in part to changes in management, such as greater use of stored roughages in later years at Reidsville and Jeanerette.

The traits for which main effects were tested in Brown Swiss were the proportions pregnant at various times. Year effects were statistically significant, but station effects were significant only for conception <90 days. In Jerseys station effects were significant for first breeding to conception, days open, calving interval, and proportion pregnant. Year effects were significant for interval from calving to first heat in Jerseys and Holsteins (Table 3).

Comparison among purebreds. Two analyses were made for differences among breeds. Analysis I involved a series of tests by parity groupings, where breeds were common to two or more locations. Main effects were station, year, and breed plus the interactions. In Analysis II Holsteins were a standard for comparison with other breeds.

Analysis I. At Reidsville and Clemson where Brown Swiss, Holsteins, and Jerseys were contemporaries, most of the F-values for breed effects were nonsignificant. Breed effects were significant ($P<.01$ or $P<.05$) only for calving to first heat in parity 1 and later parities, first breeding to conception in later parities, and calving interval in later parities.

TABLE 2. Means by location for various measures of reproduction in purebreds.

Trait	Beltsville	Jeanerette	Reidsville	Clemson
	(Days)			
Calving to 1st heat	60	54	43	47
1st breeding to conception	32	33	22	27
Open	117	119	115	112
Calving interval	396	398	394	394
No. breeds	3	2	3	3

TABLE 3. F-values and tests of significance for various measures of reproductive performance of Holsteins, Brown Swiss, and Jerseys.

Source	d.f.	Calving to 1st heat	1st breeding to conception	Days open	Calving interval	Proportion pregnant <90	<120	<145	<200 days
				Holsteins four locations					
Station (L)	3	11.8**	2.9*	1.4	.9	1.0	1.6	4.9**	2.3
Year (Y)	9	3.2**	.6	1.9	1.8	.9	2.2*	1.6	.9
Parity (P)	2	6.4**	.8	1.7	2.3	.1	.0	1.1	3.4*
L × Y	27	1.4	1.1	1.7*	1.5*	1.9**	1.3	1.4	.9
L × P	6	5.0**	1.3	2.1*	1.7	1.9	3.1**	2.0	2.0
Y × P	18	.9	.9	1.9**	1.7*	1.7*	1.7*	1.8*	1.0
L × Y × P	44-50[a]	.9	1.1	1.1	1.7**	1.0	1.0	1.4*	1.0
Error (MS)	750-1,168	1,114	2,344	2,954	3,197	.2	.2	.1	.1
				Brown Swiss three locations					
Station (L)	2	20.1**	1.1	.6	1.1**	3.8*	1.1	1.2	1.6
Year (Y)	9	.5	2.8**	3.2**	2.9**	2.2*	2.0*	2.2*	2.3*
Parity (P)	2	7.0**	1.1	3.7*	2.6	.6	1.8	1.9	2.2
L × Y	18	2.3**	.9	1.4	1.2	1.6	1.2	.6	1.1
L × P	4	8.4**	2.6*	2.8*	3.2*	1.8	.5	.7	1.0
Y × P	18	1.1	1.3	1.0	.9	.8	1.0	1.4	.7
L × Y × P	28-32	1.0	3.1**	2.1	2.2**	1.2	1.2	1.6*	1.8*
Error (MS)	426-648	889	2,405	2,886	3,102	.2	.2	.2	.1
				Jerseys three locations					
Station (L)	2	2.8	9.1**	3.4*	3.8*	3.0*	3.0*	2.2	5.6*
Year (Y)	9	6.8**	1.9*	1.7	1.7	2.0*	1.2	1.1	1.1
Parity (P)	2	4.7**	.7	.4	.7	.2	1.6	.2	.6
L × Y	13	1.5	1.3	1.1	1.5	.7	.6	1.0	.4
L × P	4	1.3	3.4**	.5	1.2	.1	.2	.3	1.2
Y × P	18	1.2	1.0	1.9*	2.3**	1.8*	1.3	1.4	.7
L × Y × P	16-17	.6	2.7**	1.7*	1.2	1.2	1.1	1.0	1.2
Error (MS)	445-567	722	1,502	1,718	1,996	.2	.2	.1	.1

[a] Range of degrees of freedom.
* P < .05.
** P < .01.

Breed effects were significant (P<.01) for calving to first heat in parity 1 and later parities in the comparison of Jerseys versus Holsteins at Jeanerette, Reidsville, and Clemson. At Beltsville, Reidsville, and Clemson (Brown Swiss vs. Holsteins), F-values for breed effects were significant (P<.01) in parity 1 for first breeding to conception, in parity 2 for calving to first heat, and in later parities for days open and calving interval. Breed effects were nonsignificant among Ayrshires, Brown Swiss, and Holsteins at Beltsville. In all the analyses there were more instances where the F-values for breed were larger and significant in later parities than for parity 1 or 2.

Few of the 2-way interactions for breed by year or breed by location were significant. The same was true for the 3-way interactions of location, year, and breed. In the comparisons there are some indications of variation among breeds in reproductive efficiency, but the inconsistent association of significant breed effects with any of the eight measures of breeding efficiency or parity suggest much larger samples would be required to measure these differences accurately.

Analysis II. Least squares estimates of differences of Ayrshire, Brown Swiss, and Jerseys from the mean for Holsteins by parity groupings are in Table 4. A positive value indicates a possible advantage for the respective breeds over Holsteins while minus values suggest superiority of Holsteins. In general, Jerseys were most consistently superior to Holsteins, but the differences were nonsignificant except in five instances (Table 4). The differences for Ayrshires and Brown Swiss were highly variable and significant for only 6 of the 48 estimates.

Repeatability estimates between parities of the same cow were low in all traits and for all breeds with few being significant (P<.05). Ranges were .13 to .28 for calving to first heat, .00 to .14 for first breeding to conception, .09 to .13 for days open, .08 to .17 for calving interval, and .00 to .11 for percent pregnant <90 days. These repeatabilities are similar to those reported for Holsteins by Dunbar and Henderson (4) and Pou et al. (13).

Breed of sire. Indications of similarities among the breeds are supported by the number of services to obtain pregnancies. When the purebred females were mated to sires of their own breeds, the mean for services per pregnancy was 1.77 (2,441 pregnancies) and 1.79 (864 pregnancies) when mated to sires of other breeds. Effects of breed of sire were nonsignificant. Variation for sires within breed and years was much larger than for breed of sire. Ayrshire sires bred to Ayrshires, Brown Swiss, Holsteins, and 5 crossbred groups averaged 1.67 services per pregnancy; Brown Swiss sires averaged 1.80 services when mated to all 4 breeds and 21 crossbred groups; Holstein sires averaged 1.70 services for 4 pure breeds and 27 crossbred groups; and Jersey sires averaged 1.76 services for Jersey cows and 6 crossbred groups. The small differences for breed of sire follow the findings of Donald and

TABLE 4. Least squares estimates of differences (LSED) and test of significance from Holsteins of Ayrshires, Brown Swiss, and Jersey according to parity grouping.

	Days				% pregnant			
Breed group	Calving to 1st heat	1st breeding to conception	Open	Calving interval	<95	<120	<145	<200
				Parity 1				
Ayr	−8.3[a]	−8.8	−18.2	−16.7	−10	−19	−14	−3
Swiss	2.8	−8.8	−4.3	−11.6	−3	−12	−9	2
Jer	10.9**	−7.2	5.6	8.4	4	0	−2	5
				Parity 2				
Ayr	12.8	7.9	14.6	−13.3	2	2	3	1
Swiss	3.9	−4.9	−.5	−6.7	−8	−3	−4*	2
Jer	7.8	2.1	10.7**	15.9*	7	12**	4*	3
				Later parities				
Ayr	−8.9*	6.5*	3.5	2.0	4	5	2	−1
Swiss	7.1	−6.0*	−10.4*	−21.2**	−4	−8	−9	−4
Jer	8.5*	4.6	4.2	3.3	5	3	1	1

[a] Sign in economic direction.
* P<.05.
** P<.01.

Russell (3) when Friesian, Ayrshire, Jersey, and Hereford sires were mated to Ayrshire, Friesian, and Jersey cows.

In the comparisons on the four pure breeds, there were some indications of variation among breeds in reproductive efficiency, but the inconsistent association of significant breed effects with the eight measures of breeding efficiency for parity suggest much larger samples would be required. However, even in larger samples, environmental effects may make interpretation of breed differences tenuous (4, 13). In herds where all females born are given an opportunity to complete one or more gestations and where breedings were scheduled to commence at a fixed time following parturition, irrespective of age, season, body weight, or milk yield, none of the four breeds showed distinct advantages in reproductive efficiency.

Estimates of heterosis. Due to limitations of numbers or because all parent breeds were not contemporaries at the various stations, only six 2-breed crossbred groups were suitable for estimation of heterosis (interaction of breed of sire and breed of dam). F-values for heterosis were nonsignificant with the exception of first breeding to conception in S × H crosses (Table 5). F-values for breed of sire were significant (P<.05) for A × S and S × A crosses but not in the other groups. The results indicate heterosis for reproductive performance is small.

In view of the low F-values for heterosis, further tests were made by parity groupings comparing the crossbreds to Holsteins or Brown Swiss. Least squares estimates of differences are in Tables 6, 7, and 8. The high frequency of positive values, 36 of 48 classifications (Table 6), suggest advantages for H × S and S × H crosses over pure Holsteins and Brown Swiss. The crosses were consistently superior in early conception (percent pregnant <90 days). The advantage of the H × S crosses appeared greater after parity 1, but F-values were significant only for calving interval in parity 1 (P<.05) and calving to first heat in later parities (P<.01).

For A × H and H × A crosses (Table 7), the high percentage of positive values (66%) also suggests advantages for the crosses. However, none of the F-values was significant. Pari-

TABLE 5. F-values and tests of significance of the interaction of breed of sire × breed of dam (heterosis) for various measures of reproductive performance of several crossbred groups.

Source	d.f.	Calving to 1st heat	1st breeding to conception	Days open	Calving interval	Proportion pregnant <90	<120	<145	<200 days
		S × H and H × S vs. Holsteins and Brown Swiss							
Station	1	8.2**	.7	1.9	2.0	2.0	1.7	.1	.9
Year	8-9	.3	1.1	.5	.3	.7	1.1	1.0	.9
Breed of sire	1	.8	.0	1.2	1.5	.0	.7	1.4	2.5
Breed of dam	1	3.7	.4	.1	.1	1.1	2.7	2.1	.1
Heterosis	1	2.1	7.3**	.6	.1	1.8	.4	.1	.9
Interactions	33-52[a]	2.0	.7	1.1	1.0	1.1	1.0	.8	.4
Error (MS)	276-633	1,173	2,190	2,891	4,182	.3	.2	.2	.1
		A × H and H × A vs. Holsteins and Ayrshires							
Year	6-8	2.0	.9	1.5	1.3	1.5	1.3	1.5	1.2
Breed of sire	1	1.2	1.4	.2	.1	.1	.4	.5	.0
Breed of dam	1	2.2	.3	.0	.1	.7	.1	.5	1.2
Heterosis	1	.1	.0	.2	.2	2.2	.3	.1	.0
Interactions	8-20	1.2	.9	1.4	.5	1.2	1.7	1.0	.6
Error (MS)	119-318	1,056	1,789	2,008	1,847	.2	.2	.2	.1
		A × S and S × A vs. Ayrshires and Brown Swiss							
Year	8	3.3**	1.0	.4	.8	1.1	1.3	.8	1.0
Breed of sire	1	.7	4.3*	4.2*	3.3	1.3	4.0*	2.4	3.0
Breed of dam	1	.0	.1	.8	.3	1.0	1.4	3.0	.0
Heterosis	1	.2	.0	.4	.1	1.1	2.2	.0	.1
Interactions	10-20	2.0*	.6	1.7	1.6	1.3	1.6	.9	1.0
Error (MS)	89-285	974	2,345	2,842	2,779	.2	.2	.2	.1

[a] Range of degrees of freedom.
* P<.05.
** P<.01.

TABLE 6. Least squares estimates of differences (LSED) from Holstein for Brown Swiss and S × H and H × S crosses at Beltsville and Clemson.

Breed group	Cal.ing to 1st heat		1st breeding to conception		Days open		Calving interval		% pregnant <90		<120		<145		<200 days	
	LSED	SE[a]	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE
							Parity 1									
Swiss	−2.8[b]	8.8	−15.8	15.1	.6	17.1	−3.4	17.9	4	15	4	15	2	11	2	9
S × H	−.3	9.3	−8.8	9.0	23.0	11.9	29.9	10.9	14	10	19	10	12	9	9	5
H × S	−5.0	5.9	−12.6	9.5	7.0	10.5	7.3	12.1	3	9	7	8	3	8	2	6
							Parity 2									
Swiss	−8.5	13.4	4.9	14.9	11.3	17.8	.8	25.6	4	15	4	15	7	10	2	10
S × H	3.8	9.0	16.8	9.8	25.9	11.6	27.8	17.5	18	9	12	9	17	8	7	5
H × S	−1.7	8.7	8.0	10.3	11.5	12.0	1.2	16.3	9	10	5	9	3	8	0	7
							Later parities									
Swiss	−9.3	14.7	−2.5	10.2	−8.2	16.8	10.4	22.4	−3	16	−8	15	−8	13	−5	7
S × H	12.1	11.3	15.7	6.5	3.2	12.2	−9.6	16.2	17	11	9	11	3	10	−1	5
H × S	−6.7	7.8	8.8	9.8	1.7	9.6	−5.2	12.7	0	9	−7	8	7	7	4	4

[a] Standard error of differences from Holsteins.
[b] Sign in economic direction.

TABLE 7. Least squares estimates of differences (LSED) from Holsteins for Ayrshires, A × H, and H × A at Beltsville.

Breed group	Calving to 1st heat		1st breeding to conception		Days open		Calving interval		% pregnant <90		<120		<145		<200 days	
	LSED	SE[a]	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE
							Parity 1									
Ayr	−8.3[b]	13.2	−8.8	18.7	−18.2	29.9	−16.7	31.3	−10	24	−19	25	−14	24	−3	19
A × H	−4.0	9.0	−33.9	12.8	23.1	20.4	22.3	21.8	6	16	17	17	21	17	20	13
H × A	−5.1	8.3	2.3	11.4	6.3	18.8	10.3	19.4	−12	18	6	16	10	15	13	12
							Parity 2									
Ayr	22.8	21.6	10.9	28.1	34.6	32.2	−33.3	35.5	26	29	25	26	23	23	11	19
A × H	11.6	15.8	21.0	19.2	29.4	21.7	11.9	23.9	15	19	35	17	22	15	12	13
H × A	10.5	13.7	15.5	17.7	24.6	19.8	5.6	21.7	9	18	30	16	18	14	5	11
							Later parities									
Ayr	−8.9	23.6	6.5	14.3	3.5	20.2	2.0	21.5	4	22	5	20	2	17	−1	9
A × H	11.3	17.1	1.4	9.9	−3.6	13.6	−5.9	14.1	−22	15	−4	13	4	12	5	6
H × A	−13.9	15.2	2.2	9.1	−3.4	13.1	−3.4	14.3	−8	14	−4	13	−8	11	−3	6

[a] Standard error of differences from Holsteins.
[b] Sign in economic direction.

ty effects were of less importance than for S × H and H × S crosses. For A × S and S × A crosses LSED values were more frequently negative, 29 of 48 classifications, than positive (Table 8), implying possible negative heterosis, sampling error, or improper statistical model for determining changes in reproduction from crossing these two breeds. All F-values were low and nonsignificant.

The frequency of positive values for all crossbred groups was about the same in parities 1 and 2, 30 or 31 of 48 tests for each parity, but slightly higher than for later parities with 26 positive values. These small differences in frequency of positive values provide no evidence for association of superiority of the crosses and parity. Overall, differences for crossbreds were advantages in 86 of the 144 tests or about 60% (Tables 6, 7, and 8) suggesting superiority in breeding efficiency, but it is not sizable. However, from the standard errors, large numbers would be required for reliable estimates of possible advantages. There is also some indication of breed differences in general combining ability with Holstein being greater than Ayrshires or Brown Swiss.

Breed groups with same breed of sire. As a further test for differences between purebreds and crossbreds, 17 groups of 2-breed, 3-breed, backcrosses, and ⅝ crosses were compared to their breed of sire across all parities. The crossbreds by Holstein sires had positive values in 69% of the tests implying superiority for the crosses (Table 9), but for 81% of the 48 values the differences of the crossbreds from Holsteins were less than corresponding standard errors. F-values in all cases were small and nonsignificant. Effects of year and parity were significant in nearly 50% of the tests. None of the interactions was important.

Crosses by Ayrshire sires tended to exceed the mean for Ayrshires more frequently (83% + values) than did Holstein crosses over Holsteins (Table 9). Also, the frequency in which standard errors exceeded the differences was less in Ayrshire groups than in Holsteins. Differences between Ayrshires and their crosses were nonsignificant except for calving to first heat. Interactions between main effects were significant (P<.01) for interval from breeding to conception, days open, calving interval, and conception <145 and <200 days. The A × H and A × S crosses had significantly fewer days from calving to first heat than pure Ayrshires while A × SHA crosses had significantly more days than Ayrshires.

Crosses by Jersey sires did not show any

TABLE 8. Least squares estimates of differences (LSED) from Brown Swiss for Ayrshires, A × S, S × A at Beltsville.

Breed group	Calving to 1st heat		1st breeding to conception		Days open		Calving interval		% pregnant <90		<120		<145		<200 days	
	LSED	SE[a]	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE
							Parity 1									
Ayr	−6.5[b]	14.2	2.7	24.6	−24.0	27.1	18.3	27.4	−13	22	−23	23	−20	22	−10	15
A × S	3.3	9.3	−7.9	15.8	6.9	17.7	13.1	17.5	17	15	−18	15	−1	15	13	11
S × A	2.3	9.5	.2	16.2	−28.5	18.1	−20.3	18.6	−2	15	−6	15	−24	15	−16	11
							Parity 2									
Ayr	−1.7	24.8	−21.8	25.0	−4.6	28.5	13.8	32.4	9	27	13	24	6	21	−1	16
A × S	−14.5	18.7	4.6	16.4	−6.9	17.6	−6.9	20.0	−15	17	3	14	−5	13	−2	10
S × A	−16.5	13.0	−27.9	16.7	−23.1	19.4	−10.6	21.5	−15	18	−4	16	−11	14	−15	11
							Later parities									
Ayr	4.5	20.8	12.3	16.7	19.5	26.8	18.6	29.8	11	24	16	22	14	20	7	13
A × S	1.8	12.7	8.4	10.7	2.1	16.6	13.0	18.7	−10	15	9	14	−2	12	5	8
S × A	−7.8	15.7	.7	12.0	17.0	19.6	10.9	21.9	−4	18	7	16	15	15	−1	10

[a] Standard error of differences from Brown Swiss.
[b] Sign in economic direction.

TABLE 9. Least squares estimates of differences (LSED) between crossbreds and purebreds (SE = standard error of difference from respective pure breeds).

Breed group	Calving to 1st heat		1st breeding to conception		Days open		Calving interval		% pregnant							
									<90		<120		<145		<200 days	
	LSED	SE[a]	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE	LSED	SE
					Holsteins vs. crossbreds by Holstein sires											
H × A	−2.8[b]	7.6	3.0	6.5	3.8	9.3	2.0	10.3	1	9	6	9	2	8	−1	5
H × S	5.5	7.1	−1.0	6.8	5.1	8.6	−3.9	9.4	7	8	0	8	1	7	−1	4
H × AS	10.6	10.9	5.4	8.2	18.8	12.3	13.9	14.5	10	12	14	11	20	10	6	7
H × SA	−11.7	9.1	3.3	7.9	−5.7	11.7	−4.8	13.4	−3	11	−4	11	2	10	−5	7
H × SAH	−21.1	20.8	10.0	16.0	3.8	28.9	36.1	54.5	−29	28	9	26	2	24	17	16
H × ASH	30.7	36.5	−1.2	19.8	55.5	38.6	53.1	55.6	46	37	34	35	27	32	17	21
					Ayrshire vs. crossbreds by Ayrshire sires											
A × S	8.1	5.8	4.1	6.4	6.1	8.9	9.5	9.4	−12	9	0	8	2	8	9	4
A × H	7.8	6.5	−.1	6.9	17.5	9.7	11.8	10.1	−7	10	13	9	13	8	16	5
A × SH	4.6	9.2	26.7	9.2	49.3	14.6	43.1	15.7	22	14	37	13	26	13	22	7
A × SHA	−40.9	17.2	47.7	17.6	48.7	30.3	49.3	47.9	6	30	30	27	44	24	24	15
A × HSA	−2.8	12.8	29.5	10.4	28.2	17.0	17.8	18.9	−15	17	32	15	26	14	11	9
					Jersey vs. crossbreds by Jersey sires											
J × SJ	−14.3	5.8	5.5	5.1	−3.6	7.7	−8.8	.2	−3	9	−8	9	6	7	−8	4
J × HJ	−9.4	5.5	6.7	4.8	5.1	7.3	5.2	8.9	2	9	10	8	5	7	0	4
J × SHJ	5.4	5.9	.7	5.6	6.7	7.9	11.1	9.4	3	10	5	9	6	8	1	5
J × HSJ	10.5	6.7	−3.3	5.9	−3.9	8.9	.8	10.9	−9	11	−4	1	0	9	−3	6
					Brown Swiss vs. crossbreds by Brown Swiss sires											
S × A	−7.0	7.4	−9.0	8.7	−11.3	10.9	−6.7	11.9	−7	3	−1	9	−6	8	−10	6
S × H	3.3	12.2	1.9	12.7	10.6	16.8	16.6	21.5	14	3	7	4	2	3	1	2

[a] Standard error of differences from respective pure breeds.
[b] Sign in economic direction.

significant advantages over Jerseys except in interval from calving to first heat (P<.05). The positive values were less (56%) than for the two previous groups. The backcrosses (J × SJ and J × HJ) tended to be poorer compared to Jerseys than ⅝ crosses (Table 9). Year effects were important for most traits, but neither parity effects nor interactions were significant.

Brown Swiss-sired crossbreds did not differ significantly from Brown Swiss in any measures (Table 9). S × H crosses showed advantages over purebreds while S × A were inferior, lending further support to the hypothesis of possible negative heterosis from crossing Brown Swiss and Ayrshires and greater combining ability of Holsteins.

For calving to first heat, 9 of the 17 crossbred groups showed some advantage over purebreds, and 12 of the crossbred groups were superior in first breeding to conception, days open, and calving interval. In percent pregnant the crossbreds exceeded purebreds in 68% of the tests. These results give further indication of advantages for crosses in breeding efficiency.

The 32 crossbred groups (Table 1) were sorted according to breed composition into five groups, and estimates of heterosis were derived as percent deviations from the means for the theoretical contributions of the parent breeds (Table 10). Due to fewer numbers the estimates for ⅝ and backcrosses were highly variable. Daughters of crossbred sires tended to show negative heterosis in comparison to the parental mean. The average percent heterosis for daughters of purebred sires was 2.8 for calving to first heat, first breeding to conception, days open, and calving interval; 4.1% for percent pregnant by <200 days; and 3.2% overall, including services for conception.

Expected values for purebreds and crossbreds (mean for parent breeds ± % heterosis) are in the lower portion of Table 10. In comparison to the four pure breeds, the expected performance of crossbreds by purebred sires would, in general, afford some advantages, but this is questionable if both male and females are crossbreds (daughters of crossbred sires). However, there are reservations in assessment of the progeny of crossbred sires since half the sires and about the same proportion of the cows these sires were bred to contained Red Sindhi breeding. Data were not available on Red Sindhis as purebreds.

If the crossbreds equalled or exceeded the purebreds in milk yield, the slightly better breeding efficiency of crossbreds would be economically significant. In most instances crossbreds, except those by crossbred sires, tended to exceed Ayrshires, Brown Swiss, and Jerseys in milk yield (2, 6, 8, 10). With first lactation yields as a base, the estimated higher milk yield per lactation, coupled with in-

TABLE 10. Estimates of percentage heterosis for various traits and expected means for purebreds and crossbreds.

Breed group	Calving to 1st heat	1st breeding to conception	Days open	Calving interval	% pregnant <90	% pregnant <120	% pregnant <145	% pregnant <200 days	Ser./concep.
				% heterosis					
Crosses									
2-breed	−2.9	6.2	3.7	1.0	11.5	7.3	−.2	1.4	−.9
3-breed	4.4	9.9	1.1	.1	−2.1	−3.9	−3.5	3.3	−.8
5/8	1.1	27.2	3.3	1.2	−1.3	19.6	−.2	2.9	−1.2
Backcrosses	−.4	1.3	−1.3	.8	17.6	10.6	3.2	−.9	−2.2
Dtrs crossbred sires	.0	.7	−.9	−2.7	−4.1	−3.4	−5.9	−7.4	−8.4
		Expected means for purebreds and crossbreds							
All pure	50	31	118	396	46	64	79	91	1.83
Crosses									
2-breed	52	29	114	392	53	69	78	92	1.85
3-breed	48	28	117	395	45	61	76	94	1.84
5/8	49	23	114	392	45	76	78	94	1.86
Backcrosses	51	31	120	393	54	71	82	90	1.86
Dtrs crossbred sires	54	34	117	393	54	70	77	89	1.82

TABLE 11. Percentage of purebred and crossbred females reaching breeding age that did not conceive (0) or completed (2) gestations at four locations.

Breed group	Gestations completed 0	2
	Purebreds	
Ayr	7.5	81.2
Swiss	13.8	74.6
Hol	7.7	78.7
Jer	12.8	73.0
	Crosses	
2-Breed	7.0	78.9
3-Breed	13.7	68.3
5/8	14.8	58.0
Backcrosses	8.6	61.9
	Daug. crossbred sires	
Crossbred	10.0	64.4

creased breeding efficiency expressed as calving interval, the 2-breed, 3-breed, ⅝, and backcrosses would be expected to give 11 to 31% higher returns over feed costs than Ayrshires, Brown Swiss, and Jerseys (McDowell, unpublished data). This would not be true for Holsteins, however. They were superior in milk yield to crossbreds at all locations. The higher breeding efficiency of crossbreds would afford some advantages, but Holsteins could have been milked for lactations of 315 days with a higher yield at drying off than in 305 days for crosses. If Holsteins had been milked for 315 days, their advantage over crossbreds would be expected to be 7 to 37% depending on whether the crossbred contained Holstein breeding and on herd production.

Traits related to reproduction. The percentage of heifers which were exposed for breeding but did not conceive within the allowed time limit (Table 11) was the same for crossbreds and purebreds (10%). Ayrshires and Holsteins had the fewest nonbreeders of purebreds, and the 2-breed and backcrosses had the fewest among crossbreds. Culling for sterility was the main basis for removal of cows, but low yields and health problems also entered the picture; therefore, the percentages which completed two gestations (Table 11) reflect a competition estimate of longevity". The turnover rate for crosses other than 2-breed was much higher than for purebreds. The values for ⅝

TABLE 12. Percent of parturitions with reproductive disorders or calving troubles and percentage of lactations terminated by problems of health, sterility, and death by breed grouping and parity.

	Number Loc.	Rec.	Reprod. disorder	Calving troubles	Lactation terminated Health	Sterility	Death
			Breed groups				
Purebreds							
Ayr	1	333	6.1	5.4	9.3	5.1	1.2
Swiss	3	958	8.2	3.7	11.3	7.6	2.4
Hol	4	1,680	6.2	6.3	9.2	6.0	1.9
Jer	3	1,196	1.5	5.4	9.0	4.0	2.2
Crosses							
2-Breed	4	1,273	8.7	4.3	10.2	6.6	1.9
3-Breed	3	970	6.4	7.4	9.1	7.3	2.4
5/8	2	196	7.3	10.2	7.7	3.6	3.1
Backcrosses	3	278	9.2	8.3	15.1	6.1	2.5
Dtrs crossbred sires	1	183	5.0	20.7	16.3	12.0	2.2
			Parity				
1st							
Pure	4	1,019	6.1	8.9	2.9	8.0	1.5
Crosses[a]	4	931	7.8	10.8	3.6	8.6	1.4
2nd							
Pure	4	867	4.8	5.1	6.0	5.0	1.1
Crosses	4	755	8.0	4.2	11.2	4.6	2.4
Later							
Pure	4	2,281	5.2	3.3	14.7	5.2	2.6
Crosses	4	1,031	6.9	3.6	16.2	5.9	2.8

[a] Dtrs crossbred sires excluded.

crosses, backcrosses, and daughters of crossbred sires must be considered with reservations due to numbers and perhaps some bias in selection because as the projects approached termination, purebreds may have been favored for continuation of the herds. However, the 2-breed and 3-breed crosses had equal opportunity to purebreds for completing two gestations.

Percentages of parturitions for purebreds and crosses where reproductive disorders and calving difficulties were recorded are in Table 12. Reproductive disorders included mummified fetus, retained placenta, metritis, cystic ovaries, retained corpus luteum, vaginitis, and prolapsed uterus. Calving troubles were recorded as abortion <152 days after conception or >152 days, dystocia, and removal of calf by caesarian surgery. Chi-square analyses were used for testing differences among purebreds and for the deviations of crossbreds from the parental means.

Jersey cows had lower ($P<.01$) frequency of reproductive disorders among purebreds, and Brown Swiss cows were lower in calving troubles ($P<.05$). With the exception of 2-breed crosses, the frequency of reproductive disorders among crossbreds was significantly higher than expected ($P<.05$). For calving troubles the ⅝ crosses, backcrosses, and daughters of crossbred sires showed a greater percentage ($P<.05$) than anticipated from the parental mean.

Location differences were relatively small for reproductive disorders, 4.5% for Beltsville and Reidsville, 6.1% for Jeanerette, and 7.1% for Clemson. For calving troubles, there were two distinct groupings: low, 2% for Beltsville and Clemson and high, over 7% at Jeanerette and Reidsville. The major contributor to reproductive disorders was dystocia, especially among daughters of crossbred sires at Jeanerette and ⅝ crosses and backcrosses at Reidsville. The daughters of crossbred sires were about average in reproductive disorders, but frequency of dystocia was extremely high for matings to either crossbred or purebred sires. Daughters of crossbred sires from cows with Red Sindhi breeding (H $\times$ RJ and S $\times$ RJ) had more calving troubles than those containing only European inheritance. The reasons for the higher incidence of dystocia at the two locations in the hotter climates are not fully discernible, except that at first parturition the heifers at Reidsville and Jeanerette were smaller than at the other locations.

Parity effects were not important as crosses tended to have higher frequencies of both reproductive disorders and calving troubles in each parity classification (Table 12).

Lactation records associated with each parity had an out-of-herd or end-of-record-cause coded by 1 of 25 classifications. These encompassed four major classifications: (a) cows dried off, (b) death, (c) removal because of health problems, such as mastitis and physical injury, and (d) sterility. Brown Swiss were above average in frequency of lactation termination due to health problems, sterility, and death (Table 12) and Jerseys below average. Crossbreds did not differ significantly from expected (mean for parental breeds); however, losses for health reasons were lowest for 3-breed and ⅝ crosses.

Location differences were large for health, sterility, and death. Clemson had the lowest values, 1.0, 3.6, and 1.1%. This was due to a high rate of removal of cows after only two gestations. The percentages for Reidsville were 9.3, 5.7, and 4.7% and at Jeanerette 10.0, 10.4, and 2.1%. The high turnover rate by involuntary culling at Jeanerette was due in part to high losses in daughters of crossbred sires.

Results of this study do not support a widely held concept that due to hybrid vigor, crossbreds reaching breeding age may have a longer productive life than purebreds, particularly if they are in competition with purebreds.

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