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BEEF-DAIRY CROSSBREEDING: A STUDY OF BIRTH TRAITS

by

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INTRODUCTION

Crossbreeding is the mating of animals which belong to different breeds, according to Lush (1945). The term also includes the mating of purebreds of one breed to grades of another breed, or even to crossbreds.

Crossbreeding is not a new practice, but most of the efforts to improve beef cattle in the United States in the past century have been aimed at improving the pure breeds. Only recently has the attention of constructive animal breeders been directed toward the use of crossbreeding for commercial beef production.

Cundiff (1970) estimated that production per cow exposed for breeding could be increased 20 to 25 percent by the systematic crossing of the British beef breeds. Perhaps production could be increased still more by use of other breeds, especially those with possibly more genetic divergence.

Crossbreeding produces heterosis, permits rapid incorporation of desirable genetic material, and allows the breeder to combine the best features of two or more breeds into one animal. These three genetic consequences of crossbreeding, given by Willham (1970a), can be used to exploit existing genetic differences in such a way as to result in maximum economic returns.

Much of the crossbreeding research with beef cattle

has dealt with the ability of the crossbred individual to grow. Some research has been done on the reproductive performance of crossbreds. However, little research exists on birth losses. Birth losses may take many forms. They may cause death, stunting, or crippling in the cow and/or calf, and may impair the future reproductive usefulness of the cow.

Difficult parturition is only one of the causes of birth losses, but it appears to be taking on increasing importance. The current enthusiasm for crossing large bulls with whatever cows are available invites calving problems. The great variation in size, shape, and muscularity in the breeds available for crossing today is almost certain to result in some crosses which will frequently have difficult parturitions. Frequent birth losses completely overwhelm the advantages of heterosis, rapid incorporation of desirable genetic material, and combination of the best features of two or more breeds into one animal, which accompany crossbreeding.

The purposes of this study are: to describe, in terms of birth-related traits, the crossbreds which result when all possible combinations of Angus, Hereford, Holstein, and Brown Swiss breeds are crossed; to determine the general and maternal combining abilities of the four breeds; to describe the heterosis and specific and reciprocal com-

binning ability effects of particular crosses for birth traits; to investigate how well certain measurements taken on the cow and calf at birth predict the degree of calving difficulty; and to examine the effects of farm, sex, age of dam, year, and parity on the birth traits.

REVIEW OF LITERATURE

The Birth Traits in General

Parturition in cattle is a highly complex event, which requires the coordination of many of the tissue systems in the body of the cow. The biological control mechanisms involved in parturition are, even today, pretty much a mystery to man.

Expelling the fetus from the uterus always involves a certain amount of stress and labor for the cow. When more time or effort than is normal is required to deliver the calf, we refer to the problem as calving difficulty or dystocia. The degree of dystocia associated with a given birth is difficult to determine. Descriptions of calving difficulty are usually based on the amount of assistance given to the cow in delivering the calf. Such descriptions reflect both the propensity of the herdsman to render aid, and the actual incidence of dystocia.

Information from birth-related traits was used in this study to supplement the information obtained directly from the description of calving difficulty. The birth-related traits were: birth weight, height at the withers at birth, and length of the gestation period. These birth-related traits, along with calving score, will hereafter be referred to as the birth traits.

The birth traits are all measures of prenatal develop-

ment. Birth weight measures the mass of tissue development, height at the withers is a measure of skeletal development, and gestation length measures the duration of prenatal development. Calving score expresses the difficulty associated with the transition from intrauterine to extrauterine development.

All of the birth traits are greatly influenced by the dam. The phenotype, which is expelled from the uterus at parturition, is determined by the genotype of the calf, the uterine environment provided by the dam, and the interaction between them. The genotype of the calf is determined by the genotypes of its sire and dam. The uterine environment of the calf is part of the maternal ability phenotype of the cow, which is influenced by her genes for maternal ability and by environmental influences such as: nutrition, health, age, parity, and others. Thus, the dam influences her progeny in three important ways: by the sample half of her genes which she transmits to him, by her genotype for maternal ability, and by modifying the uterine environment of the calf in response to external environmental conditions which she faces.

Touchberry and Tabler (1952) reported that the influence of breed of dam on birth weight was approximately three times larger than that associated with the breed of sire.

The heritabilities of the birth traits vary widely. Warwick (1958) averaged a number of heritability estimates of birth weight. The average was 41 percent. Dawson, Yao and Cook (1955) reported obtaining an estimate of 0.65 for the heritability of wither height measured on yearling steers. Touchberry (1951) obtained an estimate of 0.73 for the heritability of height at the withers of three-year-old Holstein cows. Blackmore, McGilliard and Lush (1958) gave heritability estimates of 0.34, 0.44, and 0.86 when wither height measurements were taken on the same animals at six months, one year, and two years, respectively. DeFries, Touchberry and Hayes (1959) estimated the heritability of the length of the gestation period as 0.42 using the paternal half-sib correlation, and as 0.47 using the regression of offspring on dam. Willham (1970b) estimated the heritability of calving score in Charolais to be 0.09. Response to selection for low calving score would be very small with such low heritability.

Genetic Effects of Crossbreeding

The mean of a group of crossbreds is the mean of the straightbred parents plus a heterosis effect. Alternatively, the crossbred mean can be stated as the sum of the general combining abilities of the sire and dam breeds, the maternal combining ability of the dam breed, and the specific combining ability associated with a particular cross. Recip-

recal combining ability effects can also be included in the crossbred mean, since the effects for the two reciprocal crosses sum to zero. Analysis of the genetic effects of crossbreeding can be facilitated by study of these components of the crossbred mean, which will be defined in the paragraphs which follow.

Heterosis

Heterosis is defined as the difference between the average of the two reciprocal crossbreds and the average of the parent breeds. The amount of heterosis when breeds A and B are crossed is $1/2 [AB + BA - AA - BB]$, where AB, BA, AA, and BB are means for the matings involving A sires with B dams, B sires with A dams, straightbred matings of breed A, and straightbred matings of breed B. Heterosis effects may be either positive or negative, depending upon whether the crossbred mean is larger or smaller than the straightbred mean.

For the simple case where a trait is completely determined by a single locus with two alleles, the amount of heterosis present when two breeds are crossed is $(\Delta p)^2 d$, according to Falconer (1960). The symbol Δp represents the difference in gene frequency at the locus in the parent populations, and d is the genotypic value of the heterozygote at that locus, expressed as a deviation from the average of the genotypic values of the two homozygotes. Thus, heterosis

is a function of dominance and the squared difference in gene frequency. If, for a given locus, the gene frequency in the parent populations is the same, or if there is no dominance at the locus, there is no heterosis. On the other hand, for a given level of dominance, heterosis is maximized when different alleles are fixed in the two parent populations. Genetic divergence thus enhances the magnitude of heterosis.

Quantitative traits, however, are influenced by a number of different loci. If the genotypic values of the n loci which affect a trait all act additively, the heterosis produced by their joint effects when two breeds are crossed can be represented as,

$$\sum_{i=1}^n [\Delta p]_i^2 d_i$$

according to Falconer (1960). In this case, the sign of the dominance deviation is important, since positive dominance deviations at some loci will tend to cancel negative deviations at other loci. As a result, heterosis may be absent in spite of the presence of gene frequency differences and dominance. If the genotypic values of the n loci affecting a trait do not act additively, then epistatic effects as well as dominance effects contribute to heterosis.

. Heterosis is usually greatest for traits that are

expressed early in life. Gregory, Swiger, Koch, Sumption, Rowden and Rothlisberger (1966) reported heterosis effects were largest for birth weight and growth rate to weaning, and were smallest for feedlot gain, which was measured later in life. Shreffler and Touchberry (1959) also found that heterosis manifested itself in more rapid growth up to about two years of age. After two years, the effect became too small to be statistically significant.

General combining ability

Henderson (1952) defined general combining ability as the average merit of an indefinitely large number of progeny of an individual or line, when mated with a random sample from some specified population. If maternal effects exist for the trait of interest, either the tested individuals must be males, or general combining ability must be estimated after correcting for maternal effects. When general combining ability is expressed as a deviation from the population mean, it is half of the breeding value of the individual or line. General combining ability must be defined relative to some specified population and environment, hence, it is difficult to compare estimates made in different studies.

Maternal combining ability

Maternal combining ability is the average performance of the crossbred progeny of females of a line or breed less

the average performance of the crossbred progeny of males of the line or breed, when mated to a random sample of some specified population. Both prenatal and postnatal maternal ability are included in the effect. For the birth traits, most of the maternal effect is due to prenatal influences.

Specific combining ability

Specific combining ability describes the inferiority or superiority of a cross relative to the average performance of the parent lines, after taking into account the maternal ability of the female line. Genetically, specific combining ability results from the nonadditivity of general combining ability effects, after accounting for differences in maternal ability, and is a result of dominance and epistasis.

Reciprocal combining ability

Reciprocal effects measure the difference between using breed A as the male parent and breed B as the female parent compared to reversing the role of the breeds. This effect is the interaction of general and maternal combining abilities.

Genetic Effects of Crossbreeding on the Birth Traits Ease of calving

Sagebiel, Krause, Sibbit, Langford, Comfort, Dyer and Lasley (1969) studied calving difficulties in 529 calves from all possible mating combinations of Angus, Hereford,

and Charolais cattle. A dystocia score was assigned to each calving to indicate the degree of difficulty. The scores which were used are defined in Table 1.

Table 1. Derivation of calving score^a

Degree of assistance	Calf alive or dead	Cow alive or dead	Assigned score
No assistance	alive	alive	1
No assistance	dead	alive	2
Pulled, easy	alive	alive	3
Pulled, easy	dead	alive	4
Pulled, difficult	alive	alive	5
Pulled, difficult	dead	alive	6
Pulled, very difficult	alive	dead	7
Pulled, very difficult	dead	dead	8

^aSource: Sagebiel et al. (1969).

Sagebiel and co-workers analyzed three measures of dystocia: dystocia score as referred to in Table 1, percent calving difficulties, and percent severe calving difficulties.

Calving difficulty was defined as dystocia scores 3 through 8. Severe calving difficulty was dystocia scores 5 through 8. Each sex was analyzed separately to avoid heterogeneity of variance.

They found that heterosis effects significantly increased calving difficulty in births involving crossbred female calves, but not in births involving crossbred male calves. Not all the crosses they studied produced a heterotic effect. Hereford x Charolais crosses did not show heterosis for calving difficulty in either sex. On the other hand, crossbred females from Angus x Hereford, and Angus x Charolais crosses were calved with significantly more difficulty than straightbred females of the parent breeds, but crossbred males from the same crosses were calved with no significant heterosis effect.

The results of Monteiro (1969) contradict those of Sagebiel et al. (1969). According to Monteiro, crossbreds had a lower percentage of difficult calvings than straightbreds. He worked with all possible mating combinations of Holstein, Ayrshire, and Jersey breeds. Although tests of significance were not reported, Holstein x Ayrshire, Ayrshire x Jersey, and Holstein x Jersey crosses had 5.1 percent, 2.8 percent, and 11.4 percent fewer difficult calvings than the average of their straightbred parents. These results suggest that the three straightbreds are not as well adapted to have calves of their own breed as they are to have calves sired by other breeds, which may differ considerably in size.

Rollins, Loy, Carroll and Wagon (1969) suggested that the large birth weights of crossbred calves may increase the number of calves born, but may reduce the percentage of

those born that survive to weaning. The extra vigor of the larger calf reduces embryonic loss, but injuries at birth may reduce survival to weaning.

In summary, a heterosis effect for degree of calving difficulty has been found in all of the reports that have been cited. The reports dealing with the beef breeds agree that straightbred cows have more difficulty calving crossbred calves than straightbred calves. There is some evidence that the heterosis effect for calving difficulty is greater, in beef cattle, in births involving female calves. The single report dealing with dairy breeds indicated that crossbred calves were delivered with greater ease than straightbred calves, when all of the dams were straightbreds.

Sagebiel et al. (1969) reported breed differences in breeding value for ease of calving. He found the dystocia scores of cows having crossbred calves were smallest when the sire was an Angus, and were largest when the sire was a Charolais. Hereford sires were intermediate between the two extremes. The difference in breeding value between Angus and Hereford sires was small. Calving difficulty occurred 18 percent and 26 percent more frequently with crossbred calves sired by Charolais bulls, compared to crossbred calves sired by Hereford and Angus bulls, respectively. Nearly 1 out of 4 births involving crossbred calves sired by Charolais bulls resulted in severe calving diffi-

culty. Clearly, breed differences in breeding values for ease of calving are important.

Charolais cows had significantly fewer cases of calving difficulty than either Hereford or Angus cows, when all had crossbred calves (2.1 percent, 14.9 percent and 31.5 percent, respectively). Angus cows had significantly larger dystocia scores than either Hereford or Charolais cows. Hence, Charolais cows had a beneficial maternal effect, while Angus cows had a detrimental maternal effect.

Monteiro (1969) reported that Jersey cows had less calving difficulty than either Ayrshires or Holsteins, when all breeds had crossbred calves. He concluded that the larger breeds of cows had more calving difficulty than the smaller breeds, because their calves were larger in comparison to the size of the cow. This conclusion is not supported by Sagebiel's results, where large cows had the least calving difficulty, and small cows had the most. Both Sagebiel and Monteiro agree, however, that maternal ability has an important effect on ease of calving.

Birth weight

Birth weight is an important consideration in crossbreeding, especially where there is considerable difference in the size of the parent breeds. This may be of particular importance in first calf heifers.

Heterosis for birth weight usually ranges from 0 to 5

percent, with crossbreds being heavier than straightbreds. Rollins et al. (1969) summarized heterosis estimates for birth weight obtained at the California, Nebraska and Virginia stations. Each of the experiments involved all possible mating combinations among Angus, Hereford, and Shorthorn breeds. Expressed as a percentage of the purebred means, the heterosis estimates for Angus x Hereford, Hereford x Shorthorn and Angus x Shorthorn crosses were 4.5 percent, 4.5 percent and 4.4 percent, respectively. Pahnish, Brinks, Urick, Knapp and Riley (1969) reported heterosis estimates of 3.3 percent, 3.8 percent and 1.9 percent for birth weight in Hereford x Angus, Hereford x Charolais and Angus x Charolais crosses.

Several workers have studied the heterosis effects when British beef breeds have been crossed with Brahman cattle. In general, the heterosis effects for such crosses have been greater than those observed for British x British crosses. Mason (1966) cited two experiments where heterosis for birth weight was 11 percent and 26 percent for crosses involving British beef breeds with Brahmans.

There is some evidence that the breeds differ in their breeding value for birth weight, when used to sire crossbred calves. Gregory et al. (1965) and Gaines, McClure, Vogt, Carter and Kincaid (1966), working with Angus, Hereford and Shorthorn crosses, found that Hereford bulls sired

calves with the heaviest birth weights followed in order by Shorthorn and Angus bulls. However, Rollins et al. (1969) reported that Shorthorn bulls sired calves which were heavier at birth than those sired by Hereford bulls. Pahnish et al. (1969) reported that Charolais bulls excelled Hereford and Angus bulls for siring heavy calves at birth.

Maternal effects for birth weight among crosses of the British beef breeds were reported to be very small by both Gregory et al. (1965) and Gaines et al. (1966). In both of these experiments, Angus dams excelled Hereford dams in maternal ability for birth weight, where maternal ability is defined as the difference in average birth weight in progeny of dams and in progeny of sires. However, Shorthorns performed differently in the two experiments. Shorthorn dams had the largest maternal effect of the three breeds in Gregory's experiment, while Gaines found the Shorthorn's maternal effect was the lowest of the three breeds. Crosses involving other breeds, with more variation in body size, would probably have resulted in larger maternal effects for birth weight.

Wither height

Shreffler and Touchberry (1959) did not find any significant heterosis for height at the withers measured at 3, 6, 12, 18, 24, 30, 36, and 48 months of age. They worked

with Holstein and Guernsey straightbreds, and the reciprocal crosses between the two breeds. They also estimated heterosis for two other skeletal measures, chest depth and body length; and again found no significant heterosis effect. On the other hand, body weight, heart girth, and paunch girth, which are all influenced by amount of fat, did manifest significant heterosis.

Gestation length

Brackel, Rife and Salisbury (1952) gave estimates of 288.36 and 278.57 days for gestation length in Brown Swiss and Holstein cows, respectively. Burris and Blunn (1952) reported gestation lengths of 281.7 and 286.1 days for Angus and Hereford cows, respectively. Rollins et al. (1969) studied the length of gestation of the crossbred calf, using all mating combinations of Angus, Hereford and Shorthorn breeds. He concluded that the heterosis effect for gestation length for crosses of the British beef breeds is small. His estimates were 0.5 percent, 0.5 percent and 0.4 percent for Hereford x Angus, Hereford x Shorthorn, and Shorthorn x Angus crosses, respectively. Gerlaugh, Kunkle and Rife (1951) gave an estimate of heterosis for gestation length for Angus and Hereford crossbreds of 0.4 percent.

Prediction of Calving Difficulty

Sagebiel et al. (1969) found a correlation of 0.11 between birth weight and dystocia score, when all breeds of cows were pooled together. When only Angus cows were considered, the correlation between birth weight and dystocia score was 0.36, for Herefords alone the correlation was 0.24, and for Charolais alone the correlation was 0.16. Correlations between gestation length and dystocia score, calculated separately for Angus, Hereford and Charolais cows, were generally not significant, although, for calves from Angus cows, the correlation was 0.23, which was highly significant. The correlation between cow weight and dystocia score, reported by Sagebiel, was -0.24, when all breeds were pooled together. This correlation, which was highly significant, was a result of easy calving in the large Charolais cows, and difficult calvings in the smaller Angus cows.

Lasley, Day and Comfort (1961) working with Herefords, reported a phenotypic correlation of 0.18, and a genetic correlation of 0.44 between gestation length and birth weight.

The correlations just given indicate that some of the birth traits are related, but they do not show that the relationship is one of cause and effect. If a strong cause and effect relationship between some easily obtained measurements on the cow, and calving score could be dis-

covered, perhaps a practical way to predict calving difficulty could result.

SOURCE OF DATA

Data for this study resulted from 895 births involving all mating combinations of Angus, Hereford, Holstein and Brown Swiss breeds. The data were collected in 1968 and 1969 at two Iowa State University research farms.

Two hundred heifers of each of the four breeds were purchased in the fall of 1967, and were bred artificially, beginning in January and February of 1968, using semen from 10 bulls of each of the four breeds. Five females of each breed were inseminated with semen from each bull.

Angus and Hereford sires were selected for maximum growth rate. Selections were made from among all bulls in artificial insemination studs across the country. The dairy bulls were chosen differently, since no growth data were available for them. Half of the dairy bulls were selected for highest available predicted difference for milk, and the other half were selected for the lowest predicted difference available.

The breeding females were maintained during the winter on a ration of corn silage or haylage supplemented with a concentrate mix, and were kept on pastures in the summer. Table 2 gives the wintering rations.

The 1968 calf crop was calved in October and November. Four hundred thirty-nine births were recorded. All of the cows that calved in 1968 were at least two years old. Actual

Table 2. Pounds of total digestible nutrients in wintering rations

Farm	Breed type	Heifers 1967-1968		Cows and calves 1968-1969	
		Concentrate	Roughage	Concentrate	Roughage
Ankeny	Beef	2.6	5.2 ^a	3.6	8.2 ^a
	Dairy	2.6	6.8 ^a	8.4	9.2 ^a
Chariton	Beef	2.8	2.9 ^b	10.2	4.2 ^b
	Dairy	4.1	3.8 ^b	13.7	4.9 ^b

^aCorn silage.

^bHaylage.

ages were not known on the purchased cows.

An entirely different set of 40 bulls was used for the 1969 calf crop, although the bulls were selected on the same criteria, and the mating plan was the same as before. The number of births resulting from each of the 16 mating combinations is given in Table 3, which includes data from both years.

The 1969 calf crop was born in September through December. All of the cows that calved in 1969 were at least three years old. Thus, year and age of dam effects were completely confounded in the data. Two hundred eighty-seven cows calved for the second time, and 167 cows had their

Table 3. Number of births classified by breed of sire and breed of dam

Breed of sire	Breed of dam			
	Angus	Hereford	Holstein	Brown Swiss
Angus	47	53	62	56
Hereford	49	57	68	58
Holstein	58	60	65	42
Brown Swiss	56	55	62	45

first parity in 1969. To remove extraneous variation due to age of dam, year and parity in the statistical analysis, the three sources of variation were grouped into one combined effect with three levels; first parity of two year olds in 1968, first parity of three year olds in 1969, and second parity of three year olds in 1969.

One hundred ninety-two cows were injected, in 1969, with 20 milligrams of Azium for the purpose of hastening the onset of parturition. Azium is the trade name for the compound dexamethasone, which is manufactured by Schering Corporation, Bloomfield, New Jersey. No Azium was used in 1968.

At calving, the herdsman identified the calf, recorded its birth date, dam, weight, the presentation and position of the calf at birth, and the amount of assistance given at

birth.

Each week, calves that were born during the week were measured for height at the withers and width at the hip bones. The cows which had calved were weighed, and a veterinarian took measurements of the width and depth of the pelvic opening in the cows.

The length of the gestation period was calculated for each birth, by subtracting the conception date from the date of birth. The conception date was considered to be the date of the last insemination before calving. However, the dates of earlier inseminations were used as the beginning of gestation when the pregnancy examinations at 60 and 120 days, and the subsequent calving date, left little doubt that the last insemination date was not the date of conception.

A calving score, ranging from 1 through 17 was calculated for each birth, based on numerical codes for presentation, position and degree of assistance at birth. The calving scores are defined in Table 4.

For the statistical analysis, the births which were not observed were given a calving score of 2, the same as the births which were observed, but were unassisted. This probably biases the scores for unobserved births downward slightly from what they would have been if they had been observed. However, this small bias seemed preferable to

Table 4. Definition of calving scores

Score	Condition of calf at birth	Description of observation	Presentation	Position	Assistance
1	alive	not observed	-	-	-
2	alive	observed	normal	normal	none
3	alive	observed	_a	_a	none
4	dead	observed	-	-	none
5	alive	observed	normal	normal	manual
6	alive	observed	_a	_a	manual
7	dead	observed	-	-	manual
8	alive	observed	normal	normal	chains
9	alive	observed	_a	_a	chains
10	dead	observed	-	-	chains
11	alive	observed	normal	normal	chains and jack
12	alive	observed	_a	_a	chains and jack
13	dead	observed	-	-	chains and jack
14	alive	observed	normal	normal	caesaerian section
15	alive	observed	_a	_a	caesaerian section
16	dead	observed	-	-	caesaerian section
17	dead	observed	-	-	embryotomy

^aIndicates that the presentation or the position or the presentation and position were abnormal.

the larger one which would result if unobserved calvings were given a lower calving score than observed but unassisted calvings.

METHODS OF ANALYSIS

The distribution of calving scores for the two years is shown in Figure 1, which suggests a wide departure from normality. Further evidence of nonnormality was obtained using a chi-square goodness of fit test. The mean and standard deviation of calving score were calculated. The x axis under the standard normal curve was divided into eight segments. The leftmost segment included those values of x that were less than $(\mu - 3/2\sigma)$. The upper boundary of each succeeding segment was moved to the right a distance of $\sigma/2$ until the last segment, which included all values of x greater than $(\mu + 3/2\sigma)$. The area under the curve in each of the eight segments was calculated using tabled values of the standard normal distribution. The areas represent the probability that a random value of x will fall within the range of x values which determine the borders of the area. These probabilities were then multiplied by the total number of calving scores to determine the expected number of scores which would fall within that segment under the curve if the data were normally distributed. These expected numbers, and the numbers actually observed, were used to compute the chi-square. The computed value of the chi-square with 5 degrees of freedom was 870. The critical value of a chi-square with 5 degrees of freedom is 11.1, when $P = 0.05$. The test shows there is no reason to

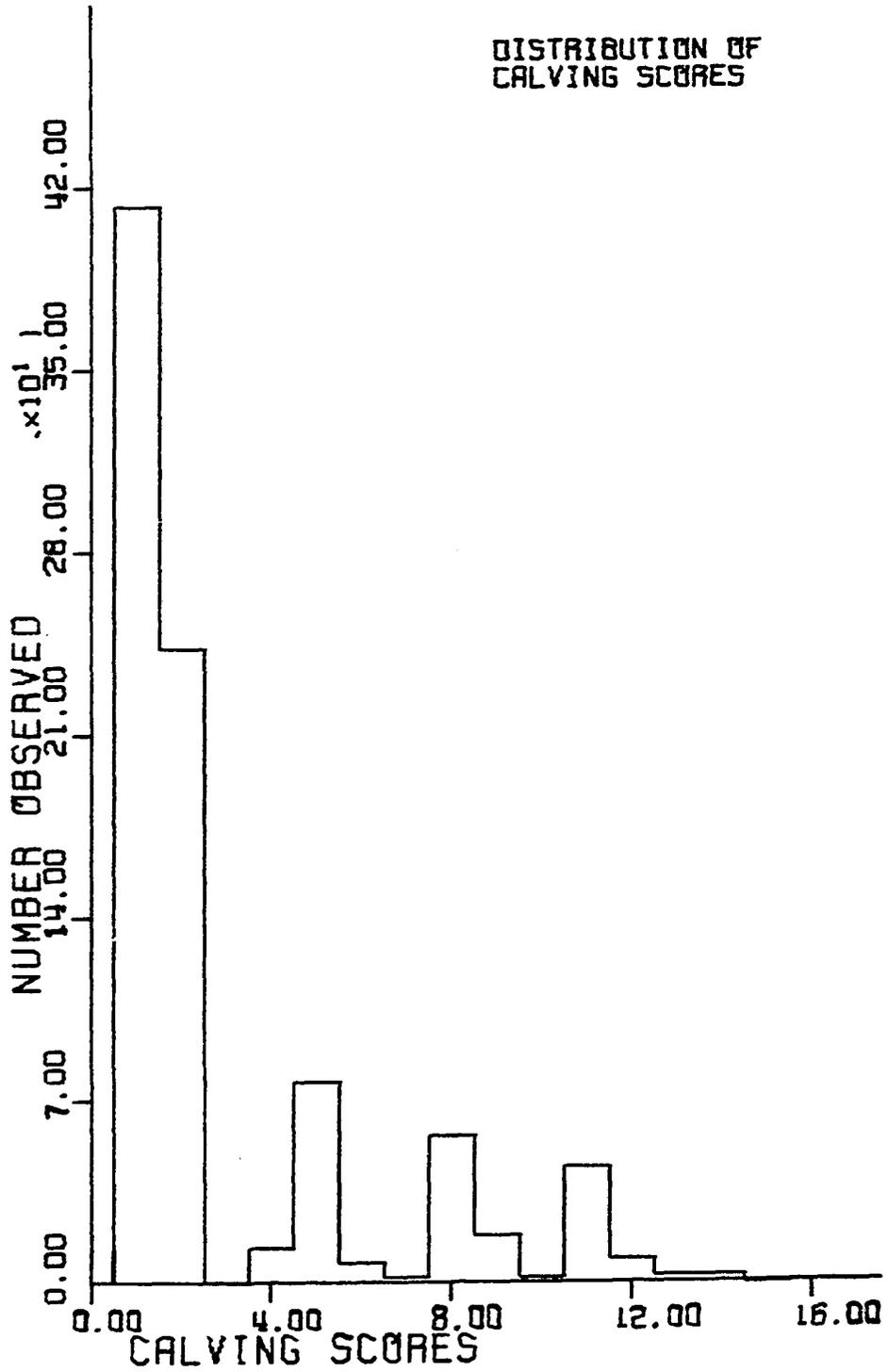


Figure 1. Distribution of all calving scores from 1968 to 1969

believe the calving scores are normally distributed.

Attempts were made to transform the data, so that it would more nearly conform to the normal distribution. Transformations using the common logarithm of the observed score plus one, the square root of the observed score plus one, the inverse sine of 0.23 multiplied by the square root of the observed score, the inverse tangent and the inverse sine of 0.055 multiplied by the observed score and the hyperbolic sine of the observed score were tested, using the chi-square goodness of fit test. Some of the transformations reduced the size of the chi-square, but not enough to suggest that any of the transformed data sets were normally distributed. The smallest value of chi-square for the transformed values was 490, with 5 degrees of freedom.

Cox (1962) described a method for approximating a normal distribution from discrete data. The calving scores from this study were transformed using Cox's method. The distribution of the transformed values were tested using the chi-square test. The test indicated there was no reason to believe that the transformed values were normally distributed.

No further attempt was made to transform the data. Means and variances calculated from the data are not influenced by the distribution, but valid probability statements for tests of significance are not possible with-

out knowledge of the underlying distribution. Scheffé (1959), however, points out that this problem is not serious when one is concerned with tests of means, since the random variable

$$t = n [\bar{y} - \mu]/s$$

approaches a normal distribution with mean zero and variance one when n is large. So that, for large n , the distribution of t is independent of the form of the population. Hence, inferences about the mean, which are valid in the case of normality, are also correct for large n , regardless of the form of the population. On the other hand, inferences concerning variances are strongly affected by nonnormality. This fact is of little concern in this study, since interest is centered on the means.

To determine the effect of each of the four breeds on the birth traits, a least-squares analysis of variance of nonorthogonal data was completed. The mathematical model assumed to describe the biology was

$$\begin{aligned} x_{hijklmno} = & \mu + A_h + P_{1ii} + G_{2i} + G_{2j} + M_{2j} + C_{2ij} \\ & + R_{2ij} + F_k + S_l + T_m + J_n + e_{hijklmno} \quad (1) \end{aligned}$$

where

$x_{hijklmno}$ = an observation made on the o^{th} individual
from a mating of a dam from the j^{th} breed

and a sire from the i^{th} breed, where the h^{th} breeding system was used, the individual was born on the k^{th} farm, had the l^{th} sex, his dam was in the m^{th} azium treatment group, and the n^{th} age of dam-year-parity group,

μ = the overall mean when equal subclass frequencies exist and there are equal frequencies of straightbreds and crossbreds,

A_h = an effect common to all progeny of the h^{th} type of breeding (crossbred or straightbred),

P_{1ii} = an effect common to all straightbred progeny of the i^{th} breed,

$G_{2i}(G_{2j})$ = the general combining ability effect common to all crossbred progeny with a parent from the $i^{\text{th}}(j^{\text{th}})$ breed,

M_{2j} = the maternal combining ability effect common to all crossbred progeny whose dam was from the j^{th} breed,

C_{2ij} = the specific combining ability effect common to all crossbred progeny who had one parent of the i^{th} breed, and one parent of the j^{th} breed,

R_{2ij} = the reciprocal combining ability effect common to all crossbred progeny whose

sire and dam were from the i^{th} and j^{th} breeds, respectively,

F_k = an effect common to all progeny born on the k^{th} farm,

S_1 = an effect common to all progeny of the 1^{th} sex,

T_m = an effect common to all progeny whose dams received the m^{th} Azium treatment,

J_n = an effect common to all offspring whose dams were in the n^{th} year-age of dam-parity group, and

e_{hijklmno} = a random deviation associated with the observation x_{hijklmno} .

All effects in the model except the random deviation are considered fixed effects in the statistical sense. The subscript 1, accompanied by a lower case letter subscript (or subscripts), denotes that the effects are measured only in straightbred progeny, while the subscript 2 denotes effects measured only in crossbreds.

The least-squares normal equations for estimating type of breeding, straightbred; and general, maternal, specific and reciprocal combining ability effects have been described by Harvey (1960). The normal equations for model (1) do not have a unique solution, because dependencies exist among the equations. Harvey has suggested restrictions on the constant estimates, which will remove the dependencies from the

equations. The restrictions used to give a unique solution for all effects in the model, are given in (2).

$$\begin{aligned}
 \sum_h A_h &= \sum_i P_{1ii} = \sum_i G_{2i} = \sum_j M_{2j} = \sum_i C_{2ij} \\
 &= \sum_j C_{2ij} = \sum_i R_{2ij} = \sum_j R_{2ij} = \sum_k F_k \\
 &= \sum_l S_l = \sum_m T_m = \sum_n J_n = [R_{2ij} + R_{2ji}] = 0
 \end{aligned}
 \tag{2}$$

These restrictions cause the constant estimates for farm, sex, Azium treatments, year-age of dam-parity and type of breeding to sum to zero about μ , the straightbred estimates to sum to zero about $(\mu + A_1)$, and the constants for each of the remaining effects to sum to zero about $(\mu + A_2)$.

After the normal equations have been reduced to a non-singular set, the matrix of coefficients of the reduced equations can be inverted. The matrix inverse is post-multiplied by the reduced right hand sides to give estimates of the constants.

Sums of squares and mean squares were calculated for each of the effects in model (1), using procedures outlined by Harvey (1960). Each of the fixed effects in the model was tested for significance by dividing its mean square by the error mean square.

The standard errors of the constant estimates are

obtained from the inverse of the reduced normal equations and the error mean square. The standard error for the hypothetical constant a_1 is given by

$$\sqrt{Ca_1a_1 \sigma_e^2} \quad (3)$$

where C is an element of the inverse of the reduced normal equations, and σ_e^2 is the error mean square. The subscripts a_1a_1 refer to the diagonal element of the C matrix, corresponding to the a_1^{th} row and column.

The least-squares mean for the general combining ability of the i^{th} breed is given by

$$\mu + A_2 + T_1 + G_1 \quad (4)$$

where A_2 indicates the mean involves crossbreds, and the T_1 effect specifies that the dam of the offspring received no Azium. If the T_1 effect were not included, the mean would be appropriate for the case where half of the cows were injected with Azium, and half of the cows were untreated. However, the mean when no Azium was used was of most interest, so T_1 was included.

The least-squares mean for the maternal combining ability effect of the j^{th} breed can be computed using the expression,

$$\mu + A_2 + T_1 + M_j \quad (5)$$

where A_2 and T_1 are the same as defined for (4).

Differences among the general combining ability effects can be tested for significance using Duncan's multiple range test, as modified by Kramer (1957). The method makes use of the inverse elements, and the standard deviation for error. If the quantity

$$[G_i - G_j] \sqrt{\frac{2\sigma_e^2}{c^{G_i G_j} + c^{G_i G_j} - 2c^{G_i G_j}}} \quad (6)$$

is greater than $\sigma_e Z_{p,n_2}$, then the difference between G_i and G_j is significant. Z_{p,n_2} is the significant studentized range value which is tabled for $P = 0.05$. The number of means in the range is given by p , and n_2 is the number of degrees of freedom for error. σ_e is the square root of the error mean square. When all pair-wise comparisons are tested, the exact probability level of the test becomes greater than 5 percent, because each of the G_i values is used more than once; hence, the tests are not independent of each other. Despite this difficulty, the tests still indicate the relative significance of observed differences. Differences among maternal combining ability effects can be tested in the same way.

In terms of the model given in (1), the least-squares mean of the i^{th} breed of straightbreds is

$$\mu + A_1 + P_{1ii} + T_1 \quad (7)$$

where A_1 is an effect common to all straightbreds, P_{1ii} is

the effect of the i^{th} breed of straightbreds, and T_1 is an effect common to animals whose dam was not injected with Azium.

The least-squares mean of crossbred progeny resulting from mating a female of the j^{th} breed, and a male from the i^{th} breed is

$$\mu + A_2 + G_{2i} + G_{2j} + M_{2j} + C_{2ij} + R_{2ij} + T_1 \quad (8)$$

where μ , G_{2i} , G_{2j} , M_{2j} , C_{2ij} and R_{2ij} are as described in (1); A_2 is an effect common to crossbreds, and T_1 is as described in (7).

The standard error for the mean of the i^{th} breed of straightbreds is the square root of (9).

$$\left[C^{\mu\mu} + C^{A_1A_1} + C^{P_1P_1} + C^{T_1T_1} + 2C^{\mu A_1} + 2C^{\mu P_1} + 2C^{\mu T_1} + 2C^{A_1P_1} + 2C^{A_1T_1} + 2C^{P_1T_1} \right] \sigma_e^2 \quad (9)$$

The standard error for the crossbred mean, when sires of breed i are mated to dams of breed j , is the square root of (10). In both (9) and (10), the C 's denote elements in the inverse of the variance-covariance matrix. The superscripts give the effects whose equations correspond to the row and column desired. σ_e^2 is the error mean square.

The heterosis effect from crossing two specific breeds is of more interest than the average heterosis effect of all crosses, which is obtained from $A_2 - A_1$. Heterosis

$$\left[\begin{array}{l}
 c^{uu} + c^{A_2A_2} + c^{G_1G_1} + c^{G_jG_j} + c^{M_jM_j} + c^{C_{1j}C_{1j}} + \\
 c^{R_{1j}R_{1j}} + c^{T_1T_1} + 2c^{uA_2} + 2c^{uG_i} + 2c^{uG_j} + 2c^{uM_j} + \\
 2c^{uC_{1j}} + 2c^{uR_{1j}} + 2c^{uT_1} + 2c^{A_2G_i} + 2c^{A_2G_j} + 2c^{A_2M_j} + \\
 2c^{A_2C_{1j}} + 2c^{A_2R_{1j}} + 2c^{A_2T_1} + 2c^{G_iG_j} + 2c^{G_iM_j} + \\
 2c^{G_iC_{1j}} + 2c^{G_iR_{1j}} + 2c^{G_iT_1} + 2c^{G_jM_j} + 2c^{G_jC_{1j}} + \\
 2c^{G_jR_{1j}} + 2c^{G_jT_1} + 2c^{M_jC_{1j}} + 2c^{M_jR_{1j}} + 2c^{M_jT_1} + \\
 2c^{C_{1j}R_{1j}} + 2c^{C_{1j}T_1} + 2c^{R_{1j}T_1}
 \end{array} \right] \sigma_e^2 \quad (10)$$

resulting from crossing breeds i and j can be obtained from the least-squares means by computing the quantity.

$$1/2 [ij + ji - ii - jj] \quad (11)$$

where the letters inside the brackets denote least-squares means of progeny from dams of breed j and sires of breed i , dams of breed i and sires of breed j , and straightbreds of the i^{th} and j^{th} breeds, respectively.

The three degrees of freedom for straightbreds, and general and maternal combining abilities can be broken down into single degree of freedom orthogonal comparisons. The comparisons were chosen to compare beef versus dairy breeds, and the two breeds within each type against each other. Harvey (1960) has given procedures for calculating the sums of squares for orthogonal comparisons.

Estimating the percent of the total variance due to general, maternal, specific, and reciprocal combining abilities, after removing variation from other fixed effects in the model, involves equating the computed mean squares with their expectations. The expected values of the mean squares are specified in Table 5.

Table 5. Expected values of mean squares for genetic effects on the birth traits

Source of variation	Expected value of mean square
General combining ability	$\sigma_e^2 + 147.94 K_G^2$
Maternal combining ability	$\sigma_e^2 + 110.19 K_M^2$
Specific combining ability	$\sigma_e^2 + 110.85 K_C^2$
Reciprocal combining ability	$\sigma_e^2 + 77.24 K_R^2$
Error	σ_e^2

The K^2 terms are defined by Snedecor (1956) as the variance associated with a fixed effect. The coefficients with the K^2 terms were obtained by means of a formula given by Harvey (1960). The formula is given in (12).

$$\frac{1}{m} \left[\sum_i z^{ii} - \frac{1}{df} \sum_i \sum_{i \neq j} z^{ij} \right] \quad (12)$$

In (12), m is the number of classes in the classification; Z is the inverse of the square, symmetrical segment of the variance-covariance matrix inverse which corresponds, by row and column, to the equations for the effects being considered; and df is the number of degrees of freedom for the classification. The superscripts on Z identify the matrix element by row and column.

Multiple regression methods were used to determine the effect of ten independent variables on the dependent variable calving score. Separate analyses were carried out for each of the four breeds of dam. The mathematical model used was

$$\begin{aligned}
 x_{ijklm} = & \mu + F_i + S_j + B_k + J_l + b_1z_1 + b_2z_2 + b_3z_3 \\
 & + b_4z_4 + b_5z_5 + b_6z_6 + b_7z_7 + b_8z_8 + b_9z_9 \\
 & + b_{10}z_{10} + e_{ijklm} \qquad (13)
 \end{aligned}$$

where

x_{ijklm} = the calving score of the m^{th} individual born on the i^{th} farm, with the j^{th} sex, sired by a bull of the k^{th} breed, and from a dam in the l^{th} year-age of dam-parity group,

μ = the overall mean,

F_i = an effect common to all animals born on the i^{th} farm,

- S_j = an effect common to all animals of the j^{th} sex,
 B_k = an effect common to all animals sired by a bull
 from the k^{th} breed,
 J_l = an effect common to all animals whose dam
 belonged to the l^{th} year-age of dam-parity
 group,
 b_1 = the partial regression coefficient of calving
 score on birth weight,
 z_1 = the birth weight of x_{ijklm} less the average
 birth weight of all progeny,
 b_2 = the partial regression coefficient of calving
 score on the weight of the dam,
 z_2 = the weight of the dam of x_{ijklm} less the
 average weight of all dams,
 b_3 = the partial regression coefficient of calving
 score on width of the dam's pelvic opening,
 z_3 = the width of the pelvic opening in the dam of
 x_{ijklm} less the average width of the pelvic
 opening in all dams,
 b_4 = the partial regression coefficient of calving
 score on the depth of the pelvic opening in
 the dam,
 z_4 = the depth of the pelvic opening in the dam of
 x_{ijklm} less the average depth of the pelvic
 opening in all dams,

- b_5 = the partial regression coefficient of calving score on wither height of the calf at birth,
- z_5 = the wither height of x_{ijklm} less the average wither height, at birth, of all calves,
- b_6 = the partial regression coefficient of calving score on width at the hips at birth,
- z_6 = the width at the hips at birth of x_{ijklm} less the average width at the hips of all calves at birth,
- b_7 = the partial regression coefficient of calving score on the length of the dam's gestation period,
- z_7 = the length of the gestation period which resulted in x_{ijklm} less the average gestation length,
- b_8 = the partial regression coefficient of calving score on day of birth,
- z_8 = the day of birth of x_{ijklm} less the average birth date of all calves,
- b_9 = the partial regression coefficient of calving score on the area of the pelvic opening in the dam,
- z_9 = the area of the pelvic opening in x_{ijklm} 's dam less the average area of the pelvic opening in all dams,

b_{10} = the partial regression coefficient of calving score on birth weight divided by cow weight,

z_{10} = the ratio of x_{ijklm} 's birth weight to the weight of his dam less the average birth weight divided by cow weight, and

e_{ijklm} = a random deviation associated with x_{ijklm} .

Birth weight and cow weight were measured in pounds. Pelvic width and depth, height at the withers, and width at the hips were measured in centimeters. Pelvic area was computed from pelvic width and depth measurements. The pelvic opening was assumed to be an ellipse, whose equation is

$$\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1 \quad (14)$$

and whose area is given by

$$4 \int_0^a \frac{b}{a} \sqrt{[a^2 - x^2]} dx = \pi ab \quad (15)$$

where a and b are lengths of the semiaxes of the ellipse. The pelvic width measurement was considered to be $2a$, and the pelvic depth was considered $2b$. Hence, the calculated pelvic area was

$$\pi/4 [\text{Pelvic width} \times \text{Pelvic depth}] \quad (16)$$

The ten independent variables make use of the regression equations cumbersome for prediction purposes. Hence, a

satisfactory subset of variables was sought. The best subset of variables might be that subset which results in the smallest residual mean square. One way to insure that the chosen subset is best by this criterion, is to examine all possible regression equations, and their corresponding residual mean squares, and then choose the subset which achieves the condition. The problem is that 1024 regressions would have to be compared for each of the four cow breeds!

An alternative method of choosing a subset of independent variables is the backward elimination procedure, which begins with all of the variables in the regression equation, and proceeds to eliminate the least important independent variables. The variable deleted at any stage is the one which, if deleted, causes the smallest nonsignificant increase in the residual sum of squares. The procedure was given by Macpherson (1968).

RESULTS AND DISCUSSION

Preliminary analyses, using only data from 1968, were used to investigate the importance of various interactions. A model was fitted for each of the four birth traits. The model included farm, sex, breed of sire, and breed of dam as main effects; sires within breed of sire as nested effects; two-factor interactions of main effects including breed of sire with breed of dam, farm with sex, farm with breed of sire, farm with breed of dam, and sex with breed of sire; and interactions of main and nested effects including farm by sire within breed of sire and sex with sire within breed of sire. The error term contained the sex by breed of dam and the breed of dam by sire within breed of sire interactions, plus all interactions of more than two effects. The interactions included in the error term were not fitted because of limitations on the size of the matrix which could be handled with the computing programs available.

The farm by sire within breed of sire and the sex by sire within breed of sire interactions were not significant for any of the birth traits, and were dropped from the model. The farm by sex, breed of sire by farm, breed of sire by sex and breed of dam by farm interactions were also found to be nonsignificant sources of variation for all of the birth traits, and were dropped from the model.

A second model was fitted using the remaining effects

of farm, sex, breed of sire, breed of dam, sires nested within breeds of sire, and the two-way interaction of breed of sire by breed of dam.

The farm effect was significant only for calving score. Differences between the sexes were significant for all of the birth traits except gestation length, and breed of sire differences were significant for all of the birth traits. Differences among breeds of dam were the largest source of variation for all of the birth traits. Sires within breed of sire differences were significant for birth weight, wither height, and gestation length, but not for calving score. The breed of sire by breed of dam interaction was significant only for birth weight and wither height. The F ratio of the mean square for breed of sire by breed of dam divided by the remainder mean square was less than one for calving score.

Since most of the interest was in calving score, the breed of sire by breed of dam interaction was dropped from the model, leaving the effects of farm, sex, breed of sire, breed of dam, and sires within breed of sire left in the model.

Sires within breeds of sire effects were absorbed, and constants were fitted for farm, sex, and breed of dam for all four of the birth traits. These constants were used to correct the data for a completely nested analysis of breed of sire, sires within breeds of sire, and progeny

within sires within breeds of sire. The percentages of the variances attributable to breed of sire, sires within breeds of sire and progeny within sires, for each of the birth traits, are given in Table 6.

Table 6. Percentages of variance attributable to breed of sire, sires within breeds of sire and progeny for the birth traits

Source of variation	df	Birth weight	Wither height	Gestation length	Calving score
Breed of sire	3	14.8	41.1	7.5	3.1
Sires: breeds of sire	36	9.8	5.9	7.0	2.2
Progeny	399	75.4	53.0	85.5	94.7

Differences among breeds of sire and differences among sires within a breed of sire contribute about equally to the variance in gestation length. Differences in breeds of sire account for about $3/2$ as much of the variance as differences between sires within breeds of sires for birth weight and calving score, while differences among breeds of sire dominate variation in height at the withers.

Most of the variation in calving score was due to sources other than breed of sire or sire within breed of sire, whereas breed of sire and sire within breed of sire

effects accounted for nearly half of the total variation in wither height. There appears to be less individual sire effect on calving score than has sometimes been suggested.

Perhaps the small individual sire effect was due to selection which tended to make the bulls alike. There is some evidence to support this conjecture. The calving score mean squares for sires within dairy breeds of sires were larger than the mean squares for sires within beef breeds of sires (15.5 and 11.2 versus 10.4 and 6.1). Beef sires were all selected for growth rate, and growth rate is genetically correlated, in some fashion, with calving score. There was a correlated response in calving score as a result of selection for growth rate. This correlated response reduced the variability in calving score among those beef bulls that were selected. Hence, the small sires within breed of sire effect within the beef breeds. Calving score may be correlated with predicted difference for milk, so that selection for two extremes in predicted difference for milk resulted in selecting for differences in calving score. The difference in breeding value for calving score between high and low predicted difference bulls gave more variability among sires within the dairy breeds than was found among sires within the beef breeds.

Analyses of variance were performed for birth weight,

height of the calf at the withers, gestation length, and calving score using model (1), given in the methods of analysis section. The results are presented in Table 7. Estimates of the constants, and their standard errors, are given in Table 8.

Nongenetic Fixed Effects

The farm, sex, Azium treatment, and year-age of dam-parity classifications were included in the model to adjust the data for more precise estimates of the genetic effects. These nongenetic sources of variation were of interest.

A significant farm difference existed for birth weight and wither height, traits which measure prenatal growth. Calves born at the Ankeny farm weighed 4.74 pounds more at birth than those born at Chariton, and were 0.46 centimeters taller at the withers. The difference in growth at the two farms was probably due to differences in the nutrition of the dams. The appearance of the cows indicated that the level of nutrition was higher at the Ankeny farm. This conclusion is consistent with the results.

The difference in average gestation length at the two farms was small. Gestations averaged 1/12th of a day longer at Chariton than at Ankeny.

The difference in calving scores between the two farms was even smaller than the difference in gestation lengths. The differences in birth weight, height at the withers, and

Table 7. Analyses of variance for four birth traits

Source	df	Birth weight	Wither height	Gestation length	Calving score
Farm	1	4568.21**	43.06*	1.53	0.07
Sex	1	5150.31**	227.20**	237.21**	112.48**
Heterosis	1	371.93	8.75	0.83	25.30
Azium	1	263.68	31.94	252.62**	25.19
Age-year-par.	2	2370.32**	12.50	299.21**	201.75**
Purebreds	3	7970.02**	1684.67**	926.26**	7.30
General C	3	3481.75**	981.42**	306.58**	53.63**
Maternal C	3	2550.31**	150.61**	167.11*	150.71**
Specific C	2	618.92**	26.80	6.33	6.57
Reciprocal	3	95.64	26.92*	43.71	15.23
Error	872	98.24	9.93	49.95	7.18

*P < 0.05.

**P < 0.01.

Table 8. Constant estimates and their standard errors

Constant	Birth weight	Wither height	Gestation length	Calving score
μ	77.44 \pm 0.50	67.51 \pm 0.16	281.00 \pm 0.34	3.30 \pm 0.13
Farm 1	2.37 \pm 0.35	0.23 \pm 0.11	- 0.04 \pm 0.24	- 0.01 \pm 0.09
Farm 2	- 2.37 \pm 0.35	- 0.23 \pm 0.11	0.04 \pm 0.24	0.01 \pm 0.09
Males	2.42 \pm 0.33	0.51 \pm 0.11	0.52 \pm 0.23	0.36 \pm 0.09
Females	- 2.42 \pm 0.33	- 0.51 \pm 0.11	- 0.52 \pm 0.23	- 0.36 \pm 0.09
St. bred	- 0.76 \pm 0.39	- 0.12 \pm 0.12	0.04 \pm 0.27	- 0.20 \pm 0.11
Crossbred	0.76 \pm 0.39	0.12 \pm 0.12	- 0.04 \pm 0.27	0.20 \pm 0.11
No Azium	0.87 \pm 0.53	0.30 \pm 0.17	0.85 \pm 0.36	- 0.27 \pm 0.14
Azium	- 0.87 \pm 0.53	- 0.30 \pm 0.17	- 0.85 \pm 0.36	0.27 \pm 0.14
T ₁ ^a	- 3.63 \pm 0.53	0.22 \pm 0.17	0.77 \pm 0.36	1.06 \pm 0.14
T ₂ ^b	1.13 \pm 0.60	- 0.25 \pm 0.19	0.76 \pm 0.41	- 0.36 \pm 0.16

^aT₁ refers to cows that had their first calf in 1968 as two year olds.

^bT₂ refers to cows that had their first calf in 1969 as three year olds.

Table 8. (Continued)

Constant	Birth weight	Wither height	Gestation length	Calving score
T_3^c	2.50 ± 0.63	0.03 ± 0.20	- 1.53 ± 0.43	-0.70 ± 0.17
P_1^d	-13.49 ± 1.23	- 5.89 ± 0.39	- 1.75 ± 0.84	0.52 ± 0.33
P_2	- 7.74 ± 1.16	- 3.92 ± 0.37	2.32 ± 0.79	-0.34 ± 0.31
P_3	9.57 ± 1.11	4.37 ± 0.35	- 4.86 ± 0.76	0.04 ± 0.30
P_4	11.66 ± 1.25	5.44 ± 0.40	4.29 ± 0.86	-0.22 ± 0.34
G_1^d	- 5.90 ± 0.70	- 2.47 ± 0.22	- 0.85 ± 0.48	-0.65 ± 0.19
G_2	- 2.28 ± 0.70	- 2.07 ± 0.22	- 0.24 ± 0.48	-0.40 ± 0.19
G_3	4.46 ± 0.73	2.17 ± 0.23	- 0.98 ± 0.50	0.53 ± 0.20
G_4	3.72 ± 0.69	2.38 ± 0.22	2.07 ± 0.47	0.52 ± 0.19

^c T_3 refers to cows that had their second calf in 1969 as three year olds.

^dThe numeric subscripts for the P, G, M, C, and R constants refer to breeds, where 1 = Angus, 2 = Hereford, 3 = Holstein, and 4 = Brown Swiss. For the C and R effects, the double subscripts refer to the breeds of the parents of a two breed cross. The order of the breeds is important for the R effects, where the first subscript denotes the breed of the sire, and the second subscript denotes the breed of the dam. Order of subscripts is unimportant for C effects since $C_{ij} = C_{ji}$.

Table 8. (Continued)

Constant	Birth weight	Wither height	Gestation length	Calving score
M_1^d	- 4.92 ± 0.83	- 1.40 ± 0.26	- 1.25 ± 0.57	1.09 ± 0.22
M_2	- 2.58 ± 0.81	- 0.01 ± 0.26	1.72 ± 0.56	0.64 ± 0.22
M_3	5.61 ± 0.81	1.44 ± 0.26	- 0.09 ± 0.55	- 0.17 ± 0.22
M_4	1.89 ± 0.83	- 0.03 ± 0.26	- 0.38 ± 0.57	- 1.56 ± 0.22
C_{12}^d	1.95 ± 0.56	0.41 ± 0.18	0.19 ± 0.38	0.10 ± 0.15
C_{13}	- 0.65 ± 0.54	- 0.16 ± 0.17	- 0.15 ± 0.37	- 0.20 ± 0.15
C_{14}	- 1.29 ± 0.53	- 0.25 ± 0.17	- 0.04 ± 0.37	0.10 ± 0.14
C_{23}	- 1.29 ± 0.53	- 0.25 ± 0.17	- 0.04 ± 0.37	0.10 ± 0.14
C_{24}	- 0.65 ± 0.54	- 0.16 ± 0.17	- 0.15 ± 0.37	- 0.20 ± 0.15
C_{34}	1.95 ± 0.56	0.41 ± 0.18	0.19 ± 0.38	0.10 ± 0.15
R_{12}	- 0.68 ± 0.67	- 0.51 ± 0.21	- 0.04 ± 0.46	- 0.10 ± 0.18
R_{13}	0.75 ± 0.66	0.26 ± 0.21	- 0.05 ± 0.45	- 0.17 ± 0.18
R_{14}	- 0.07 ± 0.67	0.25 ± 0.21	0.08 ± 0.46	0.27 ± 0.18
R_{21}	0.68 ± 0.67	0.51 ± 0.21	0.04 ± 0.46	- 0.10 ± 0.18

Table 8. (Continued)

Constant	Birth weight	Wither height	Gestation length	Calving score
R ₂₃	0.19 ± 0.65	0.02 ± 0.21	0.62 ± 0.44	- 0.28 ± 0.18
R ₂₄	- 0.87 ± 0.67	- 0.53 ± 0.21	- 0.66 ± 0.46	0.18 ± 0.18
R ₃₁	- 0.75 ± 0.66	- 0.26 ± 0.21	0.05 ± 0.45	0.17 ± 0.18
R ₃₂	- 0.19 ± 0.65	- 0.02 ± 0.21	- 0.62 ± 0.44	0.28 ± 0.18
R ₃₄	0.94 ± 0.68	0.28 ± 0.21	0.57 ± 0.46	- 0.45 ± 0.18
R ₄₁	0.07 ± 0.67	- 0.25 ± 0.21	- 0.08 ± 0.46	- 0.27 ± 0.18
R ₄₂	0.87 ± 0.67	0.53 ± 0.21	0.66 ± 0.46	- 0.18 ± 0.18
R ₄₃	- 0.94 ± 0.68	- 0.28 ± 0.21	- 0.57 ± 0.46	0.45 ± 0.18

husbandry were not great enough to alter calving scores at the two farms. Factors other than farm differences caused most of the variation in calving score.

The sex difference was significant in all of the birth traits. At birth, bull calves were 4.84 pounds heavier and 1 centimeter taller at the withers than heifers. The gestation length for males was 1.04 days longer than for females. The extra day of gestation for bulls explains part of the difference in birth weight and wither height, but not all of it. Prenatal rate of gain averaged 0.29 pounds per day in males, and 0.27 pounds per day in females. Sex differences influenced calving score. Males had higher calving scores than females (0.71 score units). Thus, males were calved with more difficulty. The difference in size between the sexes does not fully explain the difference in calving difficulty. The farm difference in birth weight and wither height was almost exactly the same as the sex difference in size. Yet, the larger calves from the Ankeny farm were calved just as easily as the smaller calves from Chariton. Size was not the only factor making the birth of male calves more difficult than the birth of female calves.

Azium was injected into 192 cows in 1969 to hasten the onset of parturition. Eighty percent of the cows that received Azium calved within 72 hours after the injection. The Azium injections were made before the gestations had reached full term in order to end the calving season. The

use of Azium decreased birth weights by 1.74 pounds, decreased height at the withers by 0.6 centimeters, shortened gestations by 1.7 days, and increased calving scores by 0.54 scores. Only the difference in gestation length was significant. The evidence indicates that Azium does hasten the onset of parturition.

The analyses of variance in Table 7 show that differences in years, age of dam, and parity contribute significantly to variation in birth weight, gestation length, and calving score. The year-age of dam-parity sum of squares for each birth trait was partitioned into a portion attributable to year-age of dam effects, and a portion due to parity effects in Table 9. Year and age of dam effects were completely confounded, and could not be separated.

Table 9. Sums of squares for orthogonal comparisons among year-age of dam-parity effects on four birth traits

Comparison	Birth traits			
	Birth weight	Wither height	Gestation length	Calving score
2 vs. 3 year olds ^a	2514.72**	24.96	0.00	225.69**
1st vs. 2nd parity ^b	149.14	6.61	417.90**	8.94

^aIncludes only 1st parities.

^bBoth first and second parities occurred in 1969.

**p < 0.01.

The year-age of dam effect was larger than the parity effect on birth weight. Calves of three year olds were 4.76 pounds heavier at birth than calves of two year olds. Part of this difference may be due to years, or the fact that different sire groups were used each year. Cows that had their second calf in 1969 had calves that weighed 2.5 pounds more at birth than calves from cows having their first calf in 1969. This difference in birth weight due to parity was not significant. Birth weight was influenced more by size and maturity of the dam than by the parity of cows of equal size and maturity.

The year-age of dam effect also contributed a larger portion of the variation in wither height than the parity effect, but neither of the effects were significant.

Parity contributed all of the variation in gestation length attributed to the joint effects of year-age of dam-parity. Gestation lengths in two and three year old cows having their first parities were about identical. Gestation length averaged 1.53 days less in second parity cows, compared to first parity cows.

Most of the year-age of dam-parity effect for calving score is due to year-age of dam. The calving scores of two year olds were 1.4 score units greater than the scores of three year olds. The calving scores of cows having their second parity in 1969 were 0.7 units less than the

scores of cows having their first parity in 1969. The growth that the cows made between two and three years of age greatly reduced calving scores as three year olds. The three year old cows calved easier in spite of the fact that their calves were 4.76 pounds heavier at birth. The ratio of calf weight to cow weight was smaller for three year old cows, however, because cow weights increased much more than calf weights.

Performance of the Breeds as Straightbreds

Differences among straightbreds existed for all of the birth traits except calving score. These differences are sources of genetic variation, which can be exploited to maximize profit from crossbreeding.

Dairy breeds excelled in prenatal growth. The rank of the breeds for birth weight and wither height was, from largest to smallest; Brown Swiss, Holstein, Hereford, and Angus.

Single-degree-of-freedom comparisons of straightbred effects are given in Table 10. Beef and dairy types differed greatly in birth weight and wither height. Birth weights averaged 22 pounds heavier in the dairy breeds. Dairy calves were 10 centimeters taller at the withers than beef calves. Herefords were 5.76 pounds heavier at birth than Angus, and were also two centimeters taller at the withers.

The rank of the breeds for gestation length, from

Table 10. Sums of squares for orthogonal comparisons among straightbred effects on four birth traits

Comparisons	Birth traits			
	Birth weight	Wither height	Gestation length	Calving score
Beef vs. Dairy	23466.32**	5010.52**	16.92	1.69
Angus vs. Hereford	850.90**	99.88**	426.32**	19.03
Brown Swiss vs. Holstein	115.67	30.32	2216.99**	1.79

**P < 0.01.

longest to shortest was; Brown Swiss, Hereford, Angus, and Holstein. The gestation length in Herefords and Angus differed significantly (284.21 versus 280.14 days). Gestation lengths in Brown Swiss and Holsteins also differed (286.2 versus 277.03 days).

All of the breeds calved straightbred calves with about equal ease, as evidenced by the nonsignificant F test (P = 0.05) for calving score in the analysis of variance in Table 7. The difference in calving score between Herefords and Angus borders on significance at P = 0.1. The rank of the breeds for calving score as straightbreds from easiest to hardest was; Hereford, Brown Swiss, Holstein, and Angus. Natural selection acts to keep the breeds at nearly the same level of fitness for ease of calving. This does not imply

that all breeds are able to calve crossbred calves with equal ease.

Performance of the Breeds as Crossbreeds

The performance of the breeds as parents of crossbred progeny was evaluated on the basis of general and maternal combining ability.

General combining ability

General Combining ability (GCA) is the additive genetic effect of a breed in cross combinations with other breeds. It is half of the breeding value of the breed in crosses with other breeds.

Significant differences exist among breeds for general combining ability in all four birth traits. Thus, one can select among breeds for improved performance. The rank of the breeds for GCA is almost the same as the rank of the straightbreds for all of the birth traits except calving score. The superior prenatal growth that was apparent in the dairy breeds as straightbreds was also found in their crossbred progeny, who also excelled in birth weight and wither height. The rank of the breeds for GCA for gestation length was exactly the same as the rank of the straightbreds.

The GCA's of the breeds for calving score differed considerably from the performance of the breeds as straightbreds. General combining ability was strongly influenced

by the size of the breed relative to the size of other breeds with which it was crossed. Angus cows had the highest average calving score of any of the straightbreds. Yet, when Angus bulls were crossed with other breeds of cows, the calving difficulty scores were low, because all of the other breeds were larger than the Angus. Hence the birth weight divided by cow weight ratio was smaller than what it would have been if the dam had been mated to a sire of her own breed. On the other hand, large breeds tended to have general combining abilities which were higher than their pure-bred effects.

Single-degree-of-freedom comparisons were calculated to compare GCA's for beef versus dairy breeds, Angus versus Hereford, and Brown Swiss versus Holstein. The comparisons are given in Table 11.

The GCA's of the dairy breeds were greater for birth weight (8.18 pounds) and wither height (4.54 centimeters) than those of the beef breeds. Beef breeds had a lower GCA for calving score than did the dairy breeds. This means that beef breeds had breeding values which contributed to easier calving compared to the dairy breeds.

Most of the differences in breeding value as parents of crossbred calves were due to the difference in size and growth potential in dairy compared to beef type. Two significant differences in GCA's between breeds within a

Table 11. Sums of squares for orthogonal comparisons among general combining ability effects on four birth traits

Comparisons	Birth traits			
	Birth weight	Wither height	Gestation length	Calving score
Beef vs. dairy	9430.34**	2912.47**	165.81	155.86**
Angus vs. Hereford	1007.57**	12.10	28.74	4.77
Brown Swiss vs. Holstein	40.32	3.18	690.83**	0.02

**P < 0.01.

type did exist, however. The GCA for birth weight in Herefords was 3.62 pounds greater than that for Angus, and the general combining ability effect for gestation length of Brown Swiss was greater than that for Holsteins by 3.04 days.

Tests for all pair-wise comparisons of GCA's were made using Duncan's new multiple range test, as modified by Kramer (1957). The results of these tests are given in Table 12. The number of comparisons exceeds the number of degrees of freedom. Therefore, not all of the comparisons are independent, and the error rate over the entire set of comparisons may be different than indicated by the level of probability. At least, the tests can be taken as rough

Table 12. Comparisons among the general combining abilities of breeds for birth traits using Duncan's multiple range test as modified by Kramer (1957)

Comparisons ^a	Birth weight difference	Wither height difference	Gestation difference	Calving score difference
G ₁ vs. G ₂	3.63**	0.40	0.61	0.25
G ₁ vs. G ₃	10.36**	4.64**	0.13	1.18**
G ₁ vs. G ₄	9.63**	4.85**	2.91**	1.17**
G ₂ vs. G ₃	6.73**	4.24**	0.74	0.93**
G ₂ vs. G ₄	6.00**	4.45**	2.30**	0.92**
G ₃ vs. G ₄	0.74	0.21	3.05**	0.02

^aG refers to a general combining ability effect. The digits used as subscripts refer to breeds, where 1 = Angus, 2 = Hereford, 3 = Holstein, and 4 = Brown Swiss.

**p < 0.01.

guides concerning the likelihood that the observed values could have occurred by chance.

All comparisons of GCA's involving a beef with a dairy breed were significantly different for birth weight, wither height, and calving score. The GCA of the Brown Swiss breed for gestation length differed significantly from all other GCA's for that trait.

We would like to have the lowest possible general combining ability for calving score consistent with satisfactory performance in other traits at all stages in the life of the animal. Small birth weights contribute to low calving scores. Compromise is probably required between the small birth weight desirable for easy calving, and the larger birth weight associated with more rapid growth later in life, since a rather high genetic correlation probably exists between prenatal and postnatal growth. About the same compromises are required for height at the withers. Short gestation lengths are most desirable. The largest difference between the GCA's of two breeds for gestation length was 3.04 days, which is a very small difference in terms of change in the calving interval of a group of cows.

The Angus breed has the smallest general combining ability for calving score, birth weight, and height at the withers. It also has next to the shortest combining ability for gestation length. From the standpoint of the four birth

traits being considered, the Angus meets most criteria for GCA.

Maternal combining ability

The maternal combining ability (MCA) of a breed is the difference in the performance of crossbred progeny of dams of the breed, less the performance of crossbred progeny of sires of the breed. The great effect of the dam on the birth traits of her progeny has already been noted.

The four breeds differed in maternal ability for all four of the birth traits in cross combinations. This means some breeds of dam will suit a certain purpose better than other breeds.

Orthogonal comparisons were calculated to compare the maternal ability of beef versus dairy breeds, Hereford versus Angus, and Brown Swiss versus Holstein. The results of the comparisons are given in Table 13. The comparisons show that most of the variation in maternal ability for birth weight, wither height, and calving score results from differences between beef and dairy breeds. This is consistent with the observations of Gregory *et al.* (1965) and Gaines *et al.* (1966), who found little difference in maternal ability among the British beef breeds.

There were, however, a few differences in maternal ability between breeds of the same type. Holsteins had a significantly greater maternal effect than Brown Swiss for

Table 13. Sums of squares for orthogonal comparisons among maternal combining ability effects on four birth traits

Comparisons	Birth traits			
	Birth weight	Wither height	Gestation length	Calving score
Beef vs. dairy	6553.07**	232.83**	25.77	349.86**
Angus vs. Hereford	288.52	102.39**	467.05**	10.63
Brown Swiss vs. Holstein	742.41**	116.06**	4.71	104.44**

**P < 0.01.

birth weight, and height at the withers. Brown Swiss had lower average calving difficulty scores than Holsteins, and thus had the beneficial maternal effect of easier calving. Hereford dams had larger maternal effects for wither height and gestation length than Angus dams.

The MCA's of the breeds pretty well parallel the rank of the breeds as straightbreds. MCA's rank in almost opposite order compared to GCA's for calving score. There is a reasonable explanation for this. Crossbred calves from Angus bulls were calved by Hereford, Holstein, and Brown Swiss cows which were larger than Angus cows. Therefore, the calves from these dams that were sired by an Angus bull were small relative to the size of the dam, resulting in

easy calvings and a low general combining ability effect for Angus. On the other hand, Angus cows were mated to bulls of larger breeds to produce crossbred calves. The larger bull breeds caused the crossbred calf to be large relative to the size of the Angus cow. Hence, calving was relatively difficult for Angus cows, and their maternal combining ability for calving score was high.

All possible pair-wise comparisons between maternal combining abilities, using Duncan's new multiple range test, are given in Table 14.

To make calving scores as small as possible, the maternal effect, as a deviation from the crossbred mean, should be less than zero. Birth weight and height at the withers should be no more than the straightbred mean, and we would like for gestation length to be as short as possible.

Performance of Specific Crosses

The performance of all 16 mating combinations of the four breeds in this experiment are given in terms of least-squares means in Table 15.

Specific combining ability

Specific combining ability (SCA) describes the inferiority or superiority of a cross, relative to the average performance of the parent lines, after correcting for the maternal ability of the female line. The analyses of variance in Table 7

Table 14. Comparisons among the maternal combining abilities of breeds for birth traits using Duncan's multiple range test as modified by Kramer (1957)

Comparisons ^a	Birth weight difference	Wither height difference	Gestation difference	Calving score difference
M ₁ vs. M ₂	2.33	1.39**	2.97**	0.45
M ₁ vs. M ₃	10.52**	2.84**	1.16	1.26**
M ₁ vs. M ₄	6.81**	1.37**	0.87	2.65**
M ₂ vs. M ₃	8.19**	1.45**	1.81*	0.81*
M ₂ vs. M ₄	4.47**	0.02	2.10*	2.21**
M ₃ vs. M ₄	3.72**	1.37**	0.30	1.39**

^aM refers to a maternal combining ability effect. The digits used as subscripts refer to breeds, where 1 = Angus, 2 = Hereford, 3 = Holstein, and 4 = Brown Swiss.

*P < 0.05.

**P < 0.01.

Table 15. Least-squares means and standard errors for the birth traits

Breed of sire ^a	Breed of dam ^a	Birth weight	Wither height	Gestation length	Calving score
A	A	64.05 ± 1.48	61.81 ± 0.47	280.14 ± 1.01	3.35 ± 0.40
H	H	69.81 ± 1.34	63.77 ± 0.43	284.21 ± 0.92	2.49 ± 0.36
F	F	87.11 ± 1.28	72.07 ± 0.41	277.03 ± 0.87	2.88 ± 0.35
B	B	89.21 ± 1.52	73.13 ± 0.48	286.17 ± 1.04	2.61 ± 0.41
A	H	69.58 ± 1.41	63.27 ± 0.48	282.60 ± 0.96	2.82 ± 0.38
A	F	83.32 ± 1.33	69.17 ± 0.42	279.70 ± 0.91	2.58 ± 0.36
A	B	77.42 ± 1.39	67.81 ± 0.44	282.69 ± 0.95	1.90 ± 0.38
H	A	68.60 ± 1.44	62.91 ± 0.46	279.71 ± 0.98	3.47 ± 0.39
H	F	85.75 ± 1.25	69.23 ± 0.40	281.09 ± 0.85	3.01 ± 0.34
H	B	80.89 ± 1.33	67.52 ± 0.42	282.45 ± 0.91	1.77 ± 0.36
F	A	71.31 ± 1.32	65.81 ± 0.42	278.63 ± 0.91	4.17 ± 0.36
F	H	77.18 ± 1.31	67.75 ± 0.42	281.65 ± 0.89	4.39 ± 0.35
F	B	92.02 ± 1.57	73.13 ± 0.50	283.28 ± 1.07	2.37 ± 0.42

^aA = Angus, B = Brown Swiss, F = Holstein, and H = Hereford.

Table 15. (Continued)

Breed of sire ^a	Breed of dam ^a	Birth weight	Wither height	Gestation length	Calving score
B	A	70.75 ± 1.36	65.93 ± 0.43	281.65 ± 0.93	4.02 ± 0.37
B	H	78.15 ± 1.38	68.59 ± 0.43	285.87 ± 0.94	3.61 ± 0.37
B	F	93.87 ± 1.89	74.05 ± 0.41	282.43 ± 0.88	4.66 ± 0.35

indicate that SCA is a significant source of variation only for birth weight.

It is possible to test all pair-wise combinations of specific combining ability effects by testing only three comparisons instead of the expected number of 15 comparisons. The restrictions imposed on the specific combining ability constants in order to solve the normal equations make this simplification possible. The pertinent restrictions are

$$\begin{aligned}
 \text{(a)} \quad C_{ij} &= C_{ji} && \begin{array}{l} i = 1, 2, 3, 4 \\ j = 1, 2, 3, 4 \end{array} \\
 \text{(b)} \quad \sum_i C_{ij} &= \sum_j C_{ij} = 0 && (17) \\
 \text{(c)} \quad \sum_i \sum_{j \substack{ > \\ <}} C_{ij} &= 0 && \\
 &&& i < j
 \end{aligned}$$

where C_{ij} is the specific combining ability effect associated with crossing breeds i and j . Since C_{ij} effects exist only in crossbreds, i is never equal to j .

The relationships given in (17) lead to the equalities given in (18).

$$\begin{aligned}
 \text{(a)} \quad C_{12} &= C_{34} \\
 \text{(b)} \quad C_{13} &= C_{24} \\
 \text{(c)} \quad C_{14} &= C_{23}
 \end{aligned} \tag{18}$$

The equalities in (18) imply those given in (19).

$$\begin{aligned}
 (a) \quad C_{12} - C_{13} &= C_{12} - C_{24} = C_{34} - C_{13} = C_{34} - C_{24} \\
 (b) \quad C_{12} - C_{14} &= C_{12} - C_{23} = C_{34} - C_{14} = C_{34} - C_{23} \\
 (c) \quad C_{13} - C_{14} &= C_{13} - C_{23} = C_{24} - C_{14} = C_{24} - C_{23} \\
 (d) \quad C_{12} - C_{34} &= C_{13} - C_{24} = C_{14} - C_{23} = 0
 \end{aligned} \tag{19}$$

Hence, it is necessary to test only the pair-wise combinations of C_{12} , C_{13} , and C_{14} to test all combinations of SCA pairs. The results of testing all pairs of SCA effects are given in Table 16.

The results in Table 16 show that C_{12} was always as large, or larger, than C_{13} or C_{14} for all of the birth traits. Thus, the SCA effects were smaller for dairy x beef or beef x dairy crosses than they were for beef x beef or dairy x dairy crosses.

The significant difference between C_{12} versus C_{14} shown for height at the withers was unexpected, since the F test in the analysis of variance for wither height, given in Table 7, was not significant. This case of borderline significance probably resulted from the lack of independence among the comparisons made in the multiple range test, which caused the probability level of the test to vary from the stated level.

SCA's did not vary much for any of the birth traits.

Table 16. Comparisons among specific combining abilities for birth traits using Duncan's multiple range test as modified by Kramer (1957)

Comparisons ^a	Birth weight difference	Wither height difference	Gestation difference	Calving score difference
C ₁₂ vs. C ₁₃	2.60**	0.57	0.34	0.30
C ₁₂ vs. C ₁₄	3.24**	0.66*	0.23	0.00
C ₁₃ vs. C ₁₄	0.64	0.10	0.11	0.29

^aC is a specific combining ability effect from crossing time straightbreds. The numeric subscripts indicate the breeds used to make the cross. The number pair 12 means that breeds 1 and 2 were crossed. The breeds are identified by number with 1 = Angus, 2 = Hereford, 3 = Holstein, and 4 = Brown Swiss.

*P < 0.05.
**P < 0.01.

Little attention to SCA seems justified when selecting crosses to optimize performance in the birth traits.

Reciprocal combining ability

Reciprocal combining ability effects did not differ significantly for any of the birth traits except height at the withers. The largest reciprocal differences for wither height were for Angus x Hereford and Brown Swiss x Hereford crosses, where $HA - AH = 1.03$ and $BH - HB = 1.06$. Both of these differences were probably significant.

Reciprocal combining ability effects were of very little importance for determining the crossbred's performance for the birth traits.

Heterosis

Heterosis is the superiority or inferiority of the crossbred average relative to the average of the straightbred parents. It is positive if the crossbred average is greater than the straightbred average, but is negative if the crossbred average is less than the average of the straightbreds. A positive heterosis effect probably is not desirable for any of the birth traits. Increasing birth weights and height at the withers tends to make the cow's job of delivering the calf more difficult. Increasing the length of gestation period lengthens the calving interval, which means a cow can produce fewer calves in a

given length of time. Certainly we do not want a positive heterosis effect for calving score, which would increase calving difficulty.

The analyses of variance given in Table 7 show that the heterosis effect was not significant ($P = 0.05$) for any of the birth traits. The difference between crossbreds and straightbreds approaches significance for birth weight and calving score, however. The crossbred average was greater than the straightbred average for all of the traits except gestation length. The differences, however, were small enough to be due to chance.

Heterosis effects for all 12 groups of crossbreds are given in Table 17.

Brown Swiss x Holstein crosses produced a sizable, positive heterosis effect for each of the four birth traits. Hereford x Holstein crosses had a large, positive heterosis effect for calving score. At the other end of the heterosis scale, Angus x Brown Swiss crosses always had negative heterosis effects.

Thinking in terms of the theoretical explanation of heterosis, one would expect greater genetic diversity in crosses involving beef x dairy or dairy x beef matings, and hence more heterosis than for crosses where both parents were of the same type. Similar selection goals for the two dairy breeds should have resulted in similar frequencies

Table 17. Heterosis in the birth traits

Heterosis effect ^b	Birth traits							
	Birth weight		Wither height		Gestation length		Calving score	
	Pounds	% ^a	cm	% ^a	Days	% ^a	Scores	% ^a
AH	2.16	3.23	0.30	0.48	-1.02	-0.36	0.23	7.71
AF	1.74	2.30	0.55	0.82	0.58	0.21	0.26	8.35
AB	- 2.55	-3.32	-0.60	-0.89	-0.99	-0.35	-0.02	-0.67
HF	3.01	3.83	0.57	0.84	0.75	0.27	1.02	37.80
HB	0.01	0.01	-0.40	-0.58	-1.03	-0.36	0.14	5.49
FB	4.79	5.43	0.99	1.36	1.26	0.44	0.77	28.05

^a[(Average of the crossbred reciprocals - Average of straightbred parents)/ Average of straightbred parents] x 100.

^bThe abbreviation AH refers to $1/2 [\overline{AH} + \overline{HA} - \overline{AA} - \overline{HH}]$ where \overline{AH} , \overline{HA} , \overline{AA} , and \overline{HH} are means of A x H^c, H x A^c, A x A^c, and H x H^c matings. A = Angus, B = Brown Swiss, F = Holstein, and H = Hereford; c refers to the breed of sire precedes the x and the breed of dam follows it.

for genes which affect milk production. Likewise, the beef breeds have had similar selection goals and should be similar to each other, but different from the dairy breeds. The large heterosis effects for dairy x dairy and beef x beef matings compared to beef x dairy and dairy x beef matings suggest either that genetic diversity was not decisive in influencing the amount of heterosis found, or that beef and dairy breeds are not as different genetically as believed.

The amount of heterosis for birth weight in this study compares closely with results reported by Gregory et al. (1965), Gaines et al. (1966) and Rollins et al. (1969). Their estimates ranged from -4% to 5%.

Wither height and gestation length show very little heterosis. The small heterosis effect observed for gestation length was negative, since crossbred gestation lengths averaged a bit shorter than straightbred gestations.

Heterosis effects for calving score ranged from less than zero, for Angus x Brown Swiss crosses, to more than 37% for Hereford x Holstein crosses. The average heterosis effect for all crosses was 14%.

The heterosis effect was helpful for gestation length, but was so small (-0.1 day) that it has little practical importance. The results of this experiment suggest that there is a tendency for calving difficulty to increase

with crossbreeding, even though this difference was not statistically significant at $P = 0.05$.

Variance Attributable to Genetic Effects

Variation among crossbred individuals for each of the birth traits was partitioned into portions attributable to general, maternal, specific and reciprocal combining abilities, after variation from farm, sex, Azium treatment and year-age of dam-parity effects were removed. The results are given in Table 18.

Table 18. The percentages of the total variance attributable to genetic combining abilities

Source of variability	Birth traits			
	Birth weight	Wither height	Gestation length	Calving score
General combining ability	15.5	36.2	3.6	3.5
Maternal ability	15.0	7.0	2.3	14.6
Specific combining ability	3.2	0.8	0.0	0.0
Reciprocal	0.0	1.2	0.0	1.2
Error	66.3	54.8	94.1	80.7

GCA and MCA accounted for about equal portions of the total variance for birth weight. GCA was easily the most important source of variation for the trait wither height,

and contributed about equally with MCA as a primary source of variation in gestation length. Variation arising from differences in MCA's dominated variation in calving score.

Differences in SCA's and reciprocal effects contributed very little of the total variation in any of the birth traits except birth weight, where SCA contributed 3.2% of the total variation.

Most of the variation in both GCA's and MCA's for birth weight, wither height and calving score arose from differences in combining ability between beef and dairy breeds. Most of the variation in GCA's for gestation length arose because the Brown Swiss breed differed from all of the other breeds. Likewise, the Hereford breed differed from all of the other breeds in MCA for gestation length.

Ease of Calving for Various Beef-Dairy Type Combinations

The means for calving score were highest for those crosses where a dairy sire was mated to a beef dam (4.05), and were lowest for beef sires mated to dairy dams (2.32). The means for straight beef and straight dairy were intermediate, and were very nearly the same (3.13 for dairy versus 3.03 for beef).

An analysis was carried out to test the significance of calving score differences among beef x beef, beef x dairy, dairy x beef and dairy x dairy matings. The model employed was

$$x_{ijklm} = \mu + F_i + S_j + T_k + M_l + (TM)_{kl} + e_{ijklm} \quad (21)$$

where x_{ijklm} was an observation on the m^{th} animal from the i^{th} farm, with the j^{th} sex, in the l^{th} mating type, and whose dam was in the k^{th} year-age of dam-parity group.

The mating types considered were beef x beef (M_1), beef x dairy (M_2), dairy x beef (M_3), and dairy x dairy (M_4), where the type of the sire is given first. The mating type beef x beef, for example, included Angus x Angus, Hereford x Hereford, Angus x Hereford and Hereford x Angus crosses. Likewise, the other mating types included all possible combinations of breeds within the given types.

The F test for mating types was highly significant for calving score. Dairy x beef crosses had the highest calving scores followed in order by dairy x dairy, beef x beef, and beef x dairy. However, the interpretation is not clear-cut, because of a significant interaction between mating type and the year-age of dam-parity classification. This interaction is graphed in Figure 2.

T_1 was an effect common to all two year olds that had their first parity in 1968. T_2 was an effect common to all three year olds that had their first parity in 1969. T_3 was an effect common to all three year olds that had their second parity in 1969. Figure 2 shows that the mating types performed differently with T_3 than with T_1 and T_2 . T_3 included only second parity cows, and T_1 and

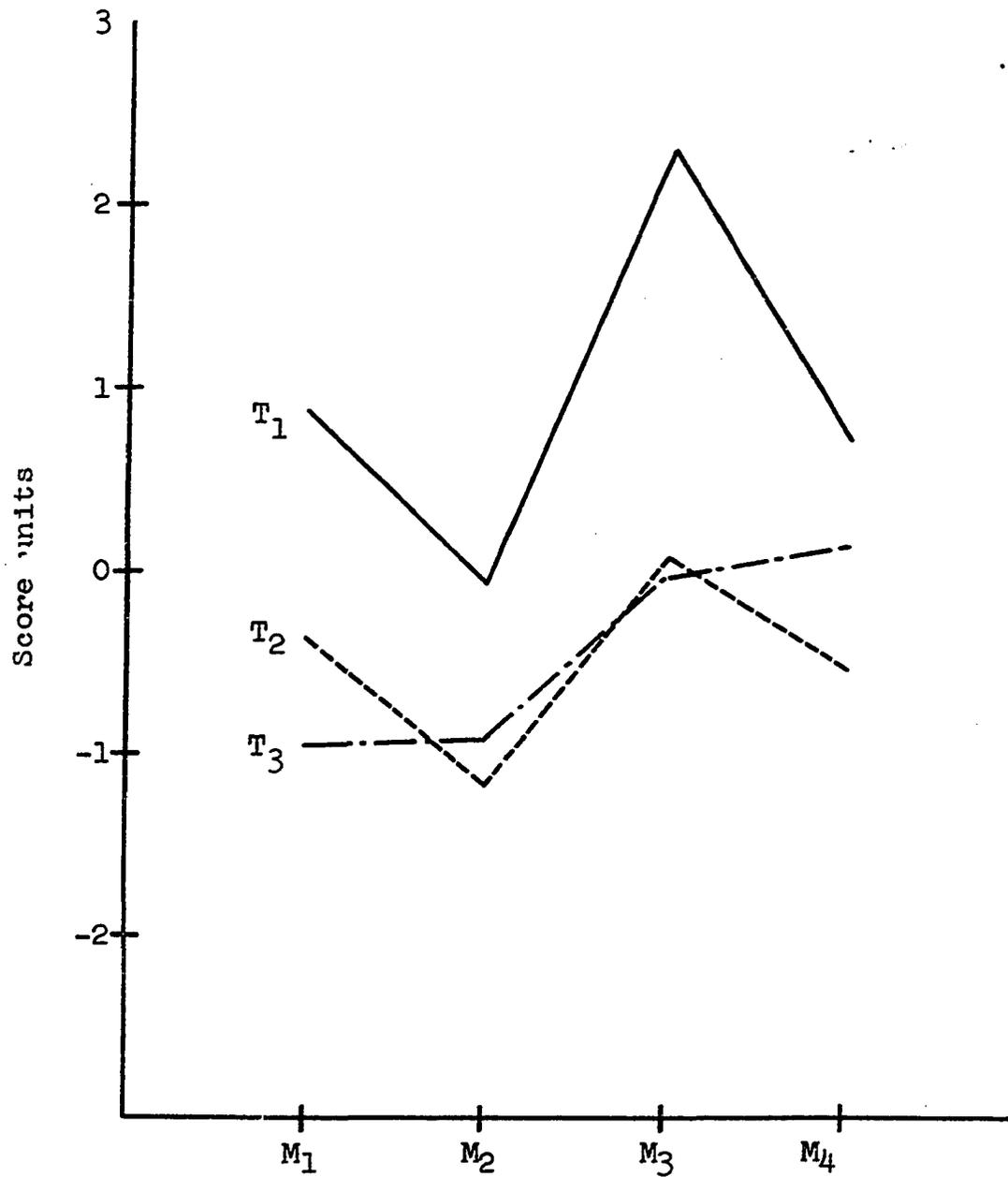


Figure 2. The interaction of mating types (M) and year-age of dam-parity groups (T) for calving score as deviations from the mean

T₂ included only first parity cows. According to Figure 2, beef cows improve more in ease of calving from first parity to second parity than dairy cows. In fact, beef x beef crosses had the lowest calving scores (easiest parturitions) and dairy x dairy crosses had the highest calving scores, when only second parities were considered. The difference in rate of decrease of calving score in beef and dairy cows must be due to some physical change which takes place during or after the first parturition. Perhaps the beef cows lost more fat after the first calving than did the dairy cows. Beef cows could have made more growth between their first two calvings than dairy cows, which were well grown at the time of first calving.

It seems safe to conclude that for all first calvings (T₁ and T₂) beef x dairy crosses calved easiest, dairy x beef crosses calved with the most difficulty, and the difference between the two was significant.

Relation of Calving Score to Economic Loss

Economic loss can result from calving difficulties in several ways. Calving difficulty can decrease the number of live calves, cause stunting or crippling of cows or calves injured at birth, increase the labor input during the calving season, or impair the future reproductive usefulness of the cow. Information on death loss was available. There was a 4.48% preweaning death loss. Forty-eight percent

of these deaths were stillbirths, few of which were due to calving difficulties. Another 25 percent of the deaths occurred more than 10 days following parturition. It seems safe to assume that these deaths were not the result of calving difficulties. The remaining 27 percent died within 10 days after birth. A high percentage of these deaths occurred on the day of birth, and probably did result from difficult parturition. At worst, all of the stillbirths and all of the group that died within 10 days after birth could have resulted from calving difficulties. Even so, the death loss due to difficult calving would be only 3.36 percent. If $1/4$ of the stillbirths and $3/4$ of the group that died within 10 days after birth actually died as a result of difficult parturition, the percent death loss due to difficult parturition would be 1.46 percent. This seems realistic.

It is clear that little death loss occurs due to dystocia when sufficient labor is available so the cows can be constantly observed during the calving season. Information is not available from this study to determine if the amount of death loss differs among the mating types when cows are observed only once or twice a day. Likewise, information is not available to examine losses due to crippling or stunting of the cow and/or calf. Hence, it is difficult to critically evaluate the effectiveness of

the calving score criterion as a measure of economic loss at calving.

Prediction of Calving Score

A cause-effect relationship was postulated between 10 measurements made on the cow or the calf at birth, and the degree of difficulty in calving, as measured by calving score. Multiple regression methods were used to determine if the supposed relationship could be used to predict calving score. The regressions were fitted within farm, sex, breed of sire, and year-age of dam-parity subclasses. Separate regressions were calculated for each breed of dam. Two hundred ten, 225, 257 and 201 offspring of Angus, Hereford, Holstein, and Brown Swiss dams were measured. When linear and quadratic effects were fitted for all 10 independent variables, the resulting coefficients of determination were; 0.38, 0.32, 0.32, and 0.30 for Angus, Hereford, Holstein, and Brown Swiss dams respectively. When only the linear effects for the 10 variables were fitted, the corresponding coefficients of determination were; 0.33, 0.29, 0.26, and 0.16. Almost as much variation in calving score could be explained by omitting some of the independent variables. Variables were deleted from the regression equation in a systematic manner described in the methods of analysis section. Table 19 summarizes the regression equations remaining after the step-down procedures were completed.

Table 19. Summary of multiple regression analysis

Breed of dam	R ²	R	Partial regression coefficients			
			Birth weight	Cow weight	Pelvic width	Pelvic depth
Angus	0.31	0.55		.018		
Hereford	0.27	0.52		.013		
Holstein	0.25	0.50	.279			- .476
Brown Swiss	0.14	0.38				

$\frac{a_{BW}}{CW}$ refers to the ratio of birth weight divided by the weight of the cow.

of calving score on independent variables					
Wither height	Width at hip	Gest. length	Birth date	Pelvic area	$\frac{Bwa}{CW}$
		- .068		- .021	128.502
					107.160
	- .564				
		- .024			42.809

Coefficients of determination (R^2) were slightly smaller than when all linear effects of the 10 independent variables were fitted. R^2 is the proportion of the total sum of squares that is due to regression. R is the multiple correlation coefficient which measures the correlation between fitted points on the regression plane and the actually observed points.

Birth date, height at the withers, and width of the pelvic opening did not remain in the reduced regression equation for any of the breeds. The equations for Hereford and Angus cows were similar. All of the variables in the Hereford equation were also in the equation for Angus. Likewise, all of the variables in the Brown Swiss equations were in the equation for Angus. The variables in the Holstein equation, however, were completely different from those of any other breed.

Calving scores in Holsteins increased almost 0.3 of a score unit for each additional pound of birth weight when pelvic depth and width at the hips were held constant. One extra centimeter of depth in the pelvic opening of Holsteins reduced the calving score by 0.48 units when other variables were held constant. Holsteins had lower calving scores when their calves were wider, if birth weight and the depth of the pelvic inlet were held constant. Perhaps long, tall, rangy calves are more difficult to get into the

proper birth position, and are more often presented abnormally than shorter, thicker calves.

Brown Swiss cows had lower calving scores when gestation lengths were shorter. As expected, calving scores increased in Brown Swiss when the weight of the calf relative to the weight of the cow increased, but this rate of increase in calving score was much smaller than in either Angus or Herefords. Probably this was due to the fact that some of the Angus and Hereford cows were mated to Holstein and Brown Swiss bulls, which resulted in larger calves than if they had been mated to bulls of their own, or a smaller breed. On the other hand, the Brown Swiss cows were never mated to bulls which produced calves significantly larger than bulls of their own breed and were often mated to smaller breeds.

Calving scores increased only slightly in both Hereford and Angus cows when cow weight increased, holding other factors constant. Thus a larger cow with a given pelvic area had no calving advantage over a small cow with the same pelvic area.

These regression analyses failed to verify that large birth weights were the major reason for calving difficulties. While birth weight is a factor in ease of calving, especially in extreme cases, yet the mating types with the heaviest birth weights were not the ones

with the greatest amount of calving difficulty. The correlation between birth weight and calving score when all mating types were grouped together was 0.14. The correlation between calf weight and calving score was 0.27, 0.30, 0.22, and 0.17 for Angus, Hereford, Holstein, and Brown Swiss cows, respectively. The ratio of birth weight divided by cow weight is probably more pertinent than birth weight alone in determining calving difficulty. The correlations between calving score and the ratio of birth weight divided by cow weight were: 0.41, 0.43, 0.37, and 0.31 for Angus, Hereford, Holstein, and Brown Swiss cows. These correlations indicate that the relationship between calving score and birth weight divided by cow weight is not very strong, but that it is better than not having the extra information about cow weight relative to calf weight. The pelvic measurements were disappointing as predictors of calving difficulty. Pelvic measurements are difficult to obtain, and are certainly not worth the trouble, based on this study.

Correlations between calving score and each of the 10 independent variables are given in Tables 20, 21, 22, and 23.

Table 20. Correlations among birth measurements for parturitions involving Angus cows

Row var. no. ^a	Column variable number ^a											
	1	2	3	4	5	6	7	8	9	10	11	
1	1.00											
2	.23	1.00										
3	.10	.34	1.00									
4	.11	.37	.52	1.00								
5	.59	-.10	.03	-.03	1.00							
6	.68	.24	.19	.15	.56	1.00						
7	.32	-.08	-.08	-.13	.32	.23	1.00					
8	-.06	-.16	-.18	-.18	.04	-.09	.09	1.00				
9	.12	.42	.87	.87	.01	.19	-.13	-.21	1.00			
10	.54	-.68	-.21	-.24	.53	.31	.31	.09	-.26	1.00		
11	.27	-.21	-.25	-.20	.31	.12	.11	.05	-.26	.41	1.00	

^aThe variables are: 1 = birth weight, 2 = cow weight, 3 = pelvic width, 4 = pelvic depth, 5 = wither height, 6 = width at hips, 7 = gestation length, 8 = birth date, 9 = pelvic area, 10 = birth weight divided by cow weight, and 11 = calving score.

Table 21. Correlations among birth measurements for parturitions involving Hereford cows

Row var. no. ^a	Column variable number ^a											
	1	2	3	4	5	6	7	8	9	10	11	
1	1.00											
2	.26	1.00										
3	.18	.37	1.00									
4	.14	.26	.43	1.00								
5	.67	-.05	.03	-.05	1.00							
6	.68	.16	.11	.08	.56	1.00						
7	.32	-.12	-.04	-.01	.28	.32	1.00					
8	.11	.09	-.11	.04	.09	.19	.15	1.00				
9	.19	.37	.84	.85	-.01	.12	-.03	-.04	1.00			
10	.57	-.63	-.16	-.10	.55	.39	.34	-.01	-.16	1.00		
11	.30	-.22	-.06	-.04	.28	.20	.12	.15	-.06	.44	1.00	

^aThe variables are: 1 = birth weight, 2 = cow weight, 3 = pelvic width, 4 = pelvic depth, 5 = wither height, 6 = width at hips, 7 = gestation length, 8 = birth date, 9 = pelvic area, 10 = birth weight divided by cow weight, and 11 = calving score.

Table 22. Correlations among birth measurements for parturitions involving Holstein cows

Row var. no. ^a	Column variable number ^a											
	1	2	3	4	5	6	7	8	9	10	11	
1	1.00											
2	.47	1.00										
3	.29	.54	1.00									
4	.37	.48	.57	1.00								
5	.71	.18	.09	.18	1.00							
6	.78	.36	.16	.22	.67	1.00						
7	.44	-.01	-.06	.03	.38	.36	1.00					
8	.10	.14	.10	.16	.05	.01	.05	1.00				
9	.38	.59	.90	.87	.16	.22	-.02	.15	1.00			
10	.49	-.53	-.26	-.13	.49	.39	.43	-.05	-.22	1.00		
11	.22	-.17	-.11	-.20	.29	.13	.14	.07	-.17	.37	1.00	

^aThe variables are: 1 = birth weight, 2 = cow weight, 3 = pelvic width, 4 = pelvic depth, 5 = wither height, 6 = width at hips, 7 = gestation length, 8 = birth date, 9 = pelvic area, 10 = birth weight divided by cow weight, and 11 = calving score.

Table 23. Correlations among birth measurements for parturitions involving Brown Swiss cows

Row var. no. ^a	Column variable number ^a											
	1	2	3	4	5	6	7	8	9	10	11	
1	1.00											
2	.39	1.00										
3	.26	.55	1.00									
4	.31	.45	.57	1.00								
5	.75	.14	.10	.15	1.00							
6	.77	.22	.13	.14	.73	1.00						
7	.37	-.07	-.02	.03	.39	.35	1.00					
8	.14	.17	.23	.16	.04	.06	.18	1.00				
9	.33	.57	.89	.88	.14	.15	.01	.23	1.00			
10	.58	-.50	-.24	-.10	.57	.51	.38	-.02	-.19	1.00		
11	.17	-.16	-.08	-.04	.24	.11	.05	.09	-.07	.31	1.00	

^aThe variables are: 1 = birth weight, 2 = cow weight, 3 = pelvic width, 4 = pelvic depth, 5 = wither height, 6 = width at hips, 7 = gestation length, 8 = birth date, 9 = pelvic area, 10 = birth weight divided by cow weight, and 11 = calving score.

SUMMARY AND CONCLUSIONS

Birth weight, wither height at birth, length of gestation, and calving score were studied in 893 births involving all mating combinations of Angus, Hereford, Holstein, and Brown Swiss breeds.

Straightbred performance was studied. The dairy breeds excelled in traits that measured prenatal growth; birth weight and wither height. The dairy breeds had slightly smaller calving scores than the beef breeds, but the differences were not significant. Gestation lengths for straightbreds were: 286.2, 284.2, 280.1, and 277.0 days for Brown Swiss, Hereford, Angus, and Holsteins.

Crossbred performance was evaluated using general, maternal, specific, and reciprocal combining ability. The breeds differed significantly for both general and maternal combining ability. The dairy breeds had larger general combining ability (GCA) effects for birth weight and wither height than the beef breeds. The rank of the GCA's for gestation length was the same as the rank of the straightbreds. Use of beef breeds in crosses reduced calving scores, because they had smaller GCA's for calving score than the dairy breeds.

Differences among specific combining abilities (SCA's) were significant only for birth weight. SCA's were smaller for dairy x beef and beef x dairy crosses than they were for

beef x beef and dairy x dairy crosses. Reciprocal combining ability effects were not significantly different for any of the birth traits except height at the withers. Specific and reciprocal combining ability effects added little information about crossbred performance.

The heterosis effects for all of the birth traits except calving score were too small to be of much practical value. Average heterosis effects were: 2% for birth weight, 0.35% for wither height, -0.03% for gestation length, and 14% for calving score. Calving was more difficult when crossbred rather than straightbred calves were born, but the difference was not significant. Heterosis in beef x beef and dairy x dairy crosses averaged slightly higher than that in beef x dairy and dairy x beef crosses. Either beef and dairy types are not as diverse genetically as previously thought, or other factors were responsible for what was observed as heterosis. Heterosis was distinctly harmful for calving score.

Together, GCA's and MCA's accounted for 30.5, 43.2, 5.86, and 17.2 percent of the total variance in birth weight, wither height, gestation length, and calving score, respectively. GCA's and MCA's were about equally important as sources of variance in birth weight and gestation length. GCA's explained five times as much of the variation in wither height as MCA's, whereas MCA's accounted for four

times as much of the variation in calving score as GCA's.

MCA was the most important source of variation influencing calving score. Differences between beef and dairy type cows accounted for most of the maternal effect in calving score. However, differences in Brown Swiss and Holstein MCA's also contributed to variation in calving score.

Beef-dairy differences were responsible for most of the GCA and MCA variation in birth weight, wither height, and calving score. Variability in GCA's for gestation length resulted because the GCA of Brown Swiss differed from all other GCA's, while variation in MCA's for gestation length resulted because the MCA of the Hereford differed from all other MCA's.

SCA and reciprocal combining ability effects did not contribute much variation for any of the birth traits.

Differences among sires within breeds of sire accounted for 9.8, 5.9, 7.0, and 2.2 percent of the total variance in birth weight, wither height, gestation length, and calving score, respectively. The corresponding percentages for differences among breeds of sire were: 14.8, 41.1, 7.5, and 3.1. Most of the variation in calving score (94.7%) resulted from sources other than breed of sire and sires within breeds of sire. The effect of individual sires on calving score has, perhaps, been overestimated.

Sires within breed of sire variation for calving score was larger in the dairy breeds than in the beef breeds. Perhaps the method of selecting beef and dairy sires accounts for the differences in variability of individual sires in beef and dairy breeds.

Prediction of calving score from other measurements made on the cow and calf at the time of birth was of little value. Prediction equations were calculated for each breed of dam. When all linear and quadratic effects were fitted, the coefficients of determination were 0.38, 0.32, 0.32, and 0.30 for Angus, Hereford, Holstein, and Brown Swiss dams, respectively.

There was a significant farm effect for birth weight and wither height. These traits measure prenatal growth, and could easily have been influenced by differences in nutritional level at the two farms.

Azium treatment significantly shortened gestations (1.7 days shorter), but did not have a significant effect on other birth traits.

The combined effects of year, age of dam, and parity were highly significant for all of the birth traits except height at the withers. Most of the combined effect of year-age of dam-parity for birth weight and calving score was due to differences in year and age of dam, but differences due to parity accounted for almost all of the year-age of

dam-parity effect for gestation length.

Beef-dairy crossbreeding can be practiced without incurring serious birth difficulties. Death losses due to difficult calving were judged to be 2 percent or less in this study. The man with Angus or Hereford cows who is considering crossbreeding with any of the beef or dairy breeds used in this study must expect that calving difficulties in his herd will increase with crossbreeding. Straightbred beef cattle have lower average calving scores than beef x beef or dairy x beef crossbreds. The lowest calving scores available to him using crossbreeding with his present cow herd are found in beef x beef crosses, but even these crosses have more calving difficulty than straightbred beef matings. It is, therefore, advisable to breed first calf beef heifers to bulls of their own breed, to minimize calving scores. After the first calf, beef cows can be bred to bulls of other breeds with little risk. Angus and Hereford cows had lower calving scores when bred to Brown Swiss rather than Holstein bulls. Use of Brown Swiss bulls will result in gestations averaging 3 to 4 days longer than if Holstein bulls were used, but this small difference in calving interval is of little practical importance.

Dairy cows can be used to produce beef calves if this is economically advisable. The man with Holstein or Brown Swiss cows available for beef production could easily cross

them with one of the beef breeds. Calving scores are lower for beef x dairy crosses than for dairy x dairy crosses or even dairy straightbreds. Either Angus or Hereford bulls can be used on dairy cows with little danger of calving difficulty. Calving scores were lowest when Holstein cows were bred to Angus bulls, and Brown Swiss cows were bred to Hereford bulls.

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